An actualistic and phylogenetic approach to identifying and interpreting crocodylian bite marks

Stephanie Katarina Drumheller-Horton
University of Iowa

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AN ACTUALISTIC AND PHYLOGENETIC APPROACH TO IDENTIFYING AND INTERPRETING CROCODYLIAN BITE MARKS

by

Stephanie Katarina Drumheller-Horton

An Abstract

Of a thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Geoscience in the Graduate College of The University of Iowa

December 2012

Thesis Supervisor: Associate Professor Christopher A. Brochu
Bite marks provide direct evidence of trophic interactions, feeding behavior, and inter- or intraspecific conflict in the fossil record. However, their utility as a source of taphonomic and paleoecologic data requires differentiation from traces left by other processes. Since the 19th century, taphonomists have often relied on actualistic observations of modern bite marks and feeding behaviors in order to identify diagnostic traces and patterns. A recent increase in interest in taphonomic research has resulted in a large body of work describing patterns of bite marks from many different clades. Most research has been focused on mammalian taxa, but a smaller number of non-mammalian groups, including crocodylians, have also drawn interest.

Crocodylians are taphonomic agents who consume and modify bones, often depositing them in the active depositional systems in which they live. However, actualistic observations of crocodylian bite marks have been limited to forensic case studies and surveys of two taxa: *Crocodylus niloticus* and *Crocodylus porosus*. Both surveys utilized captive animals, which often exhibit atypical morphologies that may bias ensuing bite mark datasets. In order to address this issue, a 2D morphometric analysis of *Alligator mississippiensis* crania from captive and wild specimens was performed. A principal component analysis and a canonical variates analysis revealed some statistically significant differences between the two groups, while crossvalidation had mixed results. An ANCOVA test of the covariance of centroid size and origin against shape (principal component scores) revealed that the effects of ontogeny introduced a stronger signal than captivity. This implies that while using captive crocodylians in fine scale analyses should be avoided, they are suitable for gross scale research, such as bite mark analyses.

To explore crocodylian bite mark patterns in greater depth, a large scale survey of
traces left by *A. mississippiensis* was performed. Bite mark types on samples taken from individual feedings were discussed in light of vital statistics and collection protocols. Bite mark types on samples taken from group feedings were classified by location and orientation on bone and type. The results were compared to pre-existing crocodylian datasets with regards to potentially diagnostic traits: bisected marks, hook scores, and a lack of furrows. Bisected marks were found in rates similar to those seen in *C. niloticus*, and rates of hook scoring and bone breakage were higher. These traces were present in higher rates than those reported in *C. porosus*. Furrows were identified, but rare.

Finally, a survey of bite marks from 21 of the 23 generally recognized species of extant crocodylians was performed to better characterize marks found across Crocodylia and to test methods for synthesizing taphonomic datasets. Bite marks were identified, and specimens were then coded for presence or absence of mark subscores. Attempts to find statistical correlation between mark types, animal vital statistics, and sample collection protocol were unsuccessful. Mapping bite mark character states on a eusuchian phylogeny successfully predicted the presence of bisected marks in previously published, extinct taxa. Predictions for clades that may have created multiple subscores, striated marks, and extensive crushing were also generated. Inclusion of fossil bite marks which have been positively associated with extinct species allow this method to be projected beyond the crown group. The results of this study indicate that phylogenies can and should be explored further for use as predictive tools in a taphonomic framework.

Abstract Approved:

______________________________________________
Thesis Supervisor

______________________________________________
Title and Department

______________________________________________
Date


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Stephanie Katarina Drumheller-Horton

A thesis submitted in partial fulfillment of the requirements for the Doctor of Philosophy degree in Geoscience in the Graduate College of The University of Iowa

December 2012

Thesis Supervisor: Associate Professor Christopher A. Brochu
This is to certify that the Ph. D. thesis of

Stephanie Katarina Drumheller-Horton

has been approved by the Examining Committee for the thesis requirement for the Doctor of Philosophy degree in Geoscience at the December 2012 graduation

Thesis Committee:

Christopher A. Brochu, Thesis Supervisor

Ann F. Budd

James G. Enloe

Walter E. Klippel

Hallie J. Sims
For my husband, Jake Horton, and my parents, Fred and Janet Drumheller, whose yards often served as my lab.
I would like to thank my advisor, Chris Brochu, for guidance and advice throughout the course of this research. Nancy Budd, Jim Enloe, Jonathan Adrain, Hallie Sims, and Walter Klippel, the members of my comprehensive exam and defense committees provided further support and suggestions which helped shape the research presented in this dissertation. The following people also provided helpful discussion, feedback, and encouragement: Michelle Stocker, Colin Sumrall, Linda Kah, Troy Fadiga, Julia McHugh, Talia Karim, Dorothy May, and the UI Paleontological Discussion Group.

The Saint Augustine Alligator Farm and curator of reptiles David Kledzik made this research possible by generously allowing me access to their animals. Southeastern Provisional and Swaggerty’s Farms provided the partially butchered cow and pig samples used in this dissertation. I would also like to thank the following institutions and individuals for allowing access to their modern research collections: Florida Museum of Natural History, American Museum of Natural History, The Field Museum of Natural History, and Rudyard Sadlier. Fossil collections made available for this research include the Utah Museum of Natural History, the University of California Museum of Paleontology, the University of Texas at Austin Vertebrate Paleontology Laboratory, and the University of Texas at Arlington.

The research presented in this dissertation was funded by the University of Iowa Department of Geosciences Littlefield Family Fund. The Iowa Department of the State Archaeologist provided storage, equipment, and space for sample processing. The Frank H. McClung Museum provided further storage as well as photographic and laboratory
facilities. I would also like to thank the University of Iowa Central Microscopy Research Laboratories for providing training on and access to their scanning electron microscopes.

Finally, I would like to thank my husband, Jake Horton, and my parents, Fred and Janet Drumheller. A support structure is vital for successful completion of any postgraduate degree, but few families are called upon to allow taphonomic experiments to run in their suburban backyards. As I predicted, the grass grew back relatively quickly and the neighbors seem to find it all very funny in retrospect.
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CHAPTER I

ACTUALISTIC BITE MARK STUDIES: HISTORY, NOMENCLATURE, AND METHODOLOGY

Introduction

Bite marks exist at an intersection of ichnology and taphonomy which is broadly applicable to variety of research topics. As trace fossils, they provide direct evidence of feeding behavior, dietary selection, and even intraspecific fighting in extinct organisms (e.g. Buffetaut, 1983; Davidson and Soloman, 1990; Williamson, 1996; Forrest, 2003; Fuentes, 2003; Avilla et al., 2004; Katsura, 2004; Cisneros, 2005; Mead et al., 2006; Steadman et al., 2007; Riviera-Sylva et al., 2009). As a taphonomic process, the act of feeding and scavenging can be destructive to remains, but taken in another light, the process can provide a great deal of positive information as well. Feeding and caching sites can create predator-mediated assemblages that not only provide potentially fruitful localities for excavation and research, but also insight into the behavior of the specific predators involved (e.g. Berger and Clark, 1995; Rogers et al., 2003; Njau and Blumenschine, 2006; Noto et al., 2012). Vertebrate bite marks are distinct from other types of bone surface modifications, including the use of tool marks, trampling, insect borings, etc. (e.g. Behrensmeyer et al., 1986; Blumenschine et al., 1996; Roberts et al., 2007). Additionally, the ever-growing body of bite mark studies focusing on different clades demonstrates that bite marks made by various actors not only can be differentiated from other types of bone surface modifications, but also from one another. Though computer and mechanical simulation methods are showing great promise when
addressing extinct groups (Gignac et al., 2010), most diagnostic marks and patterns of
marks are still identified and defined using actualistic techniques (e.g. Haynes, 1980;
1983; Haglund et al., 1988; 1989; Marean and Spencer, 1991; Murad, 1997; Pickering
and Wallis, 1997; Labisky and Boulay, 1998; Lotan, 2000; Njau and Blumenschine,
2006; McGraw et al., 2006; Drumheller, 2007; D’Amore and Blumenschine, 2009).

Bite marks provide direct evidence of trophic interactions in the fossil record, but
they can also shed light on a number of other avenues of research. In a medico-legal
context, forensic anthropologists have used bite marks to determine cause of death, make
time-since-death estimates, and identify patterns of destruction and disarticulation related
to scavenging, all with an eye towards identifying modern human remains and resolving
criminal investigations (e.g. Willey and Snyder, 1989; Haglund, 1997a; 1997b; Rathbun
and Rathbun, 1997; Klippel and Synstelien, 2007). Conservation biologists successfully
have used bite marks to focus management of natural predation on modern, threatened
populations (Lyver, 2000). A broad zooarchaeology and paleoanthropology literature
exists using bite marks to discuss domestication, determine if early hominids were
predators or scavengers, and to identify specific hunting strategies among predators,
including humans (e.g. Shipman, 1987; Stiner, 1990; Steele and Weaver, 2002).

Paleontologists have used bite marks to make broader interpretations of
paleoenvironmental conditions, reconstruct food web structure in paleoecosystems, and
explore the biomechanics of bite method and force (e.g. Erickson et al., 1996; Selvaggio
and Wilder, 2001; Faith and Behrensmeyer, 2006; Gignac et al., 2010; Longrich et al.,
2010).

However, those types of studies are made possible only when there exists a solid
foundation of literature detailing actualistic observations of bite marks. Whereas the bite marks made by many mammalian clades have been subjected to fairly rigorous exploration, non-mammalian predators and scavengers have not. Forensic case studies have provided tantalizing glimpses into some non-mammalian groups (e.g. chondrichthians - Rathbun and Rathbun, 1997; crocodylians - Caldicott et al., 2005; Langley, 2005; Harding and Wolf, 2006), but the broad surveys so necessary for positive identification and interpretation of non-mammalian bite marks are few and far between (McGraw et al., 2006; Njau and Blumenschine, 2006; D’Amore and Blumenschine, 2009).

Here I explore the history of bite mark studies, with an emphasis placed on non-mammalian predators and scavengers in general, and crocodylians in particular. I address the different methodologies used for collecting modern bite marks, mark identification and nomenclature, previously identified diagnostic marks and patterns of marks among extant groups, and paleontological examples of marks, with the goal of characterizing the current state of the bite mark research across scientific disciplines and demonstrating that, though great strides have been made in filling the gaps in our understanding of bone modifying behaviors, there is still a great deal of work yet to be done.

**History**

Taphonomic studies were performed for some time prior to Efremov coining the term (1940). The origins of the field have been projected as far back as Leonardo da Vinci in the 15th century, who observed living and dead populations of bivalves in order to determine if the Biblical flood could have created the fossil assemblages found in the Monferrato mountains of Lombardy (translated in MacCurdy, 1938; Cadée, 1991;
Martin, 1999). In the 17th century, the father of geology, Niels Stenson (Nicolas Steno), demonstrated that ‘Glossopterae,’ the so-called tongue-stones he instead identified as shark teeth, often showed signs of decay, which was incongruent with the interpretation that these, and other fossils, grew in situ (Plotnick and Speyer, 1989; Cadée, 1991; Martin, 1999). Research performed by Robert Hooke, on the structure of plant cells in Recent cork and fossil wood, Georges Cuvier, on biostratigraphic zones, Charles Lyell and Edouard Lartet, on the processes which created marks on ancient bone, all included aspects of taphonomic reasoning (Grayson, 1986; Cadée, 1991; Lyman, 1994; Martin, 1999).

The first documented, actualistic study of bite marks was undertaken by William Buckland in 1823 (Binford, 1981; Lyman, 1994). Buckland’s research on the vertebrate assemblage in Kirkdale cave led him to interpret the site as a hyena den, because of the abundant hyena skeletal elements and associated coprolites. The cave also contained many other bones that were damaged in a manner that Buckland suspected represented evidence of gnawing. A travelling menagerie near Oxford provided the opportunity to test that interpretation using observations of a living spotted hyena (Crocuta crocuta) gnawing on an ox tibia. Buckland described both the gnawing behavior of the animal itself and the damage patterns created on the bone in great detail, noting that the punctures created by the hyena’s teeth, the removal and consumption of the proximal end of the tibia, and the splintering of the remaining shaft in order to access the marrow all were consistent with the condition of ancient bison bones present at Kirkdale cave (Buckland, 1823).

These types of studies continued throughout the 19th century, growing to include
the study of human bone modifications through experimental and ethnographic means
and the effects of bone density, structure, and nutritional value on element survival
(Lyman, 1994). Having recognized that animals could exhibit behavior that accumulates
and modifies bone, archaeologists turned a great deal of attention to determining how
best to differentiate between animal- and man-made sites. Tournal (1833) expanded upon
Buckland’s case study and pointed out that hyenas were not the only predators to gnaw
bone or bring prey items to a den or caching site. Morlot (1861) reviewed observations of
bird bone modification by canids, and compared the reported patterns to his own
observations of damaged deer bones. Lyell (1863) looked beyond carnivores as a source
of bone modifications, supplying porcupines held at the London zoo with samples of
bone and antler to gnaw on in order to explore whether marks on bones found in Saint-
Prest, France were created by human tools or non-human agents. Wyman (1868) found
what he interpreted to be bite marks of varying sizes when surveying his collections, and
presented this as evidence that physically smaller carnivores could modify bones as well.
Dawkins (1874) specifically praised Buckland’s approach to site interpretation and called
for more such research to be performed.

However, changing interests within the field appear to have led to the
abandonment of those lines of inquiry, and archaeological taphonomic research became
scarce in the first half of the 20th century. There was a general shift towards the
assumption that human behavior could explain all patterns within a site (Lyman, 1994).
That mindset, taken to extremes, resulted in the idea that any pattern found in an
archaeological site had to be the direct result of human behavior. For example, the
presence of a bone exhibiting bite marks became direct evidence of domestication. Sites
which a 19th century archaeologist would have identified as a carnivore den became the foundation for 20th century discussions of specialist hunting and ritualistic treatment of carnivores. Patterns of bone modification which had previously been demonstrated to occur naturally, such as spiral fractures and bone surface wear, suddenly became ‘diagnostic’ indicators of human behavior. Those types of studies persisted throughout the first half of the 20th century (Binford, 1981).

In the meantime, paleontologists developed their own, completely separate body of taphonomic research. Spearheaded by German paleontologists, this wave of taphonomic inquiry occurred just as interest among archaeologists waned at the end of the 19th and the beginning of the 20th centuries. Like the archaeologists before them, paleontologists used actualistic observations and uniformitarian principles to better recognize and understand patterns of fossil preservation and site formation (Behrensmeyer and Kidwell, 1985; Cadée, 1991; Martin, 1999). Documentation of patterns seen in modern ecosystems was a major focus in order to better interpret the paleoenvironmental conditions responsible for preservational differences in the fossil record (e.g. Walther, 1904; Abel, 1912; 1927; Wasmund, 1926; Weigelt, 1927). In particular, the processes which would result in assemblages of unusually well-preserved remains (i.e. lagerstätten) were studied intensely, but less spectacular pathways of site formation were not neglected (Cadée, 1991; Martin, 1999).

Within the framework of interpreting modes of preservation and site formation, bone surface modifications received renewed attention. Abel (1927) discussed bite marks in this context, using them as a tool to understand the patterns of preservation found in the Miocene Pikermi bone beds. He noted that the prevalence and condition of ungulate
bones at the site was consistent with remains deposited and scavenged at a mass mortality event. He cited observations of modern African carnivores to further suggest that the ungulate remains at Pikermi must have undergone fairly rapid burial in order to avoid the near total destruction of similarly deposited skeletal elements by these modern scavengers. Work by von Nopsca (1902) and Weigelt (1927) both suggested that feeding behavior, including that of non-mammalians such as crocodylians, could also result in paleontologically informative assemblages.

However, due in part to a lack of translations for non-German speakers and the socio-political atmosphere in Europe at the time, this research did not receive a great deal of attention in the greater paleontological community until after World War II (Cadée, 1991; Martin, 1999). Many of those early 20th century studies were not rediscovered by paleontologists until independently derived taphonomic data started revealing patterns which echoed these earlier results. For example, observing the presence and prevalence of bite marks as a way to interpret the preburial interval, as discussed by Abel (1927), was not revisited in paleontology and anthropology until the 1980s (e.g. Behrensmeyer and Boaz, 1980; Brain, 1980; Hill, 1980; Willey and Snyder, 1989). Realizing the value of those earlier studies, the paleontological community eventually started translating and disseminating some of the early 20th century German works (e.g. Weigelt, 1927; translated by Schaefer, 1989).

The potential of this type of inquiry was realized outside of Germany’s borders when Efremov coined the term ‘taphonomy’ (1940). His ‘new’ field subsumed biostratinomy (Weigelt 1927), aspects of actuopaleontology (Richter 1928), and diagenetic processes of fossilization that had not yet been widely explored in a
paleontological context. In addition to simply defining the new term, he suggested overarching avenues of research which could explore the entirety of an organism’s transition from the biosphere to the lithosphere (“laws of embedding” [Efremov 1940: 93]), in order to better understand what he understood to be the overwhelming incompleteness of the fossil record (Efremov, 1940; 1953).

Though not the first time the quality of the fossil record had been criticized – Charles Darwin had made similar statements in *On the Origin of Species* (1859) in order to explain why so few fossil transitional forms had been found to support his theory of evolution through natural selection – this time, the criticism stuck. As a field, paleontological taphonomy became the study of biases in the fossil record (Gifford, 1981; Cadée, 1991; Martin, 1999). Instead of a focus on collecting positive paleoecological and geomorphological data, which had been the philosophical drive behind the German school of research, this new wave of taphonomic research instead aimed to “strip away the taphonomic overprint” (Lawrence, 1979: 903). In practice, this meant identifying biases, quantifying, and sometimes mitigating their effects through changes in collection and analytical techniques, and using them to determine when certain methods of paleontological interpretation were appropriate and when they were not (Gifford, 1981).

Throughout the 1950s and 1960s, the majority of taphonomic paleontology remained focused on understanding and addressing the issues of megabiases and information loss (e.g. Olson, 1952; 1958; Johnson, 1957; 1960; 1962; Lawrence, 1968). As this area of research generally focused on very large-scale biases, taphonomic studies of predation and scavenging were scarce because these processes were viewed as a few minor natural destructive processes among many, and when bite marks were mentioned,
it was as little more than interesting anecdotes.

The German school of taphonomy experienced a resurgence in the 1970s (Seilacher, 1970; 1976; Schäfer, 1972; Seilacher et al., 1985), fostered by the rediscovery of the earlier German works (Behrensmeyer and Kidwell, 1985). Once again, this research focused on modes of fossilization and site formation with an eye towards unusual processes and results. This branch of taphonomic research also has been highly prolific, expanding our understanding of peri- and post-burial taphonomic processes by more firmly incorporating aspects of stratigraphy and sedimentology (Cadée, 1991).

However, as in the 1950s and 1960s, the focus of most taphonomists was not centered at a scale at which bite marks and feeding traces were of wide interest, and publications on bone surface modifications were still rare.

In the meantime, the lack of widespread taphonomic research and the anthropocentric mindsets of early 20th century archaeologists continued. Bone modifications which had previously been demonstrated to occur naturally, such as spiral fractures and surface abrasion, were increasingly cited as evidence of human hunting, tool use, and even cannibalism (Breuil 1939; Weidenreich, 1941). There were a few taphonomic papers published during this time which demonstrated that these types of marks were not diagnostic of human behavior and that many of the marks and patterns attributed to human actors could be created by non-human actors and processes, particularly the feeding behavior of carnivores and scavengers (e.g. Pei, 1938; Zapfe, 1939). However, that work received little attention until after the publication of Raymond Dart’s proposed osteodontokeratic society.

Dart attributed patterns of bone damage and accumulation found in cave sites in
South Africa to australopithecine behavior, proposing that early hominids not only hunted and killed a wide variety of animals (including each other), but also used the bones, teeth, and horns of their prey as tools long before the first stone tool users of genus *Homo* (Dart, 1949; 1956; 1957; 1960). He too cited bone modifications such as spiral fractures and surface abrasion as supporting evidence for his interpretation, but his work garnered much more attention than previous, similar claims. Dart’s ideas were provocative, and they almost single-handedly catapulted taphonomy back into the forefront of archaeological research. A significant body of literature grew in direct response to, and in refutation of, Dart’s work (e.g. Brain, 1969; Bonnichsen, 1973; Hill, 1976; Shipman and Phillips, 1976). That new research not only overhauled our understanding of early hominids by shifting general interpretations away from murderous hunters and more towards marginalized scavengers or potential prey items, but also highlighted the need for more rigorous research exploring the processes of bone modification and accumulation in order to differentiate human from non-human traces.

This momentum continued through the 1970s and 1980s. In particular, actualistic research in Africa flourished, aimed at answering paleoecological questions surrounding paleoanthropological sites (e.g. Boaz and Behrensmeyer, 1976; Gifford and Behrensmeyer, 1977; Behrensmeyer and Boaz, 1980; Behrensmeyer, 1981). This bridged the gap between the fields of paleontological and archaeological taphonomy, which until then had been developing on effectively separate, if somewhat parallel, trajectories. Scientists in both fields pushed for more systematic, rigorous research across all facets of taphonomy, including bite mark studies (e.g. Haynes, 1980; 1982; 1983).

This explosion in taphonomic research also was felt outside of the paleontological
and zooarchaeological communities. Forensic anthropologists quickly recognized the
value of those taphonomic studies to medico-legal investigations. Previously recognized
taphonomic patterns, such as skeletal disarticulation order, weathering stages, and agents
of bone surface modification, were adopted as useful tools for recognizing cause of and
time since death (e.g. Morse, 1983).

Forensic taphonomists also recognized that as useful as the existing data were to
their own investigations, an important niche remained which they were uniquely
positioned to fill. Because of the age of most paleontological and zooarchaeological sites
and the rarity of soft tissue preservation within that context, almost all previous research
had been narrowly focused on processes related to bone. Forensic anthropologists work
on significantly younger, fresher remains, and the geologically short-term processes
which affect soft tissue decomposition were of particular interest to them. Also, in
studying these processes, it became apparent that soft tissue can and does affect the final
disposition of skeletal remains, even after it has completely decayed (Haglund and Sorg,
1997; Sorg and Haglund, 2002). Therefore, forensic studies of bite marks often included
not only information on bone modifications, but also soft tissue modifications and
descriptions of processes in terms of hours, days, or months which had only been
addressed by zooarchaeologists and paleontologists on scales which ranged over years,
centuries, or millennia (e.g. Willey and Snyder, 1989; Rathbun and Rathbun, 1997;
Klippel and Synstelien, 2007).

Interest in taphonomic research in paleontology, archaeology, and forensic
anthropology shows little sign of waning. This is probably due to the large amount of
primary data yet to be collected, and bite mark studies are no exception. While the bite
marks created by some mammalian taxa have been studied in great detail, many other groups have not enjoyed the same level of attention. Actualistic discussions of the bite marks created by non-mammalian predators and scavengers are still fairly rare. Birds long have been thought to modify remains (e.g. Morse, 1983), but systematic actualistic observations outside of pellet studies largely are restricted to marks specifically created on primates by *Stephanoaetus coronatus*, crowned hawk-eagles, in Uganda and the Ivory Coast (McGraw et al., 2006; Trapani et al., 2006; Berger and McGraw, 2007). Taphonomic descriptions of modern shark (Rathbun and Rathbun, 1997) and piranha (Sazima and Guimarães, 1987) bite marks are lone examples in forensic case studies. A single survey of bite marks in captive *Varanus komodoensis*, Komodo dragons, characterized the many extinct and extant ziphodont reptiles (D’Amore and Blumenschine, 2009). Crocodylian bite marks have been explored in a few forensic case studies (Caldicott et al., 2005; Langley, 2005; Harding and Wolf, 2006) and two surveys of *Crocodylus niloticus*, the Nile crocodile (Njau and Blumenschine, 2006) and *Crocodylus porosus*, the salt water crocodile (Westaway et al., 2011). Though these studies form foundations for future research, there is a great deal of territory left to explore.

**Nomenclature and Classification**

In 1981, Lewis Binford published his influential and provocative *Bones: Ancient Men and Modern Myths* in response to what he saw as a lack of actualistic and experimental research in archaeology. He used examples from his own work to demonstrate the utility of what he called middle-range research, including a lengthy discussion on bite marks. This facet of his research is particularly notable in that in
addition to describing patterns of canid bite mark damage in great detail, Binford also suggested a system of nomenclature for future bite mark studies which has been adopted by most archaeologists and forensic anthropologists (Haglund and Sorg, 1997) and some paleontologists (D’Amore and Blumenschine, 2009). Borrowing heavily from the descriptive terms scientists had used in the past – pits, punctures, scores, and furrows – Binford’s system is simple enough that effectively any vertebrate bite mark can be categorized with it. His classifications are defined as follows:

Pit – A bite mark in which a tooth contacts a bone, but the force behind it is not powerful enough to break through its surface. This crushes the outermost layer of cortical bone, leaving a depression behind.

Puncture – A bite mark in which the tooth breaks through the outer surface of the bone, leaving a hole in the cortical bone.

Score – A bite mark in which the tooth drags along the surface of the bone, crushing the outermost layer of bone and creating a channel which does not fully pierce the cortical bone.

Furrow – A bite mark in which the tooth drags along the surface of the bone, breaking though the cortical bone and creating a deep channel or elongated hole (Figure 1.1).

These basic descriptions can be elaborated upon to describe the majority of vertebrate bite mark patterns. Specialized tooth morphologies or specific feeding behaviors may create unique, diagnostic traces that nevertheless can be described in some way to Binford’s succinct classifications for ease of comparison. For example, serial

pits or punctures are multiple tooth marks in a row are created by a single biting event and preserve the general shape of the tooth row, making them potentially useful when
using comparative jaw morphology to identify potential actors (Lyver, 2000; Gignac et al., 2010). Crenulated and chipped back margins (sensu Binford 1981) are a type of breakage caused by repeated biting or gnawing. That type of damage is created by medium to large mammalian carnivores, such as canids, bears, and hyenas (e.g. Haynes, 1983), and is effectively caused by a preponderance of punctures and furrows in a localized area. Forked or bifurcated scores can be caused by the high crowns or browsing herbivores who sometimes gnaw bone in search of certain minerals to supplement their diets (Morse, 1983). Paired, flat-bottomed, or U-shaped scores, particularly along naturally occurring ridges on bone, are diagnostic of some rodents’ incisor gnawing (Morse, 1983; Haglund, 1997b; Klippel and Synstelien, 2007).

Bite marks are often also associated with different types of secondary alterations in the form of breakage patterns which can explain other deviations from Binford’s basic descriptions. These features are caused by any kind of impact damage to bone, not just that caused by bite forces (Byers, 2002).

Depressed Fractures – This type of breakage is caused when bone collapses under the pressure of a tooth, creating broken, concentric or irregular edges beyond the margin of the primary bite mark.

Fracture Lines – These fractures are also caused when the bone breaks under the force of a bite, but instead of collapsing, it splinters in a linear, radiating fashion away from the site of tooth impact.

Spiral Fractures – These fractures are caused by particularly powerful bites and are thus named because they propagate in a spiral fashion away from the site of impact, often ending as roughly diagonal fractures across the shafts of long bones (Figure 1.2).
Forensic anthropologists have been able to observe patterns of feeding and bite mark location on a fine temporal scale, and in doing so have succeeded in compiling a generalized scavenging sequence (Haglund, 1997a). Their findings closely mimic previously described disarticulation sequences, because carnivores seem to take advantage of the same physical weaknesses of skeletal structures to dismember prey as the comparatively longer processes of decomposition (e.g. Hill, 1980; Binford, 1981). Deviations from these sequences have been used to compare scavenging behavior, discuss structural differences in prey morphology, and in forensic case studies, indicate
time since and cause of death (Haglund, 1997). While heavily biased towards mammalian predators and prey, aspects of both sequences often hold true in other vertebrate taxa as well (e.g. Hill, 1980; Behrensmeyer et al., 2003). The stages of the scavenging sequence are described below:

Stage 0 – This stage is characterized by damage to the thoracic cavity and throat. Major skeletal elements have yet to be removed, and if damage to bones is present, it is usually restricted to cranial elements around the eyes and nose.

Stage 1 – Tissues of the abdomen and thighs are particularly targeted. The proximal clavicles, sternum, and sternal ends of the ribs are destroyed to expose the viscera. This stage also includes the removal of forelimb elements.

Stage 2 – The hind limbs, having a more solid, bony connection than the forelimbs, are removed next. The method differs according to prey anatomy, predator, and possibly even climatic condition. There are two general patterns though: a scavenger either gnaws through the distal femoral condyles to free the limbs or removes the limbs and pelvic girdle en mass.

Stage 3 – At this point, all non-axial skeletal elements have been disarticulated. Long bones are often damaged at both ends.

Stage 4 – All skeletal elements are disassociated, damaged, and often scattered over a large area.

Developed separately from this scavenging sequence, but with a parallel theoretical basis, the location, number, and orientation of bite marks have been used to describe and differentiate between bite mark types and actors in archaeology and paleontology. The placement of bite marks on meat bearing bones versus anatomical
regions which lack significant nutritional value has been used to debate interpretations of predation versus scavenging in such disparate clades as hominids (e.g. Shipman, 1986) and theropods (e.g. Longrich et al., 2010). Physical restrictions of the trace maker can also restrict bite marks to certain bones or regions of bones, particularly when the prey item is significantly larger (e.g. Morse, 1983; Haglund, 1997b) or when the predator lacks socketed or structurally powerful teeth (e.g. D’Amore and Blumenschine, 2009). Certain feeding behaviors, such as the mammalian habit of gnawing bone in an attempt to access the marrow cavity, can result in statistically more bite marks than others, such as the more reptilian method of either only pursuing the surrounding meat for food or simply swallowing bones whole (Fiorillo, 1991). Comparisons of bite mark orientation are most often performed with regards to the long axis of long bones, and they are often described in terms of their angle to that axis, being rough parallel, perpendicular, or in between (Njau and Blumenschine, 2006; D’Amore and Blumenschine, 2009).

Size classification of bite marks, and particularly pits, has been explored as a potential way to identify the trace maker (Domínguez-Rodrigo and Piqueras, 2003; Coard, 2007). However, those attempts have largely demonstrated that mark size is heavily dependant on factors other than the species of the trace maker, such as the density of the affected area of bone and the strength behind the bite itself (Selvaggio and Wilder, 2001). Though some correspondence between predator body mass and bite mark size has been found (Delaney-Rivera et al., 2009), identification of trace maker based on bite mark size alone has not gained significant support. Instead, actualistic studies have focused on finding novel marks or patterns of marks to help associate traces with trace makers.
Actualistic Bite Mark Studies

Anthropologists and those paleontologists who follow Binford’s (1981) classification system often do not use binomials or other formal ichnotaxa to differentiate trace fossils. Also, since Binford’s scheme used canids as the basis for his bite mark nomenclature, many publications simply describe patterns in association with the trace maker in terms of their differences from the canid or ‘generalized carnivore’ model. Examples of bite mark patterns derived from actualistic observations of a variety of modern groups are presented below.

Dogs, Wolves, and Other Canids

Binford’s classification of bite marks into pits, punctures, scores, and furrows was largely based on observations of bone modifications created by dogs (Canis familiaris) and wolves (Canis lupus), though marks made by other groups were also discussed in lesser detail (Binford, 1981). Binford’s main collection of domestic dog bite marks was initially gathered for a study on patterns of which elements were given to animals and which were kept for human use and consumption in Eskimo groups in Alaska. When the focus of this research shifted to patterns of bone modification, those observations were compared to marks left at natural wolf kill sites. In addition to the descriptions of tooth marks in isolation, which have become the standard classification scheme across many bite mark studies, Binford named and described a number of other patterns of bite marks which have been used to a lesser extent in subsequent studies.

Crenulated Edges – These marks occur when relatively thin walled bone breaks away during a biting event, leaving behind a broken margin, notched by punctures.

Channeled Bones – After long bone ends are removed, dogs and wolves were
observed puncturing bone shafts in a progressive manner down the long axis of the bone. Margins of the ensuing channel were highly marked with chips and scores. This behavior is an effort to access marrow.

Flakes – When an animal pulls away a splinter of bone from an already broken margin, this peeling behavior creates an elongate flake Binford suggested could often be confused with the effects of human tool-making.

Chipped-back Margins – When teeth lose traction on particularly dense bone surfaces, smaller pressure flakes can be chipped away from the surface of the bitten area. Repeated marks of this kind on or around fracture surfaces can create highly modified margins which, again, Binford suggests, can be confused with human modification.

Mashed Edges – Powerful crushing bites, when partnered with leverage, such as that caused when a gnawed bone is propped against the ground, can break away pieces of the bone’s margin without creating an obvious associated tooth mark.

Polishing – This feeding trace is caused when the animal repeatedly licks an exposed section of damaged bone, such as when attempting to access bone marrow. According to Binford, this type of modification had been cited as use-wear and used to support interpretations of bone tool use.

The focus of Binford’s research was to demonstrate that many putative bone tools were, in fact, created by non-human agents. As such, additional research was needed to tease out features which differentiated canid bite marks from other groups. Initial comparisons of captive wolves, bears, hyenas, and great cats largely found that differences between bone modifications created by these four groups could be expressed in terms of degree of damage, not the presence of obviously diagnostic marks (Haynes,
1983). Using degree of damage alone for identification purposes is problematic though, considering that the extent of carcass utilization can be strongly affected by a number of other factors, including overall access to food and number of individuals involved in feeding (Haynes, 1982).

Also, the extent of canid bone modification has been demonstrated to differ depending on location and situation. Both wild and captive wolves as well as domestic dogs exhibit ‘boredom gnawing,’ or bone chewing as a source of entertainment rather than food. This behavior often occurs at or near dens and causes much more extensive bite mark damage than that found at kill sites, including reduction of dense long bone shafts into hollowed out cylinders or even smaller fragments (Haynes, 1982), further complicating the use of damage extent as a diagnosable bone modifying behavior.

Without obvious novel bite mark morphologies, some researchers have turned to documenting patterns of element selection and survival (Haynes, 1982). However, because canid bite marks, scavenging sequences, and patterns of element survival are often used as baselines in surveys of other modern mammalian bite mark, the onus of finding a pattern to differentiate other groups from the canid model falls on members outside of the group.

In the meantime, forensic anthropologists have started addressing the effects of canid feeding behavior as well, and these animals represent one of the most highly reported animal agents of human bone modification. While largely echoing the previously defined damage patterns (Haglund, et al., 1988; Haglund, 1997a) and scavenging sequences (Haglund et al., 1989), these studies are placing these data in a medico-legal context and exploring other sources of information which can be derived
from bite marks and scavenging behavior, such as estimating time-since-death (Willey and Snyder, 1989).

Hyenas

After comparing bite marks created by a variety of captive mammalian carnivores, Haynes (1983) determined that the best, if not only, way to differentiate hyena bite marks from those created by wolves, bears, and great cats, was the degree of damage on similarly-sized elements. Hyenas are well-known bone-crushers, and are more than capable of severely damaging or even completely consuming many prey bones which would survive feeding by other predators, especially when these skeletal elements are transported to a den site for further gnawing (Cruz-Uribe, 1991). For finer scale identification of trace makers, Cruz-Uribe (1991) used modern patterns of prey selection to differentiate between hyena species in archaeological contexts, but the utility of this method becomes more problematic as sampled taxa become more temporally and phylogenetically removed from their modern analogues. Also, the focus of this study was strictly to differentiate between human and non-human agents, and not to identify diagnosable feeding trace which would separate hyenas from other potential nonhuman feeding trace makers.

Since many important hominid sites formed in times and places where hyenas were also present, addressing this issue and differentiating hyena-mediated assemblages from evidence of hominid behavior is of particular import to paleoanthropologists (Cruz-Uribe, 1991). Actualistic observations on captive hyena bone ravaging behavior demonstrated that this highly destructive feeding strategy has a direct effect on estimates of element abundance by making identification of highly modified, isolated fragments
problematic (Marean and Spencer, 1991). In fact, observations of bone modifying behaviors in Amboseli National Park, Kenya, demonstrated that a shift from lions as the dominant predator to hyenas in an otherwise unchanging ecosystem can drastically alter the estimated diversity from the subfossil assemblage because of different levels of element destruction between the two predator groups (Faith and Behrensmeyer, 2006).

**Great Cats**

Diagnoses of great cat bite marks, as in similar studies of hyenas, often focus on differences in damage magnitude and location from the canid model. In Haynes’ (1983) comparison of different captive predators, none of the large cats sampled (lion – *Panthera leo*, tiger – *P. tigris*, jaguar – *P. onca*) exhibited the same extensive gnawing behavior seen in the other groups, but still exhibited powerful bite forces. This resulted in comparatively deep, relatively isolated marks when contrasted with the concentrated damage of gnawing wolves, hyenas, and bears. An unusual propensity for shearing away protruding bone surfaces, such as the greater trochanter of the femur and the tibial crest, was noted though.

Subsequent studies built on those observations, noting that felids do not exhibit the same degree of bone cracking behavior as canids, hyenas, and bears, leaving marrow largely unutilized as a food source (Domínguez-Rodrigo, 1999). This indicates that the bone modifications directly related to extensive gnawing and marrow consumption, such as chipped back margins, channeled bones, and long bone shaft cylinders (e.g. Binford, 1981; Haynes, 1983), are largely absent in felid modified remains.

Identifications of felid trace makers have also relied on comparisons of serial tooth mark spacing and arrangement. In one of the more famous paleoanthropological
examples, bite marks present on hominid cranial elements retrieved from Swartkrans cave in South Africa were shown to align with the lower canines of a leopard. This evoked an interesting paleoecological scenario since similar caves in modern, African ecosystems often have overhanging trees, attracted by the moisture and cooler condition surrounding cave openings. Since leopards often retreat to such isolated trees to avoid losing their prey to hyenas or other predators, the picture of an ancient leopard feeding on a hominid in such a tree, dropping discarded elements into the cave below was not too much of a stretch. While the author who originally proposed this interpretation of Swartkrans has expressed reservations relating to the complex nature of the cave site and the presence of multiple carnivore taxa which could have also contributed to the bone accumulations (Brain, 1981), this examples remains one of the better known and cited examples of felid bite mark identification in the fossil record.

**Bears**

Multiple examples of bear bite marks are published in the forensic literature. Since these studies were performed from a medico-legal standpoint, their main focus tended to be positive identification of human remains and cause of death instead of bite mark morphology. The presence of associated scat (Murad and Boddy, 1987; Murad 1997; Carson et al., 2000) and footprints (Haynes, 1982; De Giorgio et al., 2007) often formed the basis of bite mark actor identification. These lines of evidence are much easier to positively correlate on the time scale of a modern forensic investigation, but while both coprolites and trackways are available for paleontological research, making a case for direct association of these trace fossils with bite marked bones can be much more problematic unless the case can be made that a fossil locality represents a den or other
living surface (e.g. Binford, 1981; Cruz-Uribe, 1991). When bite mark morphology is mentioned in these forensic studies, it is usually described as either consistent with Binford’s (1981) model for mammalian bone modifications (Murad and Boddy, 1987) or restricted to comparisons of serial bite mark spacing to the dentition of the attacking animal (De Giorgio et al., 2007). Taxa included in these case studies include American black bear (*Ursus americanus* – Murad and Boddy, 1987; Murad, 1997) and European brown bear (*Ursus arctos arctos* – De Giorgio et al., 2007).

Patterns of mark placement and element destruction have been more successful in differentiating bear predation from other mammalian groups. For example, black bears (*Ursus americanus*) and polar bears (*Ursus maritimus*) have demonstrated similar tendencies of removing and consuming elements of the axial skeleton before the lower extremities (Carson et al., 2000), a pattern which statistically deviates from Haglund’s (1997a) typical mammalian scavenging sequence. It is possible that this pattern may be a sampling artifact, since previous studies indicated specific targeting of hind limbs in larger, non-human prey, at least among black bears (Haynes, 1982). Also, a recent survey of bite marks made by captive brown bears (*Ursus arctos*) demonstrated that the extent of bone breakage and number of marks created even within this one species could vary significantly depending on behavioral differences and prey size (Saladié et al., 2011).

Bear species have been included in various surveys of bite marks made by different mammalian carnivores. Most attempts to differentiate bear mediated damage from marks made by other taxa relate mark size and bone breakage to tooth shape, jaw morphology, relative size, and strength (e.g. Haynes, 1980; 1983; Domínguez-Rodrigo and Piqueras, 2003). The only discussions of diagnostic traces attributable to bears
discusses the crushing, grinding, and subsequent exfoliation and shearing caused by their cheek teeth (Haynes, 1983) or angle of bite-mediated fracturing (Saladié et al., 2012), but even these descriptions put the damage into terms of tooth shape and size in relationship to other taxa. However, researchers have questioned whether these marks are actually diagnostic of bears, or if isolated mammalian marks could be differentiated at all beyond broad size categories of the acting carnivore, citing similarities across the observed clades depending on duration and magnitude of gnawing damage (Domínguez-Rodrigo and Piqueras, 2003; Saladié et al., 2011). Without uncontested diagnostic bite marks, more positive identification of bear bite marks must therefore rely on the presence of serial marks which can be compared to jaw and tooth morphology (Haynes, 1980; 1983; De Giorgio et al., 2007).

**Pigs**

The earliest discussion of suid bone modifications come from the forensic literature and center on domestic pigs (*Sus scrofa domestica*). The primary type of bone modification identified was crushing, particularly of the sternal ends of the ribs, caused by the molars, and many smaller bones were consumed completely, suggesting a possible explanation for the not-uncommon loss of human hands and feet at crime scenes (Morse, 1983). This pattern was explored in more depth during a forensic case study, in which scavenging pigs had particularly targeted the victim’s viscera, causing significant crushing damage to the sternum, sternal ends of the ribs, medial ends of the clavicles, and pubic bones. Many of the bones of the face and hands were either missing or highly crushed, and bite marks were observed in lesser concentrations on many of the long bones (Berryman, 2002). This pattern of element destruction was broadly similar to a
previously recorded incident of scavenging by wild Bornean bearded pigs (*Sus barbatus*) on an orangutan (*Pongo pygmaeus* – Galdikas, 1978). Some individual marks were attributable to canids, but others exhibited a broad, flattened U-shaped cross-section which was better matched to the shape and orientation of a pig’s lower incisors, which these animals use in rooting type feeding behavior. Scores were the most common type of bite mark, and were described as often elongate and parallel (Berryman, 2002).

Zooarchaeological surveys, meant to differentiate bite marks from human tool marks and determine how suids might have affected archaeological sites, have also been performed as well. Isolated elements, some of which were experimentally altered to simulate hammerstone processing, were presented to domestic pigs, captive and wild boar (*Sus barbatus, Sus verrucosus, Sus salvanius, Sus scrofa scrofa*, and *Sus scrofa meridionalis*), and captive pig/boar hybrids. Though levels of modification were higher among the captive animals, both captive and wild specimens generated the shallow, U-shaped scores described in the forensic studies. A previously undocumented type of bite mark, L-shaped pits and punctures, was associated with the morphology of suid premolars and was identified as a potentially diagnostic mark for the group. Of particular note in the study, complete bones were not as heavily damaged as those which had been cracked open and the marrow removed to simulate human modification with hammerstones (Domínguez-Solera and Domínguez-Rodrigo, 2009).

**Rodents**

As a group, rodents are well known for their tendency to gnaw on a variety of substances, including bone, in order to maintain the length of their continuously growing incisors and to consume various minerals. Some species of rodent are also known to be
avid bone accumulators, caching bone in dens and gnawing on their collections. The African porcupine (*Hystrix afericaustralis*) has been particularly noted for its caching behavior (Brain, 1981), as have packrats (members of genus *Neotoma*). Rodent bite marks are most often described as series of paired, parallel scores, which are generally shallow, U-shaped, and flat-bottomed in cross section. These marks, caused by the paired upper incisors and occluding teeth of the lower jaw, most often follow natural ridges on bone, such as the rims of orbits or crests on long bones (Haglund, 1997b; Klippel and Synstelien, 2007).

These paired marks are the most common type of rodent bite mark identified in archaeological and paleontological studies (e.g. Brain 1981; Gifford, 1981). However, not all examples of rodent bite marks create this type of damage. The condition and type of bone being gnawed can affect the way these bite marks are expressed. Regions of bone with very thin cortical bone are often too fragile to stand up to even minor bite forces, and bite marks in these areas often lack distinct paired scores (Haglund, 1997b). Dry bone seems better suited to preserving distinct scores than fresh or greasy bone, a fact which is made even more interesting by the fact that different species of rodents may preferentially select bones at different stages of drying and weathering (Brain, 1981; Klippel and Synstelien, 2007). Also, if gnawing behavior or duration is particularly extensive, paired scores are often reworked and obscured by subsequent, overlapping marks. When paired incisor marks are absent, rodent bite marks are most often expressed as sets of parallel scores, scores arranged in a fan-shaped pattern, or disorganized, cross-cutting scores (Haglund, 1997b). In the fossil record, similar marks have been attributed to multituberculates, who while lacking the unrooted incisors which drive much modern
rodent bite mark morphologies, are often interpreted as having filled a similar ecological niche (Longrich and Ryan, 2010).

Rodents, such as brown rats, which preferentially gnaw regions of long bone which are particularly greasy and/or associated with epiphyseal surfaces create diagnostic, pedestalled feeding structures. While the articular surfaces and shaft of the long bone are left comparatively alone, the spongier bone in between experiences more focused attention. Taken to an extreme, this can result in only a thin strip of bone left attaching the shaft to the articular surfaces (Haglund, 1997b; Klippel and Synstelien, 2007). Rodent groups whose bite marks have been studied actualistically include the African porcupine (Brain, 1981), grey squirrels, and brown rats (Klippel and Synstelien, 2007). Marks attributed to field mice, African rats, and marsh rats have been published as graphics, if not explored in further detail (Morse, 1983). Gerbils (Brain, 1980) and other species of mice, squirrels, and rats (Brain 1970) have also been observed gnawing bone.

**Primates**

Bite marks and feeding modifications made by chimpanzees (*Pan troglodytes*) have been identified as potential sources of data for understanding hunting behavior and food selection in early human ancestors. Initial research of captive individuals on isolated, artificially flavored bones resulted in bite marks which were broadly similar to generalized carnivore damage (Pickering and Wallis, 1997). Pits, scores, crenulated margins, notches, and chipped back margins were all identified, and other than the fact that these marks were generally wider than those created by similarly sized carnivores, they were described as being very similar to other types of mammalian bite marks. The only feature that was noted as being potentially diagnostic of chimpanzees, and through
extension the pre-tool using hominids the captive animals were being used to simulate, were bone peels. These structures superficially resembled the curled peels caused by whittling wood and were caused when the chimpanzees held a bone between their teeth and pulled or twisted it away to fracture it with their hands. While the authors pointed out that some mammalian predators, such as dogs and hyenas, manipulate prey bones with their front paws in such a manner as might create similar peels, the frequency of these structures was higher in the more dexterous chimpanzees (Pickering and Wallis, 1997). Similar patterns of results have arisen in human bite mark studies as well (Saladié et al., 2012), bolstering the utility of comparisons between chimpanzee bite marks are fossil examples from early hominids.

Subsequent research has found similar feeding modifications on remains scavenged by wild populations, if not in the same extent as seen in the captive study. Peeling, fraying, and stepwise fracturing were identified again as possibly diagnostic traces associated with concentrated mastication of long bone ends. However, patterns which had proven useful in diagnosing feeding traces in other groups, such as prey skeletal element survival, were found to vary due to differences in the behavior and prey selection of populations of chimpanzees and the sampling techniques of the researchers. This suggested that further research was needed to positively identify patterns truly shared across and unique to the group (Plummer and Stanford, 2000; Tappen and Wrangham, 2000). In the largest sample of chimpanzee modified bones to date, even though previously identified diagnostic traces such as peeling and fraying were again identified, and other potentially diagnostic patterns of cranium, innominate, and rib damage were also found, the authors still stressed that direct application of their results to
the hominid fossil record would be difficult. Citing equifinality and comparing their results to examples of human bite mark damage, they recommended continued caution when identifying pre-tool using hominid hunting sites (Pobinar et al., 2007).

*Other Mammals*

A variety of other mammals have been documented creating bite marks on bone, but large scale surveys or detailed descriptions of these feeding traces have not yet been performed. For example, wolverines (*Gulo gulo*) have been observed fragmenting and caching long bones from large prey items (Haynes, 1982). Some herbivores, including deer, sheep, cattle, camels, giraffes, wildebeests, and antelopes, have been documented to gnaw bone in order to satisfy a nutrient deficiency in their diets. Bite marks made by the high-crowned molars of browsers in particular have been briefly described as forking and two-pronged (Morse, 1983). It is unclear if opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*) modify bone or if they only scavenge meat and transport bone (Morse, 1983). Research on the subject is ongoing (Synstelien, pers. comm.).

*Birds*

Birds have long been known to disarticulate and transport bone (Morse, 1983), and studies of the contents of pellets are common (e.g. Dodson and Wexlar, 1979; Kusmer, 1990; Yom-Tov and Wool, 1997), actualistic research of bone surface modifications made by this group have been scarce. Of these studies, many have been tightly focused on the African crowned eagle (*Stephanoaetus coronatus*). This narrow sampling makes sense within the framework of the original study (McGraw et al., 2006), which was attempting to determine if a particular hominid fossil, the Taung child, could have been killed and transported by a large bird of prey, as had previously been suggested
by paleoanthropologists (Berger and Clark, 1995). Crowned eagles were ideal for this analysis, since they were known to prey on small primates. However, whether the taphonomic patterns created by this one species of bird can be applied to other members of this diverse group has not yet been tested. Still, the results of the studies of this group are interesting and informative in their own right, as modifications made by talons and beaks would be predicted to differ substantially to those made by the teeth of other vertebrates (Sanders et al., 2003; McGraw et al., 2006; Trapani et al., 2006; Berger and McGraw, 2007).

These studies indicated that while prey preference seemed to change between localities, the pattern of damage did not. Long bones and crania preferentially survived feeding events, even though the crania in particular were often heavily damaged, either from the crushing grip on the eagles’ talons or from the removal of the occipital region of the skull in order to allow removal and consumption of the brain. Long bones were less modified on average, and damage was often confined to the diaphyses. Broad, flat bones, such as the scapula and pelvic elements, commonly exhibited evidence of raking by talons. Many bones, especially cranial elements, were punctured by beak and talon, and these marks varied in shape from round to rectangular to triangular. Beak marks, unlike tooth marks, left sharply V-shaped pits and scores, and were often found at the margins of breaks. These patterns were not only similar between geographically disparate groups and samples taken by different groups of researchers, they also resembled the types of damage seen at the Taung child locality, thereby supporting the interpretation of the site as an avian cache (Sanders et al., 2003; McGraw et al., 2006; Trapani et al., 2006; Berger and McGraw, 2007).
While Morse (1983) noted the role crows, hawks, black vultures, and turkey vultures play in defleshing and scattering remains, he did not directly observe any kinds of bone surface modifications made by these groups. Further exploration into black vultures and turkey vultures has had somewhat greater success. In one study, complete pig and goat carcasses were placed in an enclosure which prevented access by terrestrial predators and scavengers, but allowed birds to enter by air. Motion sensor cameras were used to capture photographs of any scavenger activity in the enclosure. While described as shallow and even ephemeral, both types of vulture left behind faint scores similar to those described as evidence of claw raking in the African crowned eagle research discussed above. However, the associated photographs taken during incidents of scavenging in this study made it unclear if the marks were created by beaks or talons. The author surmised that even small amounts of weathering or abrasion would obscure these marks. However, similar patterns of marks may be more distinct and persist longer in situations where the scavengers are larger or the prey is smaller and the bones are more fragile (Reeves, 2009).

Sharks and Other Fish

Though shark attacks on humans are statistically rare, numerous incidents have been recorded in the popular media (Hart and Sussman, 2005) and scientific publications (e.g. Coppleson 1958; İşcan and McCabe, 1995; Rathbun and Rathbun, 1997; Mendieta and Duarte, 2009). As the majority of this group’s literature is derived from forensic studies, there is a strong emphasis on modifications to soft tissue. Shark tooth marks on both soft tissue and bone are described as being crescent-shaped, reflecting the curving, twisting motions sharks use to bite and dismember prey (İşcan and McCabe, 1995;
Rathbun and Rathbun, 1997; Mendieta and Duarte, 2009). Most studied remains were retrieved from the stomach contents of sharks, which made direct association of predator and prey obvious, but also presented the issue that digestive fluids often extensively etch bone and obscure other bone surface modifications. However, this did not seem to be an issue in the presented case studies, since many sharks have been known to hold remains relatively unchanged and undigested in their stomach for days, if not weeks (Coppleson, 1958; İşcan and McCabe, 1995; Rathbun and Rathbun, 1997). Due to the fact that shark teeth are constantly replaced and are designed for cutting and slicing instead of gripping and crushing, shed or broken teeth are often left behind in both soft tissue and bones (İşcan and McCabe, 1995; Rathbun and Rathbun, 1997). These general patterns of shark bite marks on bone, including the embedding of shed teeth, have also been noted in the fossil record (e.g. Schwimmer et al., 1997; Shimada and Everhart, 2004; Shimada and Hook, 2004; Everhart, 2004; 2005). Many of these studies go so far as to note the presence (Everhart, 2004) or absence (Shimada and Everhart, 2004; Everhart, 2005) of striations within bite marks, caused by serrations on the teeth of many shark taxa.

While there are a variety of other types of fish that could potentially create bite marks on bone, very little actualistic work has been done to explore the existence and/or nature of those marks. Morse (1983) stated that while fish were more than capable of defleshing remains, he doubted that they would leave much in the way of marks on bone. A forensic study surveying incidents of known scavenging by piranhas on humans mentioned characteristic bite marks on soft tissue, but did not describe these marks in detail and mentioned no bone modifications of any kind (Sazima and Guimarães, 1987). Observing taphonomic processes in aquatic systems presents its own unique challenges
above and beyond equivalent studies on land, but this is certainly an area in which more actualistic bite mark studies are needed.

**Komodo Dragons**

Though ziphodont dentition was common in a variety of extinct taxa, especially among archosaurs, this type of laterally compressed, distally curved, serrated teeth are only represented in modern groups by some members of Varanidae. As the largest living varanid, captive Komodo dragons (*Varanus komodoensis*) were selected to provide actualistic data on bite marks created by animals with this type of dentition. Beyond patterns of bite mark frequency and location, the study discussed striations caused by denticulated carina and defined one new type of bite mark, edge marks, which are deeply incised, sharply V-shaped marks created when the distal edge of a tooth’s carina contacts a flat section of bone (D’Amore and Blumenschine, 2009). The striations themselves were found to be somewhat correlateable with body size of the bite mark actor in some taxa (D’Amore and Blumenschine, 2012).

**Crocodylians**

Bite marks and predation-mediated assemblages have been attributed to crocodylians and crocodyliforms in both fossil (von Nopsca, 1902) and modern deposits (Weigelt, 1927) for some time. However, detailed descriptions and surveys of diagnostic crocodylian feeding traces have only recently received attention (Njau and Blumenschine, 2006; Drumheller, 2007; Milàn et al., 2010; Westaway et al., 2012). Prior to these publications, crocodylian bite marks were often identified with little discussion of the methodology behind the diagnosis beyond general discussions of mark and tooth shape (e.g. Schwimmer, 2002; Cisneros, 2005; Mead et al., 2006; Steadman et al., 2007).
Many of the more detailed descriptions of fossil crocodylian and crocodyliform bite marks specifically discussed pathologies related to inferred intraspecific fighting (Buffetaut, 1983; Williamson, 1996; Avilla et al., 2004; Katsura, 2004). This association was most often based on the location of the marks, generally on the jaws and in the region of the base of the tails, which is consistent with injuries sustained by modern crocodylians during fights over access to territory or mates (e.g. Webb and Manolis, 1983).

Without the availability of large scale surveys of diagnostic feeding traces, some authors attempted to identify all potential feeding trace makers and then eliminate these contenders using a variety of ecological, morphological, and biomechanical arguments. Isolated observations of crocodylian feeding behavior, including forensic case studies, were used to both exclude (Gebo and Simons, 1984) and support (Davidson and Soloman, 1990) crocodylians as the trace maker in paleoanthropological specimens. A similar process of elimination was used by paleontologists to discuss putative *Metriorhynchus* bite marks on a plesiosaur, comparing tooth shape and spacing across available marine predators to the striated bite marks seemingly created by serrated teeth (Forrest, 2003) and *Asiatosuchus* bite marks on a turtle, again using jaw and tooth morphology to eliminate other crocodyliform actors (Fuentes, 2003).

In 2006, Njau and Blumenschine published the first large scale taphonomic study of crocodylian bite marks, focusing on both captive and wild members of *Crocodylus niloticus*. These marks proved novel in a number of ways. Furrows, scalloped edges, and other features diagnostic of the gnawing behavior of mammals (Binford, 1981) were absent in crocodylians, which utilize inertial feeding techniques rather than chewing or
shearing to process prey (Cleuren and deVree, 2000). Furrows, as defined by Binford (1981), would later be found in other crocodylian taxa (Drumheller, 2007), but never in the context of chewing or gnawing.

Additionally, two new types of bite marks were discovered by Njau and Blumenschine (2006): bisected marks and hook scores. Bisected marks were caused by the prominent carina found on relatively new, unworn crocodylian teeth. These marks were present in pits, punctures, and scores and presented as secondary indentations within the larger bite mark structure. In pits and scores, this created a subscore which effectively ‘bisected’ the larger bite mark. In punctures, portions of the carina along the sides of the teeth left notches on opposing margins of each mark (Njau and Blumenschine, 2006). Present in 10% of samples marks, these structures have since been found among other extant (Drumheller, 2007) and extinct crocodylian and crocodyliform taxa (Rivera-Sylva et al., 2009; Brochu et al., 2010; Noto et al., 2012), and seem to be diagnostic of non-ziphodont members of the clade.

Njau and Blumenschine (2006) tentatively associated hook scores, L- or J-shaped structures, with death rolling behavior, a disarticulation technique by which a crocodylian bites down on a portion of prey and rolls along its longitudinal axis using movements of head, spine, and tail to twist away a bite-sized piece (Fish et al., 2007). While this corkscrewing motion can generate hook scores, subsequent research has shown that other violent motions during a biting event, such as lateral shaking or thrashing, could also produce this type of trace (D’Amore and Blumenschine, 2009; Drumheller, unpublished data). Also, while Njau and Blumenschine (2006) considered hook scores to be diagnostic of Crocodylia, these marks have since been found in other reptiles which
utilize inertial feeding techniques (D’Amore and Blumenschine, 2009).

Putative crocodyliform bite marks on turtle shells are fairly common in the paleontological literature (e.g. Carpenter and Lindsey, 1980; Erickson, 1984; Fuentes, 2003; Karl and Tichy, 2004; Mead et al., 2006; Steadman et al., 2007; Lehman and Wick, 2010; Noto et al., 2012), a fact which prompted a taphonomic study of feeding traces created by modern crocodylians (captive specimens of Paleosuchus palpebrosus) on turtles (Trachemys scripta) (Milàn et al., 2010). The most common behavior was described as the ‘nutcracker’ technique, in which the caiman positioned a turtle’s shell roughly perpendicularly in its jaws and applied pressure, causing failure of the connection between carapace and plastron and exposing the tissue within. Portions of one shell processed in this way also exhibited crushing in areas associated with pits and scores. Another caiman resorted to eating a turtle’s exposed extremities after attempts to perform the nutcracker technique failed. The resulting bite marks in both cases were most often pits and scores, some of which occurred serially, from a single biting event. Pits and a few punctures were associated with crushed or otherwise fractured regions of the shells. Scores seemed to have occurred during shell repositioning or loss of grip within the jaws. From the illustrations, some of these examples would have been classified as hook scores, sensu Njau and Blumenschine (2006).

Forensic studies of crocodylian attacks on human beings have largely agreed with the patterns of damage and destruction described from other vertebrate prey. These studies often focus on soft tissue damage, but many cases include significant trauma to the bones as well, from the partial or complete loss of limbs (e.g. Harding and Wolf, 2006; Sartain and Steele, 2009; Mendieta and Duarte, 2009) up to near-total consumption
of remains (e.g. Cupal-Magaña et al., 2010). When damage to bone is discussed, beyond presence and location of trauma, crushing damage, spiral fractures, pits, punctures, and scores have all been described. Larger scale surveys of crocodylian attacks are often aimed at identifying patterns in location and cause of attacks, in order to predict and prevent further human injury or loss of life (Caldicott et al., 2005; Langley, 2005). Crocodylian taxa present in these types of forensic studies included *Alligator mississippiensis, Crocodylus acutus, Crocodylus niloticus*, and *Crocodylus porosus*.

**Conclusions**

Differentiation of bite marks from other types of bone surface modifications is the vital first step before any other types of interpretations can be drawn. The paleoecological, archaeological, or medico-legal information that can be derived from, for example, a bite mark versus a cut mark or an insect burrow, is very different. With such intense work on the subject of bone surface modifications, particularly since the 1980s, confidence in our ability to differentiate one basic type of bone surface modification from another has grown, reflected in reviews surveying the state of the field (e.g. Fisher, 1995) and successful blind inter-analyst tests of mark identification (e.g. Blumenschine et al., 1996). Controversies still arise through, particularly when the mark identifications are interpreted as early examples of human tool marks (e.g. McPherron et al., 2010; Domínguez-Rodrigo et al., 2011; Njau, 2012). Therefore, though significant strides have been made in differentiating mark types, more research is still required on bone surface modifications.

Having demonstrated how to differentiate bite marks from other types of bone surface modifications, the next step is to differentiate bite marks made by different
groups of animals. When that is possible, researchers have a solid line of direct evidence for addressing trophic interactions, feeding behavior, and diet in past ecosystems. Ancient bite marks have been identified and interpreted to these ends across numerous clades, including constituents of such disparate groups as temnospondyls (e.g. Reisz and Tsuji, 2006), theropod dinosaurs (e.g. Fiorillo, 1991; Van Valkenburgh and Molnar, 2002; Fowler and Sullivan; 2006), sharks (e.g. Shimada and Hooks, 2004; Everhart, 2005), and multituburculate mammals (e.g. Longrich and Ryan, 2010). Of these, some unusual examples provided evidence for specific behaviors, such as cannibalism in theropods (Rogers et al., 2003; Longrich et al., 2010), tree caching in leopards (Brain, 1981), and regional variation in diet in crocodylians (Schwimmer, 2010). Whereas the actualistic foundation of modern bite mark studies paved the way for many of these interpretations, the fossil record also has yielded a few examples where identification of the trace maker has been simplified by the preservation of embedded teeth (e.g. Currie and Jacobsen, 1995; Farlow and Holtz, 2002; Reisz and Tsuki, 2006; Drumheller and Boyd, 2011; Xing et al., 2012). Other authors have supplemented the preserved bite mark information with gut contents, coprolites, and isotope levels in order to attain a more wholistic view of trophic interactions and food web structure in paleoenvironments (e.g. Farlow and Holtz, 2002).

Being able to differentiate between active predation and passive scavenging has been addressed in both paleontology and paleoanthropology. While some have expressed doubt that making such a distinction is even possible using bite marks and other trace evidence (Farlow and Holtz, 2002), interpretations of scavenging have been made based on bite mark location on, and relative size in comparison to, prey remains (Longrich et
al., 2010). Among paleontologists, this debate has largely focused on large, charismatic theropods, particularly *Tyrannosaurus rex*, with debate ongoing (e.g. Horner and Lessem, 1993; Holtz, 2008).

The topic has enjoyed significantly more attention in the paleoanthropological and zooarchaeological literature, because of intense interest in early hominid diet and behavior, especially with regards to protein and meat consumptions, and how that affected a variety of important factors in human evolution such as brain size, cooperative hunting behavior, and tool use. Determining the order of access to prey items could help determine whether various hominids were hunters, active scavengers, or passive scavengers (O’Connell et al., 2002). As hunters, hominids would have first access to carcasses, allowing them to collect more and better portions of meat for consumption. Active scavenging, or accessing prey by chasing initial predators away from a food item, could also provide a significant amount of meat without the exertion and, in the case of human ancestors, the technology needed for outright hunting. Passive or marginal scavenging, or procuring only that meat which has been voluntarily abandoned by previous predators, would have provided the lowest quantity and quality of food items.

Debate on early hominid hunting versus scavenging remains ongoing, with actualistic experiments being performed by all sides of the argument. Simulated sites of anthropological interest, representing different order of predator access to prey items, from hominids first (e.g. Marean and Spencer, 1991), to last (e.g. Selvaggio, 1994), to somewhere in between (e.g. Selvaggio, 1998), have been created and studied in attempts to determine how to identify these different scenarios in the paleoanthropological record. Most have turned to ratios of bite marks to cut marks, whether across the entire
assemblage, on only long bones and long bone fragments, or on specific areas of bone, such as near long bone ends (Lupo and O’Connell, 2002 and references therein). While patterns in these ratios, and also tying marks on anatomical parts of higher nutritional value to earlier access to the prey remains, have been found, the application of these data to the fossil record has remained contentious.

Though bite marks are most often associated with feeding behaviors, incidents of intraspecific fighting have also been interpreted in the fossil record. This identification can be difficult to interpret, especially if the incidence of fighting resulted in a kill and subsequent feeding event. However, some animals exhibit specific patterns in intraspecific fighting events, such as focused bites directed at the base of the tail among crocodylians (Webb and Manolis, 1983). These types of pathologies have been found in a number of fossilized crocodylians and more basal crocodyliforms and crocodylimorphs (e.g. Buffetaut, 1983; Williamson, 1996; Avilla et al., 2004; Katsura, 2004). Similar arguments have been made for identifications of intraspecific fighting among other groups of extinct animals, particularly head-biting behavior in theropods (e.g. Tanke and Currie, 1998).

Other researchers are pushing the bound of what bite marks can reveal beyond descriptive interpretations of the biting event itself. For example, functional morphologists have long relied on modeling and direct sampling of modern animals to make predictions of bite force capabilities in extinct groups (e.g. Erickson et al., 2003; 2004). These predictions have recently been tested using failure rates of bone under casts of theropod teeth and comparisons of those test results to actual fossilized bite marks attributed to *Deinosuchus antirrhopus* (Gignac et al., 2010).
Conservation biologists have also started exploring bite marks as a potential aid in improving methods of protecting endangered and threatened species. In one example, predation was blamed for the loss of many adult and juvenile birds in a protected breeding area in New Zealand (Lyver, 2000). With many potential predators and no single step which could be taken to protect against all of them, researchers turned to the bite marks themselves to determine which species was preying on the nests. By comparing the size and spacing of the marks to the dentition of local predators, the biologists were able to identify the culprit and tailor a method of protection to the specific threat to the breeding population.

In addition to simply identifying bite marks, forensic anthropologists are currently exploring other ways that bite marks can provide important evidence about the cause and condition of unexplained human deaths. Estimating time since death is an important factor in building criminal cases and identifying human remains. Observations of captive wolves have demonstrated that the period of time it takes for large predators to completely deflesh and disarticulate a corpse can be very short, but is also strongly dependant on the number of animals involved in the feeding event (Willey and Snyder, 1989). This aligns well with observations of predation made in zooarchaeological contexts.

Rodent scavenging has also added an interesting temporal aspect to the timing of different feeding events (Klippel and Synstelien, 2007). Brown rats, common visitors to decaying remains, focus their attention on the greasy ends of long bones. This results in a characteristic pedastling modification of the bone. Once the bones have decayed and weathered to the point that grease is no longer readily available, brown rats lose interest
in scavenging the remains and another rodent, the grey squirrel, takes their place. The squirrels are only attracted to older, dry bone, presumably for access to nutrients such as phosphorus and calcium. Following the natural, sharp margins of these dry bones, squirrels create sets of paired scores, which have long been correlated with rodent gnawing behavior and incisor morphology (Haglund, 1997b). While less temporally focused as other methods for determining time since death, this succession of scavengers can narrow these estimates to periods of months in which two rodents are active if other techniques prove inconclusive.

Further applications of bite marks to studies of trophic interactions, functional morphology, feeding behaviors, and forensic processes are still being developed and explored. However, none of them would be possible without a solid foundation of actualistic observations across a broad spectrum of living groups. Sampling techniques and theoretical frameworks have changed and strengthened since William Buckland first compared modern and ancient bite marks in 1832. Surveys of bite marks made by previously unsampled extant groups have been published with increasing frequency, especially following the burst of taphonomic research in the 1980s. However, sampling across these groups has been uneven, with the vast majority of attention being centered on mammalian groups, and particularly on African taxa which would have interacted with early hominids and North American taxa studied in archaeological and forensic anthropological contexts.

Though highly useful within the contexts of the research questions they were designed to address, surveys of modern mammals were often of limited use to researchers interested in non-mammalian groups. The differences in morphology and feeding strategy
led to studies comparing mammalian and presumed non-mammalian bite marks in the fossil record (e.g. Fiorillo, 1991; Van Valkenburgh and Molnar, 2002). In search of better modern analogies for these groups, studies surveying non-mammalian bite marks have increased in frequency (e.g. Drumheller, 2007; D’Amore and Blumenschine, 2009; Milàn et al., 2010; Westaway et al., 2011). In response, the importance of these groups in more recent contexts has also been realized, providing a richer, more complete understanding of modern ecosystems and trophic dynamics (Njau and Blumenschine, 2006).

For this progress to continue, more surveys of modern groups need to be performed in order to fill the remaining gaps in sampling. Some important groups of large predators, such as sharks, have not yet been systematically surveyed and are only addressed in forensic case studies (e.g. Coppleson 1958; İşcan and McCabe, 1995; Rathbun and Rathbun, 1997; Mendieta and Duarte, 2009). Other groups are only represented by a very limited survey of living groups, with only a single sampled taxon among squamates (D’Amore and Blumenschine, 2009) and three sampled taxa among crocodylians (Njau and Blumenschine, 2006; Milàn et al., 2010; Westaway et al., 2011). Conducting further surveys of un- and under-sampled groups will improve our ability to differentiate between types of bite marks and broaden the types of research questions bite mark data can be used to address.

Taphonomy has been a highly multi-disciplinary field since its earliest inception, drawing upon biological, geological, and anthropological sources to address any number of research questions, including those which specifically address bite marks. However, researchers in all of the branches of science which actively study bite marks and other taphonomic processes – paleontology, zooarchaeology, paleoanthropology, and forensic
anthropology – have often remained unaware of the relevant, parallel research being performed by colleagues in their sister disciplines. More active cooperation between researchers of disparate backgrounds, partnered with the continued collection of raw actualistic data, will continue to push the boundaries of taphonomic research.
CHAPTER II
THE UTILITY OF CAPTIVE ANIMALS IN BITE MARK RESEARCH: A CASE STUDY OF \textit{ALLIGATOR MISSISSIPPIENSIS}

\textbf{Introduction}

Captive animals often differ morphologically from their wild relatives (e.g. Hard et al., 2000; Zuccarelli, 2004; McPhee, 2004; O’Regan and Kitchener, 2005; Guay and Iwaniuk, 2008). Differences in behavior (e.g. Flemming et al., 1996; Geiser and Ferguson, 2001; McPhee, 2003), functional performance (e.g. Erickson et al., 2004), and rate and type of pathology (Fitch and Fagan, 1982; Munson et al., 2005) have also been noted among captive populations. Even so, animals kept in farms and zoos are regularly used to study a wide variety of topics, from physiology to functional morphology to taphonomy. Within the bite mark literature, captive animals have been used extensively (e.g. Haynes, 1983; Willey and Snyder, 1989; Marean and Spencer, 1991; Pickering and Wallis, 1997; Njau and Blumenschine, 2005; Drumheller, 2007; D’Amore and Blumenschine, 2009; Saladié et al., 2011) even though the potential for biasing effects has been recognized (Haynes, 1982).

However, captive animals have a variety of characteristics which make them attractive as research specimens. Captive populations held in zoological parks or farms are often more accessible for research. When dealing with threatened or endangered species, captives may prove to be the only viable source of data. Also, many of these facilities keep long-term veterinary and physiological records of their animals. Some of these variables, such as mass or sex, can be collected in the field, but others, such as
exact age and measurements through ontogeny, may be difficult to impossible to collect from wild animals. Furthermore, captive specimens have habitats and routines that include regular human interaction, another potentially complicating factor which still can make data collection safer for animals and researchers alike. Therefore, if captivity can be shown to have a negligible effect on a study’s data, these animals can prove to be quite lucrative sources of information.

Among crocodylians, a variety of morphological differences have been cited anecdotally in the literature. Captive *Alligator mississippiensis* are said to have wider, blunter snouts, teeth that splay outwards (Figure 2.1), and larger fat deposits (Erickson et al., 2004). This pattern seems to be repeated in other generalized and blunt-snouted taxa. Captive tube-snouted crocodylians, such as *Gavialis gangeticus* and *Tomistoma schlegelii*, often exhibit unusual bending along the rostrum, both laterally and dorsally. Morphometric analyses of *A. mississippiensis* have also revealed that captives exhibit a raised lip along the skull table, comparatively short basioccipitals and wide lachrymals, closely set eyes, and an upturned rim around the orbits (Sadleir, 2009). Feeding behavior among captives does not appear to deviate from that seen in the wild (personal observation, Cleuren and De Vree, 1992; 1999), but bite force performance has been demonstrated to differ between the two populations, especially among older, larger animals (Erickson et al., 2004).

While the forensic anthropological literature has yielded a few case studies involving wild crocodylians (e.g. Caldicott et al., 2005; Langley, 2005; Harding and Wolf, 2006), the majority of actualistic bite mark data for this group has relied heavily on captive specimens (Njau and Blumenschine, 2005; Drumheller, 2007; Westaway et al.,
Figure 2.1
A – UF 61483, captive adult *Alligator mississippiensis*. B – UF 34886, wild adult *A. mississippiensis*. C – Generalized *A. mississippiensis* ‘captive’ morphotype with arrows indicating the regions commonly cited as differing from the wild form.

2011). These, and other modern observations of crocodileian behavior, have been used in turn to interpret past behaviors (Buffetaut, 1983; Williamson, 1996; Avilla et al., 2004; Katsura, 2004), identify fossil bite marks, and assess diets (Davidson and Soloman, 1990; Forrest, 2003; Fuentes, 2003; Cisneros, 2005; Mead et al., 2006; Steadman et al., 2007; Riviera-Sylva et al., 2009) in extinct crocodileians and more distantly related archosaurs.

Thanks to highly successful conservation efforts and extensive research collections, *A. mississippiensis* is one of the most rigorously studied species of extant crocodileians (Rowe et al., 1999). Therefore, this species is a logical candidate for a case study exploring whether captive crocodileians should be used as proxies for their wild,
living or extinct, relatives. This study utilizes two-dimensional geometric morphometric techniques to test the hypothesis that there are no significant differences between tooth placement and bite radius in captive and wild *A. mississippiensis*, thus making them acceptable proxies for bite mark collection and analysis.

**Materials and Methods**

The specimens used in this study are held in three collections: the American Museum of Natural History (AMNH), the University of Florida (UF), and Rudyard W. Sadleir’s research collection (RWS) held at the Field Museum of Natural History (FMNH). Only specimens with known provenance and which lacked extensive pathologies, postmortem damage, and remaining soft tissue obscuring areas of interest were included in the analysis (Table 2.1).

Images of the ventral view of each cranium, representing eighteen captive and seventy-two wild individuals (Table 2.1), were collected with an Olympus® Stylus™ brand, model 760 still-image camera. Both camera and specimen were oriented on a copy stand using a two-way level centered on the suture between the specimens’ maxillae in order to ensure a uniform camera angle during image and data collection.

Landmarks were chosen from the right side of each skull and represented sockets from all five premaxillary and the first seven maxillary teeth (Figure 2.2). These loci were selected to address tooth socket spacing, relative tooth position in the jaw, and overall snout shape. These features are capable of affecting bite mark expression, particularly with regard to the relative spacing of marks within serial bite structures and, to a lesser extent, the angle of tooth impact. No further maxillary teeth were sampled, following the landmark selection outlined by Sadleir (2009), because the placement and,
Table 2.1

Captive and wild *Alligator mississippiensis* specimens, listed by institution.¹

<table>
<thead>
<tr>
<th>Institution</th>
<th>Captive</th>
<th>Wild</th>
</tr>
</thead>
<tbody>
<tr>
<td>American Museum of Natural History</td>
<td>AMNH7141, AMNH9112†, AMNH61563, AMNH119220, AMNH138124</td>
<td>None</td>
</tr>
<tr>
<td>Florida Museum of Natural History</td>
<td>UF35129, UF61483</td>
<td></td>
</tr>
<tr>
<td>Rudyard W. Sadleir</td>
<td>RWSF1, RWSF2, RWSF3, RWSF4, RWSF5, RWSF6, RWSF7, RWSF8, RWSF9, RWSF10, RWSF11</td>
<td>RWS1, RWS2, RWS3, RWS4, RWS7, RWS8, RWS9, RWS10, RWS11, RWS12, RWS13, RWS14, RWS15, RWS16, RWS17, RWS18, RWS19, RWS20, RWS21</td>
</tr>
</tbody>
</table>

¹ All RWSF specimens were culled at ages 2 - 2.5 years and roughly 4 feet in length (Sadleir, 2009). * = disarticulated specimens; † = displays pathologies in the tooth row.

to a lesser extent, number of remaining teeth is variable in *A. mississippiensis*, especially when different ontogenetic stages are included in an analysis. The center of the socket was selected for each landmark instead of a feature of the tooth itself for two reasons: crocodylians continuously shed teeth, making eruption and wear patterns irregular, and
Figure 2.2

Type II landmarks on *A. mississippiensis.*
the vast majority of the specimens available for this study had lost most, if not all, of their teeth during natural decay or the collection and cleaning processes.

While all the sampled landmarks are Type II, the inclusion of suture contacts to provide solid Type I landmarks yielded statistical results dominated by suture position alone, particularly the contact between the maxilla and the ectopterygoid along the lateral margin of the jaw. This is consistent with the findings of previous morphometric analyses of the species (Sadleir, 2009). However, since the sutures themselves play no direct role in the creation of bite marks, the reported analysis was restricted to those landmarks most directly related to the question at hand: the teeth themselves.

Landmark data were collected using the program ImageJ (Girish and Vijayalakshmi, 2004). This data is presented in Appendix A. Generalized least squares Procrustes superimposition was performed in IMP 6 (Sheets, 2001) on the resulting dataset in order to remove the effects of scale and rotation. This was accomplished by anchoring each specimen’s centroid, the geometric center of a shape, on the origin of an X-Y graph (for two dimensional data such as those used in this study). Size was then removed as a factor by dividing coordinates by the centroid size, a metric of size devoid of shape information that is calculated by taking the square root of the sum of all squared distances between the landmarks and the centroid. Finally, rotational factors were removed by reorienting each specimen around the origin in order to minimize the sum of squared distances between landmarks (Zelditch et al., 2004). However, Procrustes superimposition produces more variables than the degrees of freedom allow, so another step in calculation was required. A thin plate spline mathematical model was therefore applied to the Procrustes scores to generate partial warp scores, again using IMP (Sheets,
2001). These scores have the correct number of degrees of freedom, and are therefore able to be used in additional statistical tests (Zelditch et al., 2004).

The distribution of partial warp scores were visualized with SAS® 9.2 using principal components analyses, canonical variates analyses, and box plots (PROC PRINCOMP, PROC DISCRIM, PROC BOXPLOT). Results were tested for significance using an ANOVA test, a Tukey HSB test, (PROC ANOVA), a MANOVA test, and crossvalidate (PROC DISCRIM). Deformation grids were generated with tpsUtil 1.53 (Rohlf, 2012) and tpsRelw 1.49 (Rohlf, 2010) in order to better visualize the shape changes represented by the principal component axes. In R 2.15.2 (R Development Core Team, 2004), an ANCOVA (state package) was performed in order to statistically assess the covariance between size (represented by centroid size) and origin (captive or wild) with regards to shape (represented by principal component scores). To confirm that the dataset could be explored using both ANOVA and ANCOVA tests, the assumptions of both tests were explored with a multivariate Shapiro Wilk’s test (mvShapiroTest package) and a Bartlett’s test (stats package) to determine if the data were normally distributed and the variances were statistically comparable.

**Results**

The first seven principal component (PC) axes yielded eigenvalues greater than one, and the scree plot indicates that the first four axes are potentially informative. The amount of variance explained by axes one through four is as follows: 20.29%, 12.08%, 9.55%, and 8.61%. However, only axes two and four resulted in ANOVA p values <0.05, but >0.0001. This indicates that only these two axes reject the null hypothesis that the means of the PC scores of captive and wild individuals do not statistically differ, an
Top – Principal components analysis, axes 2 (12.08% of the variance) and 4 (8.61% of the variance). Deformation grids show the estimated shapes present at 0.05 and -0.05 on axis 2 and 0.02 and -0.03 on axis 4. Open circles = captive; Solid circles = wild. Bottom – Canonical variates analysis, boxplots. C = captive; W = wild. All statistically significant axes, determined by an ANOVA (PCA) and a MANOVA (CVA), are shown.
interpretation which is further supported by the Tukey HSB test results. Even so, both of these axes still exhibit significant overlap visually between captive and wild populations (Figure 2.3).

In order to determine if these results were meaningful, a multivariate Shapiro Wilk’s test, performed on axes one through four, successfully rejected the null hypothesis with p<0.0001, which indicated that the datasets were normally distributed. A Bartlett’s test performed on each of axes one through four never generated a result of p<0.05. Therefore the null hypothesis was not rejected and the two variables (captive and wild) have equal variances. Taken together with the knowledge that whether an animal lived in captivity or in the wild are independent variables, these two tests show that the dataset meets all three assumptions for use in an ANOVA.

The area most often cited as differing between captive and wild crocodylian populations is the width of the snout, particularly around the region of the fourth maxillary tooth (Erickson et al., 2004). Deformation grids indicated that this part of the snout was driving much of the observed pattern along with shortening and broadening of the snout in captive individuals, particularly along PC axis two (Figure 2.3). However, these results were a cause for concern, because these features vary significantly through ontogeny as the fourth maxillary tooth enlarges, the surrounding teeth correspondingly move to accommodate the change, and the overall snout shape changes during growth and development (Kälin, 1937; Brochu, 1999).

The only axis generated with a canonical variates analysis found a statistical difference between captive and wild populations with a Wilk’s Lambda of p<0.05. However, visually the two populations again exhibited overlap along their total ranges
(Figure 2.3). Also, the partnering crossvalidate function was only able to positively classify captive specimens 61.11% and wild specimens 73.61% of the time.

While statistically significant division between captive and wild populations was found to exist, the pattern centered on a ontogenetically variable trait and, frankly, was not as strong as the qualitative literature would lead one to expect. Therefore, to further explore what, if any, effect ontogeny had on the dataset, an ANCOVA was performed in order to better understand the interactions of centroid size, origin (captive versus wild), and size/origin interaction with shape, represented by principal component scores for axes one through four (Table 2.2). Since the dataset previously had been found to conform to all the assumptions of an ANOVA, an ANCOVA also was deemed appropriate for this analysis. None of the four axes yielded significant differences based size/origin interactions. Axes one and two demonstrated a significant difference based on size (axis 1 - p<0.001, axis 2 – p<0.0001), and axis four demonstrated statistical differences based on origin (p<0.01).

**Discussion**

The mixed results of these analyses are surprising at first glance. One of the differences often cited between captive and wild crocodylians is snout shape (Erickson et al., 2004). Previous analyses of *A. mississippiensis* crania demonstrated strongly divergent morphologies between the two groups (Sadleir, 2009). The results of this study were not so straightforward. Initial analyses were able to find statistical differences between the sampled captive and wild specimens. However, the signal was largely dominated by potentially ontogenetic factors.

The results of the ANCOVA test indicate that ontogeny is introducing a stronger
signal in the dataset than origin. This interpretation makes sense when wild and captive
morphologies are viewed as a range of variation related to ecophenotypy rather than a
straightforward binary characteristic. Morphological differences between juvenile and
adult crocodylians have long been recognized (McIlhenny, 1935). These qualitative
observations of morphology and behavior since have been subjected to more rigorous
analysis, both within and between captive and wild populations. Erickson and colleagues
(2004) recognized that bite force in captive and wild *A. mississippiensis* was highly
similar among juveniles, but that differences arose in older, larger animals. Published
differences in crocodylian bite forces (Erickson et al., 2004), cranial morphology
(Sadleir, 2009), biomechanical performance of humeri (Meers, 2002) and geometric
dimensions of femora (Farlow et al., 2005) between captive and wild populations have all
been interpreted as the long-term effects of exposure to unnatural habitat and diet (Meers,
2002; Sadleir, 2009), pressures which act over time and ontogeny. During growth, the
ecological pressures of captivity would be expected to introduce increasingly aberrant
morphologies the longer the conditions persist, and all the while, changes in shape related
to normal growth in the taxa would persist.
While no one is questioning that differences between captive and wild crocodylians have been observed elsewhere in the body, the ANCOVA results indicate that these effects related to captivity, while present, are not as strong as the existing ontogenetic signal. Future morphometric studies also should avoid comparing any crocodylian groups from a limited size and age range to the full ontogenetic spectrum of another form, as this biased sampling will most likely artificially inflate any real differences between the two populations.

The definition of ‘captivity’ itself is another complicating factor. Qualitative observations and in-depth morphometric analyses of populations within crocodylian species have revealed the breadth of variation possible under natural conditions (Sadleir, 2009), and yet all captives are often lumped together as a single state. Living conditions for crocodylians at zoological parks and farms can range from bare concrete enclosures to fenced off areas of largely unchanged natural habitats. Animals that are held in indoor facilities often live under highly climate controlled conditions, often with unchanging temperature and light exposure (Sadleir, 2009), while those kept in open air enclosures experience much of the same light and temperature changes as their wild counterparts. Differences in captive diet and behavior level have been noted by researchers (Meers, 2002; Farlow et al., 2005), but have not yet been surveyed or studied in much detail. With so much possible variation in the conditions of captivity, differences among captive populations’ morphological reactions to these pressures would be expected, and in fact, has been observed (Figure 2.4).

**Conclusions**

When attempting to justify the utility of captive crocodylians in bite mark
analyses, the results of this study are actually quite positive. While statistically significant differences arose between captive and wild populations, the signal from this variable was not as strong as the overarching effects of ontogeny. For sensitive, quantitative analyses, such as future morphometric analyses of natural variation, captive specimens should certainly be avoided. However, for studies that work at a gross scale, such as bite mark interpretations, these results indicate that the snout shape of captive specimens should not be introducing notable bias into the data, especially if sampling across the full range of age and size groups is performed. These findings are further bolstered by the fact that comparable marks have been experimentally collected from both captive and wild specimens of *Crocodylus niloticus* (Njau and Blumenschine, 2005) and *A. mississippiensis* (Drumheller, 2007).

This study did not address all possible sources of bias when using captive
crocodylians. Tooth splay is still a cause for concern. However, the results of these analyses do seem to indicate that socket position is not affected by this process, only the angle of the tooth within those sockets. Preliminary statistical comparisons of socket shape bolster this interpretation (Drumheller, unpublished data). Tooth angle could conceivably affect the way the animals’ teeth impact bone during a bite. Even so, bite marks collected from captive and wild populations hint that this might not be the case.

Crocodylians often create a diagnostic tooth mark called a bisected pit or score. This feature is created when the prominent carina of newly erupted, relatively unworn crocodylian teeth creates a small subscore within the larger bite structure, a groove which effectively ‘bisects’ the mark (Njau and Blumenschine, 2005; Drumheller, 2007). In the surveyed bite marks from both captive and wild crocodylians, these subscores seem to fall in the approximate center of the bite marks, representing a roughly perpendicular angle of tooth impact. This could either indicate that captive animals are subtly adjusting their biting behavior in order to angle their splayed teeth more effectively or that these particular bite marks are preferentially caused by the mechanically stronger teeth in the back of the jaw, which are preferentially used for powerful killing or crushing bites (Cleurens and Devree, 2000) and do not seem to splay as strongly as more anteriorly positioned teeth.

This study also does not address the rate and type of pathology in captive and wild crocodylians. While none of the sampled wild specimens exhibited obvious, significant pathologies in the tooth row, two observed captive specimens did. AMNH 9112 had impacted teeth on both sides of the upper jaw. Holes in the dorsal surface of the snout were caused by bone resorption as a result of these impactions, leaving the roots of
the affected teeth clearly visible through the roof of the snout. AMNH 31563 also exhibited a similar impacted tooth in the left maxilla. This specimen also had extensive reaction tissue throughout much of the left maxillary tooth row, but it was unclear if this was related to the impacted tooth or an unrelated injury or infection (Figure 2.5).

However, prior research indicates that wild *A. mississippiensis* are certainly not
immune from injuries and infections that affect the tooth row (Erickson, 1996). Broken teeth and related alveolar damage and infections commonly result in partial to complete edentulism in wild members of many crocodylian species, including *A. mississippiensis*. In fact, one survey of crocodylian dental conditions directly compared captive and wild specimens, and found that the wild animals actually exhibited significantly more pathologies than their captive counterparts (Erickson, 1996). It seems that any effect pathologies might have on crocodylian feeding behavior and bite marks, excluding any obviously extreme cases, would present in both captive and wild populations, and would therefore not preferentially affect one source of data over the other.

While collecting datasets from wild populations is still preferable in the study of taphonomic processes and feeding traces, in this instance, the use of captive crocodylians as proxies for their wild counterparts seems to be justified, especially if a wild dataset is available for comparative purposes. However, that is not to say that this pattern will hold true across all taxa whose bite marks have been collected for interpretation. As a case study, this paper should serve as a suggestion for how bite mark data collected from captive members of other groups can be accepted or rejected on their own merits.
CHAPTER III

A DIAGNOSIS OF *ALLIGATOR MISSISSIPPIENSIS* BITE MARKS WITH
COMPARISONS TO EXISTING CROCODYLIAN DATASETS

**Introduction**

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

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

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

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

While the *C. niloticus* survey represented a major step forward in crocodylian bite mark studies, the authors expressed a need for further sampling of other extant crocodylians in order to independently verify the novelty of the identified marks and to determine how widely these traces occurred in the clade (Njau and Blumenschine, 2006: p. 17). Milàn and colleagues (2010) performed a short study on *Paleosuchus palpebrosus* modifications of turtle shell, but their focus centered on patterns of shell breakage and behavior specific to chelonivory and not on detailed descriptions of the bite marks themselves. Forensic case studies covering attacks by *Alligator mississippiensis*, *Crocodylus acutus*, *C. niloticus*, and *Crocodylus porosus* on humans provide potential sources of independent analyses of these groups (e.g. Harding and Wolf, 2006; Sartain and Steele, 2009; Mendieta and Duarte, 2009; Cupal-Magaña et al., 2010). These studies
often focused more on patterns of soft tissue damage and, because most only cover one or a few attack events, the sample size is limited. Still, even though these studies are not directly comparable to the Njau and Blumenschine (2006) study, discussions of feeding strategy and bone modifications were largely consistent with the patterns described for *C. niloticus*.

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

To further explore how crocodylians modify prey bone and whether these marks can be positively diagnosed in the fossil record, bite marks were collected from specimens of *Alligator mississippiensis*, the American alligator. This focus on *A. mississippiensis* stems from a number of factors that make this species ideal for
continuing actualistic research involving crocodylians. First, thanks in large part to successful conservation efforts and the ensuing relative ease of access to members of this species to researchers, the anatomy and ecology of *A. mississippiensis* has been more extensively studied than any other extant crocodylian (Brochu, 1999). Secondly, in addition to often serving as the de facto model organism for the group, in this study *A. mississippiensis* represents a completely separate lineage within Crocodylia from the previously surveyed species. *Crocodylus niloticus* and *A. mississippiensis* last shared a common ancestor in the Late Cretaceous (Brochu, 1999). Because identifications of diagnostic bite marks in *C. niloticus* (Njau and Blumenschine, 2006) were not successfully reproduced in a close relative, *C. porosus* (Westaway et al., 2011), interpreting these marks as diagnostic for all crocodylians, much less for all crocodyliforms, was called into question. This study attempts to explore and clarify this conflict between the existing crocodylian samples by broadening the phylogenetic reach of existing datasets.

*Crocodylian Feeding Behavior*

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

Prey items are then dispatched. This can be accomplished in a number of ways.
Smaller prey items can be repositioned in the mouth until a single, powerful killing bite can be performed (Cleurens and deVree, 2000). This repositioning utilizes inertial feeding behavior. The head and neck are elevated and the hyolingual apparatus presses the prey item dorsally in the mouth. Then, the rapid opening of the jaws, partnered with further elevation of the open jaws, accelerates the prey item further into the mouth cavity. This can be partnered with lateral movement when shifting the prey item to one side or the other is desired. Rapid jaw closure, partnered with reversal of any lateral movement and a retraction of the hyolingual apparatus, thrusts the head forward. The prey item is then positioned further back in the toothrow. These types of bites can occur multiple times, shifting prey position in the mouth, until a killing or crushing bite can be applied (Cleurens and deVree, 1992). This phase can be particularly important when hard-bodied prey types, such as turtles, are involved, since careful positioning is required to effectively compromise armored shell (Milán et al., 2010).

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

Once smaller prey is dead, further inertial bites can be utilized to transport food
items towards the throat, in preparation for swallowing (Cleurens and deVree, 2000). Larger prey may require further reduction before swallowing is possible. However, the conical teeth of most crocodylians, while useful for grasping prey, are not particularly good at cutting or tearing tissue on their own. Continued lateral thrashing can tear smaller portions away from a prey item, and crocodylians have been observed modifying this behavior to take advantage of hard substrate, slamming prey items against rock or fixtures in enclosures (Njau and Blumenschine, 2006; Drumheller pers. obsv.). Further death rolling can twist away bite-sized portions of food (Fish et al., 2007), a technique which can become even more effective when two or more animals utilize it on the same prey item simultaneously, moving in opposition to one another (Njau and Blumenschine, 2006). Unlike mammalian, crocodylians do not proactively seek out bones or marrow as sources of nutrition during this stage of feeding. However, incidental ingestion of bone can and does occur, and crocodylian digestion is more than capable of processing it (Fisher 1981). Swallowing is accomplished through further inertial repositioning, until the prey item is positioned where muscles of the throat can take over food transport (Cleurens and deVree, 2000).

Large prey reduction and defleshing can continue until the entire prey item is consumed. However, sections of carcass are often abandoned, particularly when large or durable prey items are involved. Violent dismemberment can scatter elements which are then discarded (Davidson and Solomon, 1990). The cracked-open remnants of turtle shell are often abandoned once the majority of soft tissues have been consumed (Milán et al., 2010). While bite marks can be left at any of the stages of feeding described above, it is to these abandoned remnants of meals that taphonomists must turn (Njau and
Blumenschine, 2006), since the digestive processes of crocodylians effectively destroy any consumed bone (Fisher, 1981).

**Materials and Methods**

*Bite Mark Sample Collection*

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

Two sets of bite mark samples were collected. The first sample (Group 1) consisted of specimens presented to fourteen individual specimens of *A. mississippiensis*.

![Figure 3.1](image-url)

Photographs of *A. mississippiensis* taken during Group 1, individual feeding (left) and Group 2, group feeding (right).
in isolation (Figure 3.1). Smaller animals were presented with the isolated pig femora while larger animals were given the partially butchered cow hind limbs. Many samples were voluntarily abandoned, but some animals had to be induced to drop the limbs to facilitate retrieval once active biting ceased. Each animal was unrestrained while bite mark samples were collected except in cases when handler and animal safety was a concern. In the event that restraint was deemed necessary by SAAF staff, individuals were held near the base of the skull by a handler seated on the animal’s back to limit movement and were given samples to bite from this position. Behaviors of note, such as death rolling or violent lateral thrashing, were recorded. Specimens were then labeled with each animal’s SAAF identification number or name for easy correlation to veterinary metadata (e.g. age, sex, length, weight, etc.) kept on site at the facility (Table 3.1). Animals whose bite marks were collected in this manner represented male and female, captive bred and wild caught individuals across a variety of ages (5 - >56 years in age) and sizes (122 - 402 cm in total length). Photographs and video footage were collected during the sampling events.

The second sample (Group 2) consisted of 27 partially butchered cow hind limbs placed in two adult *A. mississippiensis* group enclosures (Figure 3.1). Feeding events were again photographed and videotaped. Most specimens were voluntarily abandoned by the animals within hours of introduction into the enclosures. However, some were kept for longer periods (up to several days) or abandoned in the water of the enclosures where immediate retrieval was problematic. These samples were collected within a week of initial introduction into the enclosure when the water features for one of these enclosures was drained for regularly scheduled cleaning by the SAAF staff. During this
Table 3.1

*A. mississippiensis* specimens from which bite marks were collected.²

<table>
<thead>
<tr>
<th>Accession #</th>
<th>Imaged</th>
<th>Sample</th>
<th>Sex</th>
<th>Age</th>
<th>Total Length</th>
<th>Head Length</th>
<th>Snout-Vent Length</th>
<th>Weight</th>
<th>Origin</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>97062</td>
<td>Y</td>
<td>Pig</td>
<td>M</td>
<td>22Y, 11M, 23D</td>
<td>314 cm</td>
<td>45 cm</td>
<td>161 cm</td>
<td>185.97 kg</td>
<td>C</td>
<td>unrestrained</td>
</tr>
<tr>
<td>99013</td>
<td>N</td>
<td>Cow</td>
<td>M</td>
<td>~31Y</td>
<td>296 cm</td>
<td>41 cm</td>
<td>151 cm</td>
<td>143.6 kg</td>
<td>?</td>
<td>unrestrained</td>
</tr>
<tr>
<td>A05001</td>
<td>N</td>
<td>Cow</td>
<td>M</td>
<td>adult</td>
<td>244 cm</td>
<td>31.5 cm</td>
<td>120 cm</td>
<td>?</td>
<td>?</td>
<td>unrestrained</td>
</tr>
<tr>
<td>A01025</td>
<td>Y</td>
<td>Cow</td>
<td>M</td>
<td>&gt;56</td>
<td>402 cm</td>
<td>57 cm</td>
<td>193 cm</td>
<td>?</td>
<td>W</td>
<td>unrestrained</td>
</tr>
<tr>
<td>A00241</td>
<td>N</td>
<td>Pig</td>
<td>?</td>
<td>5Y, 11M, 5D</td>
<td>122 cm</td>
<td>15.25 cm</td>
<td>62.25 cm</td>
<td>7.8 kg</td>
<td>C</td>
<td>restrained</td>
</tr>
<tr>
<td>99106</td>
<td>Y</td>
<td>Pig</td>
<td>?</td>
<td>6Y, 10M, 9D</td>
<td>185.5 cm</td>
<td>25.5 cm</td>
<td>95.25 cm</td>
<td>25.4 kg</td>
<td>W</td>
<td>restrained</td>
</tr>
<tr>
<td>A00268</td>
<td>Y</td>
<td>Pig</td>
<td>?</td>
<td>5Y, 11M, 5D</td>
<td>146 cm</td>
<td>19 cm</td>
<td>73.5 cm</td>
<td>12.6 kg</td>
<td>C</td>
<td>restrained</td>
</tr>
<tr>
<td>97103</td>
<td>Y</td>
<td>Cow</td>
<td>M</td>
<td>adult</td>
<td>304 cm</td>
<td>41 cm</td>
<td>158 cm</td>
<td>?</td>
<td>?</td>
<td>unrestrained with 97064</td>
</tr>
<tr>
<td>97064</td>
<td>Y</td>
<td>Cow</td>
<td>M</td>
<td>22Y, 11M, 24D</td>
<td>353 cm</td>
<td>45.5 cm</td>
<td>169 cm</td>
<td>?</td>
<td>C</td>
<td>unrestrained</td>
</tr>
<tr>
<td>tt 00852</td>
<td>N</td>
<td>Pig</td>
<td>?</td>
<td>juvenile</td>
<td>160 cm</td>
<td>20.5 cm</td>
<td>105.5 cm</td>
<td>14.8 kg</td>
<td>?</td>
<td>restrained</td>
</tr>
</tbody>
</table>

² Vital statistics were provided by the SAAF. Missing information is indicated with a ‘?’ Collection protocol information was recorded at the time of sampling. Under ‘Imaged,’ Y = yes and N = no. Under ‘Sex,’ M = male and F = female. Under ‘Origin,’ C = captive and W = wild.
time, the enclosures were thoroughly searched in order to avoid specimen loss not related to consumption. The remaining enclosure encompassed a natural section of swamp that could not be drained. Samples uncollected from this enclosure were considered lost and not necessarily consumed. Of the 27 limbs placed in the enclosures, 6 were never retrieved, with 4 being interpreted as wholly consumed and 2 recorded as lost. Animals were observed breaking and swallowing large sections of cow limbs, and many retrieved limbs were missing large fragments or had been disassociated from the other portions of the limb.

Samples from both groups were cleaned and prepared by simmering each limb in water with an enzymatic detergent (Borax®), then by successive rounds of rinsing and hand scrubbing with a milder non-enzymatic detergent (Luminox® and Dawn®), sponges, and soft plastic brushes until no more soft tissue remained and the bones were reasonably free of grease. Though commercial and more publically available enzymatic detergents are highly successful at cleaning bone (e.g. Fenton et. al., 2003; Mairs and Rutty, 2004; Steadman et. al., 2006), concerns arise when samples are destined for long-term curation or chemical analysis. Without being thoroughly rinsed, and in some cases denatured, the active enzymes will continue to digest the bone over the course of decades until nothing but crystal deposits remain (Shelton and Buckley, 1990). Because the specimens collected from isolated individuals in particular were destined for a destructive preparation process for microscopic analyses, this was not a concern within the bounds of this study.

*Bite Mark Identification and Classification*

Bite marks were identified and differentiated from the few butchering traces using
a 10X hand lens and the method described in Blumenschine et al. (1996). Marks were then categorized according to Binford’s (1981) classification scheme, which divides all feeding traces into four broad groupings: pits, punctures, scores, and furrows. Pits are formed when a tooth contacts the surface of a bone, depressing, but never fully piercing, the cortical bone. When the tooth does break through the cortical bone, the bite marks is instead called a puncture. Similarly, when a tooth is dragged along the surface of a bone, leaving a groove that crushes and depresses the cortical bone without fracturing it, the mark is called a score. When the cortical bone is pierced as the tooth moves along the bone surface, the mark is instead called a furrow. Diagnostic bite marks take the form of novel expressions of these general classes or statistically definable patterns of marks described in terms of preferential location, orientation, density, and other variables. While a separate classification scheme for bite marks specifically attributed to crocodylians has been suggested and ichnogenera erected by Mikulás and colleagues in 2006, it is largely redundant with Binford’s (1981) earlier, more widely used nomenclature. Novel structures, including the bisected pits, punctures, and scores, and the hook scores described by Njau and Blumenschine (2006), were recorded.

Other types of bone modifications were observed and recorded as well. Biting events often cause secondary alterations to bone in the form of fracturing patterns related to impact trauma (Byers, 2002). Depressed fractures occur when the bone surrounding a bite mark collapses under the force of the impacting tooth. This can impart an irregular, jagged margin to a bite mark, particularly a puncture or furrow. If the surrounding bone does not collapse under the force of a bite, due to differences in bone structure and bite strength, it may instead fracture in linear patterns radiating from the location of the
impact. These secondary alterations are called fracture lines. If a bite is powerful enough to break a bone completely, these fractures often propagate in a spiral fashion around the circumference of the bone. These are called spiral fractures and often are expressed as diagonal breaks across the shafts of long bones. It is important to note that these types of marks are often associated with bite marks, but can also be caused by other biotic and abiotic bone modifying agents involving impacting forces.

Each bone and its associated bite marks were photographed in detail with an Olympus® Stylus™ brand, model 760 still-image camera. While it has been determined from blind inter-analyst tests that bite marks are able to be differentiated from other types of bone surface modifications using only a 10X hand lens for magnification (Blumenschine et al., 1996), the bisected marks previously identified in the *C. niloticus* actualistic survey are believed to be affected by the relative wear of the carinae of teeth, with a spectrum of tooth morphologies and wear stages being present even within the mouth of a single individual (Njau and Blumenschine, 2006). The marks were thus observed under higher magnification, where more subtle bisections caused by incompletely worn carinae might still be visible. Specimens from the first group, representing bite marks from a single known animal, were sectioned into pieces small enough (>10 cm in maximum length) to fit in the stage of a Hitachi® brand, model S-3400N variable pressure scanning electron microscope (VP-SEM). Because this is a variable pressure SEM, further processing, such as gold plating, was unnecessary. All bite marks and any tool marks created during the butchering process were imaged in the VP-SEM and the scale recorded. Any novel structures that had not been visible under the initial 10X hand lens survey were also recorded at this point.
To ensure that bite marks from only one identified individual was collected on each of these samples, the nature of Group 1’s collection was, of necessity, very limiting. Animals were often physically isolated or restrained. Periods of feeding time were limited. Therefore, information on location, density, and orientation of these marks was not collected.

Since the Group 2 bite marks were collected during more naturalistic feeding behavior and over longer periods of time than those of Group 1, these samples were inspected for presence or absence of marks as well as for preferences of mark location and orientation. Long bones from this sample, representing long-term, group feeding, were measured and marked delineating a proximal one-fourth, a distal one-fourth, and a central one-half representing the midshaft of each bone. On broken long-bones, these delineations had to be estimated using references to landmarks on the bones. Bite marks were identified and re-counted from each section. Then each specimen was oriented adjacent to a Skill® brand, model 8601-RL laser level, so that the laser level projected a laser line along the long dimension of the shaft. Measurements of the angle of individual bite marks found on each specimen in relation to the long dimension of the shaft were taken using the laser line, in partnership with a protractor, wherein the proximal end of the bone represented 0° along the laser line, and the distal end represented 180°. These angles were then entered into PAST 2.16 software (Hammer et al., 2001) to generate rose diagrams for better visualization of observed patterns.

Both legs of identified hook scores were measured in this manner, and the angle of the hook itself recorded. D’Amore and Blumenschine (2009) further refined the original definition of hook scores (sensu Njau and Blumenschine, 2006), dividing the
marks into groups based on the angle formed by two legs of the ‘hook.’ Score curvature was grouped into three categories representing the angle one leg of the hook diverted from the initial direction of movement. Marks were grouped into <45°, 45-90°, and >90°, with only scores bending more than 90°, where the legs of the hook formed an acute angle, being called a true hook score (see D’Amore and Blumenschine, 2009: Figure 3.3). While hook score curvature was collected in a slightly different manner in this study, the angle between the legs of each mark was measured in this study instead of the angle at which each mark bent, categories were selected to make direct comparison between these two datasets possible. (e.g. A hook mark that bends from the original bite trajectory >90° will have an angle between mark legs of <90°.)

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

Results

Bite marks were present on every sample from both collected groups, though individual bones within the articulated cow limbs occasionally lacked feeding traces. Following Binford’s (1981) classification scheme, pits, punctures, scores, and furrows were all identified. Bisected marks and hook scores (sensu Njau and Blumenschine, 2006) were identified in samples from both collected groups. Depressed fractures, fracture lines, and spiral fractures, secondary alterations created during structural failure
of the bone under the pressure of a bite (Byers, 2002), were also found. A few individual bite marks were associated with flakes from the denser long-bone midshafts. Other bone surface modifications and any unusual structures, including cut marks related to butchering and pathologies, were identified and excluded from subsequent consideration. Detailed findings from each sample group are addressed below.

**Group 1 – Individual Feeding**

At least one pit was present on every specimen collected for this group (Appendix B). Pits ranged from circular and ovoid, reflecting the shape of the individual tooth tip, to slightly teardrop-shaped, indicating a subtle drag-out structure from the end of the biting event. The SEM images revealed obvious crushing damage to the cortical bone inside the pits, indicative of the impact damage (Figure 3.2).

Only two punctures were identified on specimens created by animals A01025 and ‘Fluffy.’ Both individuals were large adult males, and A01025 was both the oldest (>56 years) and the largest (total length 402 cm) of the sampled animals (Table 3.1). A01025 was a wild-caught individual while Fluffy’s origin, exact age, and other statistics were not available in the SAAF’s records. Both punctures were associated with secondary alterations, giving them irregular, fractured margins. Each was located on the proximal end of the shaft of cow tibiae (Figure 3.2).

As with pits, scores were present on every sampled specimen. Crushing was again obviously visible inside the bite marks in SEM images. Individual scores ranged from a few millimeters to several centimeters in length. Often one end of the mark would be more rounded, indicating the point of tooth entry, while the other tapered to a point, where the tooth pulled away from the surface of the bone. In extreme cases, this would be
Figure 3.2

Light photography (left) and SEM images (right) of pits (top), puncture (middle), and scores (bottom). Bite marks collected from specimens SAAF 99106, top left; SAAF 2003, top right; SAAF A01025, middle left; SAAF A01025, middle right; SAAF 'Mother,' bottom left; SAAF A01025, bottom right. Photograph scale bars = 1 cm. SEM scale bars = 1 mm.
expressed as a large puncture with a drag-out score exiting the mark (Figure 3.2).

No furrows were identified on specimens from this group.

Seven specimens left bisected pits or scores on samples. Specimen 40264318 created one bisected pit that was only visible under the SEM. Specimen 99106 left two bisected pits and two bisected scores. However, only the pits’ bisections were visible with a 10X hand lens. ‘Fluffy’ left two bisected pits and ‘Mother’ left three bisected scores, all of which were visible under a hand lens. The sample modified by A01025 had three bisected scores, of which only one was visible with a hand lens alone. Specimen 99013 left one bisected pit and tt00852 left another bisected pit and one bisected score. These three marks were only identifiable under higher magnification in the SEM (Figure 3.3). The presence of bisected marks did not seem to be a function of animal age or size, with marks made by the largest, oldest specimen (A01025) and one of the smallest, youngest specimens (tt00852). While the majority of the sampled animals were male, the lone identified female, ‘Mother,’ was one of the seven animals that left bisected marks, implying that sex was also not a factor. Similarly, neither the origin of the animals (captive bred or wild caught), nor the collection protocol (restrained or unrestrained), nor the type of prey item (pig femur or cow limb) could successfully predict presence or absence of bisected marks (Table 3.1).

While most identified scores had some degree of curvature, true hook scores (sensu D’Amore and Blumenschine, 2009) were only present on samples taken from four individuals: A05001, 99013, tt00852, and ‘Mother.’ A05001 and 99013 created one hook score each, while tt00852 left two, and ‘Mother’ created three (Figure 3.3). Like the bisected marks, presence or absence of these marks was not restricted to a single size,
age, sex, origin, or collection protocol. Contra Njau and Blumenschine’s (2006) interpretation that these marks were indicative of death-rolling behavior, none of the animals that created these marks exhibited this behavior during sample collection, which aligns well with D’Amore and Blumenschine’s (2009) findings. However, ‘Mother’ in particular was noted for her violent attack on the cow limb, including powerful, repeated bites and lateral shaking of the sample. Handlers suggested that her behavior may have been less from an interest in feeding, and more in defense of her nest, which was nearby in the enclosure.

While all bite marks exhibit some level of crushing damage, a few marks exhibit further alteration and breakage meeting the criteria of secondary impact damage. Both identified punctures were associated with depressed fractures, giving them irregular, broken margins. A small number of fracture lines are also present radiating from the puncture created by specimen A01025 (Figure 3.2). The tibia from the cow limb presented to A01025 was broken, and roughly the distal half of the bone with all articulated distal elements were ingested immediately following the biting and fracturing event. The break on the recovered portion of the tibia is a spiral fracture. A large pit is present directly on the margin of the break, and the fracture was accomplished with a single, powerful bite to the tibia (Figure 3.3).

**Group 2 – Group Feeding**

Specimens from this group represent bite marks made during prolonged group feeding (Figure 3.4). Twenty-seven articulated cow hind limbs were introduced during the collection of this group. Of these, only 21 femora, 17 tibiae, and 23 other elements
(patellae, astragali, etc.) representing 61 complete or partial bones were retrieved. On these bones, 3,831 individual marks were identified. Traces on long bones, i.e. femora and tibiae, were counted and organized by location on the long-bone: proximal one-fourth, distal one-fourth, and central one-half. The results of this survey are presented in Appendix B.
The density of bite marks on bone elements varied greatly, ranging from 1 (SKD12.3) to 378 (SKD14.1) individual marks identified per bone. Scores are by far the most common type of mark, representing 59.57% of all identified traces. Pits are the second most common, comprising 31.45% of the recorded marks. Punctures constitute 8.48% of the remaining bite marks, whereas furrows are represented by a mere 0.1% of marks.

Of these, 10.37% of all pits, 9.95% of all scores, and 19.08% of all punctures exhibit bisections, representing 10.8% of all observed bite marks. Of the sampled bones, 83.61% exhibited at least one bisected mark. Hook scores constituted 6.18% of all observed scores, and were present on 62.5% of the observed bones.

Punctures and furrows were largely restricted to the proximal and distal ends of long bones. All six furrows were identified on proximal or distal portions of femora. Of the 309 total, identified punctures, 277 marks, comprising 89.64% of the sample, were present on either the proximal or distal ends of the long bones, while a comparatively scant 32 marks, or 10.36% of punctures, were located on the denser long bone shafts. Three punctures were expressed as notches (sensu Capaldo and Blumenschine, 1994) on the margin of spiral fractures. These notches, one on specimen SKD2, and two on specimen SKD22, are associated with further alteration on the interior surface of the marrow cavity of both femora, where the impact of the tooth created enough percussive force to flake away the surrounding bone. Other flakes have been identified in association with pits or scores on the exterior of the dense, midshaft bone (SKD5.2, SKD8.1, SKD21), along broken margins associated with spiral fractures (SKD17), and as the flaked away fragments themselves (SKD20).
Group 2 feeding samples. Top left – SKD 2 femur exhibits serial punctures with secondary impact alterations. Top right – SKD 4 femur exhibits significant loss of bone resulting from a spiral fracture. Middle left – SKD 2 femur exhibits a notch with associated flake on the margin of a spiral fracture. Middle right – SKD 22 femur fragment exhibit significant loss of bone resulting from spiral fractures. Bottom left – SKD 5.2 tibia exhibits a large flake associated with a pit. Bottom right – SKD 3 femur exhibits the high density of bite marks present on some crocodylian modified samples.

Individual bite marks seemed to be preferentially oriented perpendicular to the long axis of the bone, with very few marks falling in shallower, more parallel angles. A Rose diagram was generated with angle measurements taken from 1,688 individual bite marks.
(Figure 3.5). A random orientation of these marks was rejected using a Rao’s U test of uniform distribution (p<0.0001). The diagram indicates a strong peak in orientations roughly perpendicular to the long axis of the bones, with a calculated mean of 90.62618°, a median of 91°, and quartiles terminating at 73° and 109°.

Discussion

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

Observed patterns of Group 2 *Alligator mississippiensis* bite mark type, location, and proportion are largely congruent with the Njau and Blumenschine (2006) *Crocodylus niloticus* study, though interesting differences are present. Identified marks were often (but not always) present in numbers per bone that exceeded that expected in similarly collected mammalian samples (378 individual marks per element in *A. mississippiensis*, 250 in *C. niloticus*). These numbers surpass even captive mammalian-modified bones created during extensive ‘boredom gnawing’ (Haynes, 1982). Types of bone modification associated with gnawing, such as extensive furrowing and concentrated damage at long bone ends (Binford, 1981), were largely absent in both collections. However furrows, which were wholly absent in the Njau and Blumenschine study (2006), were identified in this survey, which indicates that their absence should not be used as a diagnostic characteristic of crocodylian feeding traces. These marks were largely restricted to long bone ends, as were the punctures, and they also often occurred in isolation. This indicates that their presence was most likely a function of prey bone density and not focused attention by the animals in order to access the marrow cavity, which often drives mammalian patterns of punctures and furrow expression. This result is congruent with documented crocodylian feeding behaviors and inertial feeding strategies in general (Cleurens and deVree, 2000).

Bisected marks were identified in similar amounts (10% of all observed bite
marks in *C. niloticus*, 10.8% in *A. mississippiensis*) and were present on a similar percentage of individual marked bones (82.5% in *C. niloticus*, 83.61% in *A. mississippiensis*). Similar expression of these marks in the two samples reflects a broad similarity between tooth morphology and wear pathways in the two species. While rare from the point of view of individual marks, the presence of at least one bisected mark on >80% of marked bones from both samples bolsters Njau and Blumenschine’s (2006) assertion that these marks are potentially quite strong diagnostic indicators of crocodylian feeding in the fossil record.

While Njau and Blumenschine (2006) described patterns of fracturing that seem to correlate well to depressed fractures and fracture lines (sensu Byers, 2002), wholesale bone breakage in the form of extensive spiral fractures was not observed in their *C. niloticus* sample, though incomplete fracturing was noted. Among specimens of *A. mississippiensis*, 5 femora and 9 tibiae were not retrieved and are believed to have been consumed (26.92% of all initially introduced long bones), and 6 further long bones exhibited complete spiral fracturing in which large portions of bone was consumed, representing 15.79% of the total femora and tibiae samples. This is particularly interesting, because crocodylian bite force has been shown to have a strong linear relationship with animal size (Erickson et al., 2003; 2012), and while captive specimens can be problematic to use in bite force studies (Erickson et al., 2004), similarly sized specimens of ecologically similar species (in this case, large generalists) would be expected to be capable of creating similar bite forces. The largest specimens sampled from both *C. niloticus* (Njau and Blumenschine, 2006) and *A. mississippiensis* were roughly 4 meters in length, and yet only the alligators caused extensive spiral fracturing.
It is possible that this difference, as well as the presence of furrows, which also represent bone surface modifications created during particularly powerful bites, may be the result of some type of sampling artifact. Both taxa were presented with cow limbs, but smaller *A. mississippiensis* specimens from Group 1 were given isolated pig femora while some of the *C. niloticus* specimens were instead presented with sections of goat, which may have introduced some room for variation between the samples. Although specifics are not available for comparison, published images indicate that there may have been more remaining soft tissue on the initial samples used by Njau and Blumenschine (2006) than in the current study, which could affect the animals’ ability to access and break bones. However, the presence of numerous punctures in the *C. niloticus* study does not support the interpretation that the animals were hindered from accessing and heavily modifying their bones. Duration of feeding may have also contributed to this difference, but spiral fracturing was observed occurring even in the first few moments after sample introduction to specimens of *A. mississippiensis* (i.e. Group 1 – SAAF A01025), again implying that this factor may not have contributed to the differences.

It seems more likely that the differences in gross bone modification, in the form of bone breakage and wholesale consumption, represent actual differences in feeding strategy. Why this may be the case is less clear. Crocodylian snout shape has often been used as a guiding reference when interpreting feeding ecology, with more slender-snouted forms being interpreted as piscivorous (e.g. Iordansky, 1973; Langston, 1973; Busby, 1995), or at least as small-prey specialists (McHenry et al., 2006), while boxier snouts trended more towards durophagy, and broader, medium-length snouts indicating some kind of compromise between the two, an ecological generalist (e.g. Brochu, 2001).
While these designations were largely qualitatively assigned at first (Busby, 1995; Brochu, 2001), more recent studies have relied on quantitative techniques (Pierce et al., 2008; Sadleir and Makovicky, 2008). Though differences in these studies are present, both *A. mississippiensis* and *C. niloticus* are typically folded into groups interpreted to represent an ecologically generalist lifestyle. It seems likely that as a group, *A. mississippiensis* is simply a more violent feeder than *C. niloticus*, utilizing their ability to crush similar bones to greater effect. Interestingly, the last common ancestor of *Alligator* was a small, durophagous animal whereas *Crocodylus* is descended from seemingly more generalist forms (Brochu, 2001). It may be that this difference in feeding strategy can be traced to relict behaviors reflecting this evolutionary history rather than differences in the current morphology.

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

**Conclusions**

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

Bisected marks now have been identified in members of *A. mississippiensis*. Furthermore, the rate of bisected marks and the percentage of marked bones exhibiting bisections are nearly indistinguishable from those seen in *C. niloticus* (Njau and Blumenschine, 2006). While further studies of other crocodylian species are still needed, the presence and similarity of these bisected marks on both the *Alligator* and *Crocodylus* lineages goes far to support their interpretation as diagnosable traces for other crocodylian taxa as well.

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

Similarities between bite marks identified in extinct and extant crocodylians and non-crocodylian crocodyliforms (Njau and Blumenschine, 2006; Rivera-Sylva et al., 2009; Brochu et al., 2010; Noto et al., 2012) indicate that the currently identified patterns and diagnostic types of bite marks are sufficient for broadly identifying the group as a whole. Species-level identifications can be more problematic, often relying on comparisons of mark types, size, spacing, and distribution to potential ‘contenders’ present at a particular site (e.g. Davidson and Solomon, 1990; Noto et al., 2012). This study indicates significant differences in the level of hook scoring, bone fracturing, and consumption between members of *A. mississippiensis* and the two sampled *Crocodylus* species (Njau and Blumenschine, 2006; Westaway et al., 2011). The potential for more fine scale, species-level identifications will rely on further such surveys of traces made by other extant and extinct taxa.
CHAPTER IV
A PHYLOGENETIC FRAMEWORK FOR TAPHONOMIC PATTERNS IN THE FOSSIL RECORD: AN EXAMPLE USING THE BITE MARKS OF CROCODYLIA

Introduction

Many taphonomic patterns, both in terms of fossil modification and survival, can be correlated to anatomical features, such as skeletal element structure (e.g. Lyman, 1994) and overall shape (e.g. Behrensmeyer et al., 2005). Systematists observe similar morphological features when identifying phylogenetically informative characters (e.g. dePinna, 1991). Despite this apparent source of potential overlap, correlations between phylogenetic and taphonomic patterns have not been widely investigated. Bite marks provide an excellent opportunity for exploring the potential for phylogeny to predict taphonomic patterns. They represent an intersection of ichnology and taphonomy, in which tooth shape and structure, jaw morphology and mechanics, and behavior act in concert to create patterns of element surface modification, accumulation, and destruction. As such, bite marks seem a likely taphonomic candidate to preserve some aspect of a phylogenetic signal.

Unfortunately, sampling of modern bite marks has been extremely uneven across and within clades. For example, due to their common interaction with forensic sites, importance to studies of early domestication, and habit of caching and heavily modifying bones, domestic dogs (Canis familiaris) and wolves (Canis lupus, red wolves, etc.) have an extensive bite mark literature (e.g. Binford, 1981; Haynes, 1982; Haglund, 1997a). Among mammals, hyenas (e.g. Haynes, 1983; Cruz-Uribe, 1991; Marean and Spencer,
1991), great cats (e.g. Brain, 1981; Haynes, 1983 Domínguez-Rodrigo, 1999), bears (e.g. Haynes, 1982; Domínguez-Rodrigo and Piqueras, 2003), and rodents (e.g. Brain, 1981; Haglund, 1997b; Klippel and Synstelien, 2007) have all enjoyed a significant amount of attention in the bite mark literature. On the other end of the spectrum, bite marks from only one squamate, the Komodo dragon (Varanus komodoensis), have been systematically studied (D’Amore and Blumenschine, 2009). While mammalian bite marks have been more extensively studied than non-mammalian ones, no single clade has experienced the broad sampling and directly comparable collections protocols which would make phylogenetic comparison possible.

Here, I present the results of an actualistic survey of bite marks collected from 21 of the 23 generally recognized species of extant Crocodylia. Crocodylian bite marks recently have received an increased amount of systematic attention (Drumheller, 2007; Milan et al., 2010; Westaway et al., 2011), and potentially diagnostic bite mark types were first identified in Crocodylus niloticus (Njau and Blumenschine, 2006). In addition to representing important predators and taphonomic agents in their own rights, crocodylians are popular proxies for extinct clades, including non-avian theropods (Brazaitis and Watanabe, 2011), so a better understanding of their feeding behaviors and traces has broad potential for application to a large number of paleoecological and paleobiological questions.

In order to explore potential phylogenetic patterns in this dataset, presence or absence of novel feeding trace types in this survey were then coded as binary characters and added to a published character-taxon matrix encompassing extinct and extant eusuchians (after Brochu and Storrs, 2012). When possible, these codings were cross-
checked against previous publications of crocodylian bite mark surveys (e.g. Njau and Blumenschine, 2006; Westaway et al., 2011). The efficacy of these projections in predicting similar marks in the fossil record was tested using published examples of fossil crocodylian bite marks including *Crocodylus anthropophagus* (Brochu et al., 2010) and *Deinosuchus riograndensis* (Schwimmer, 2002; Rivera-Sylva et al., 2009; Lehman and Wick, 2010). While heavily reliant on observations of extant groups, fossil bite mark examples from non-crocodylian crocodyliforms (Noto et al., 2012) and extinct morphologies currently represented by unrelated, but convergent, taxa (D’Amore and Blumenschine, 2009) will also be discussed in the context of projecting these taphonomic patterns beyond the crown group.

**Materials and Methods**

*Bite Mark Collection and Preparation*

Partially butchered cow hind limbs and pig femora were obtained from meat packaging plants and transported to the St. Augustine Alligator Farm (SAAF) in St. Augustine, Florida. Cow specimens retained significant amounts of flesh at the joints, and included articulated femora, tibiae, patellae, and varying numbers of tarsal bones depending on how much of the foot was removed during the butchering processes. The pig femora experienced more initial processing and were largely defleshed.

Bite marks were collected from seventy-six individuals from 21 of the 23 extant species. The SAAF staff requested that members of *Gavialis gangeticus* be excluded from the study, due to their recent relocation and concerns about stress affecting their ongoing breeding program. All SAAF specimens of *Crocodylus palustris* were largely edentulous, preventing bite mark collection. At least one animal from all remaining
species was sampled, for a total of 65 individuals.

Bite mark samples were collected from isolated individuals so that veterinary data kept by SAAF staff could be correlated to specific sets of bite marks (Figure 4.1).
Smaller animals were presented with the isolated pig femora while larger animals were given the partially butchered cow hind limbs. Many samples were voluntarily abandoned after a short period of time, but some animals had to be induced by handlers to abandon samples once active biting ceased. Animals were unrestrained while bite mark samples were collected except when the SAAF staff felt that handler and animal safety was a concern. In those cases, animals were held near the base of the skull by a handler and with larger animals, further secured by the handler sitting on the animal’s back.
Behaviors of note, such as death rolling or violent lateral thrashing, were recorded.
Collection protocol and vital statistics, including age, sex, length, etc., were recorded for each animals and are presented in Appendix C. Photographs and video footage were also
collected during the sampling events.

Samples were defleshed and degreased through simmering in water with Borax®, an enzymatic detergent. After rinsing and manual removal of any remaining soft tissue, bones were cleaned again with Luminex® and Dawn®, milder, non-enzymatic detergents. Sponges and soft plastic brushes were used to prevent further bone surface modifications during the cleaning process. Enzymatic detergents have proven to be highly successful at cleaning bone when long-term curation is not an end goal (e.g. Fenton et. al., 2003; Mairs and Rutty, 2004; Steadman et. al., 2006). Since these samples were destined for further, destructive preparation, efforts to prevent continued, long-term digestion of the bone by the active enzymes were not made (Shelton and Buckley, 1990).

**Bite Mark Identification and Classification**

Bite marks and butchering traces were identified using the criteria described by Blumenschine and colleagues (1996), using a 10X hand lens. While Mikulás and colleagues (2006) erected ichnogenera specifically representing crocodylian bite marks, the classification scheme defined by Binford (1981) was published earlier and has been more widely used by both paleontologists and anthropologists (D’Amore and Blumenschine, 2009). In Binford’s (1981) classification scheme, all marks are separated into four broad groupings: pits, punctures, scores, and furrows. Pits represent depressions on the surface of a bone, caused when a tooth tip contacts, but does not pierce, cortical bone. When piercing does occur, the mark is instead classified as a puncture. When the tip of the tooth drags along the surface of the bone, leaving a crushed groove which does not fully pierce the cortical bone, the mark is called a score. When a similar bite does manage to pierce the cortical bone, the mark is instead classified as a furrow.
These broad categories of bite marks can be further divided by any novel mark morphology or pattern of expression. In the case of crocodylians, Njau and Blumenschine (2006) identified two new types of bite marks in their diagnosis of *Crocodylus niloticus* feeding traces: bisected marks and hook scores. Bisected marks were pits, punctures, and scores which exhibited subsoring and/or notching on bite margins which were formed by the prominent carinae present on relatively unworn, recently erupted crocodylian teeth. Hook scores were defined as J- or L-shaped marks, created when the trajectory of a particular tooth abruptly changed directions during a biting event. Hook scores were later identified among modern Komodo dragons (*Varanus komodoensis*) and non-avian theropods (D’Amore and Blumenschine, 2009), which discounted them as diagnostic traces of crocodylians alone. Bisected marks, however, remain unique to crocodylians and non-crocodylian crocodyliforms, and have since been found in other living (Drumheller, 2007) and extinct forms (Rivera-Sylva et al., 2009; Brochu et al., 2010; Drumheller and Boyd, 2011; Noto et al., 2012).

Biting events cause impact-type trauma to bone, and often leave secondary alterations related to these forces (Byers, 2002). These include depressed fractures, which occur when the margins of a bite mark collapses irregularly under the force of the impacting tooth. Bone may also fracture in linear patterns which radiate away from the location of the impact, a secondary alteration called fracture lines. Spiral or green stick fractures occur when a bite is powerful enough to completely break the bone, and as the name suggest, these fractures typically propagate in a spiral or transverse fashion around the circumference of particularly long bones. It should be noted that these types of alterations are associated with any kind of impact trauma, and not just biting events.
Bite marks were photographed in detail with an Olympus® Stylus™ brand, model 760 still-image camera. While blind inter-analyst tests have shown that bite marks can be differentiated from other types of bone surface modifications using only a 10X hand lens for magnification (Blumenschine et al., 1996), the presence or absence of bisected marks have been related to the relative wear and chipping of the carinae of teeth, with numerous tooth morphologies and levels of wear being present even within the mouth of a single individual (Njau and Blumenschine, 2006). It was determined that observing these marks under higher magnification might reveal more subtle bisections caused by incompletely worn carinae. After light photography, specimens were sectioned into pieces small enough (>10 cm in maximum length) to fit in the stage of a Hitachi® brand, model S-3400N partial pressure, scanning electron microscope (VP-SEM). All identified bone surface modifications were recorded and imaged with the scale in the VP-SEM.

Statistical Analyses of Vital Variables and Collection Protocols

A variety of vital statistics were collected from each animal whose bite marks were sampled. These included sex, mass, age, total length, snout-vent length, cranial length, and whether each animal was born in captivity or in the wild. Variation in collection protocol, i.e. whether an animal was restrained during sampling or not and if a bite mark sample was collected on a cow limb or pig femora, was recorded for each animal as well (Appendix C). Correlation between the presence or absence of specific bite mark types with each of these variables was tested using either a one-way ANOVA for continuous or measured variables (such as total length) or a Chi squared test of independence for binary, categorical variables (such as sex). These tests were performed using PAST statistical software (Hammer and Harper, 2006) and were meant to
determine if variables other than phylogeny might be affecting the observed pattern of bite marks.

*Phylogenetic Analysis and Character Mapping*

Debate remains as to the usefulness of behavioral characters in phylogenetic analyses, based largely around concerns that behavioral traits are inherently more labile than morphological or molecular ones (de Quieroz and Wimberger, 1993; Blomberg et al., 2003). However, studies have determined that behavioral characters exhibit rates of homoplasy in analyses that are not statistically different from those generated from morphological datasets (de Quieroz and Wimberger, 1993). Also, metrics that measure the phylogenetic signal in a dataset have found worthwhile data within even demonstrably labile behavioral datasets (Blomberg et al., 2003). As bite mark morphology is caused by a combination of morphological and behavioral traits of the acting animal, it is possible that a phylogenetic signal is present in observed patterns of feeding traces.

In order to explore this avenue for synthesizing bite mark datasets, single (bisections) and multiple (trisections or quadrisections) subscores within individual bite marks from the sampled, extant taxa were coded as binary characters (i.e. presence/absence). These two, new characters were then added to a preexisting eusuchian character taxon matrix (Brochu and Storrs, 2012) comprising 121 ingroup taxa and 181 unordered characters. *Bernissartia fagesii* was designated as the outgroup taxon.

Maximum parsimony analyses were performed in TNT 1.1 (Goloboff et al., 2008) utilizing heuristic searches (specifically tree bisection resection) based on 1000 random addition sequence replicates. Separate searches were performed both including and excluding the new bite mark characters. Both analyses generated 750 most parsimonious
trees with identical strict consensus trees.

Character state changes for the bite mark characters, as well as other characters of interest from the original matrix, were mapped onto the strict consensus tree in Mesquite 2.75 (Maddison and Maddison, 2011) using the parsimony mapping parameter. Patterns of unambiguous bite mark character state changes are interpreted to be phylogenetic predictions of presence or absence in the fossil record. Areas of the tree where character states were determined to be ambiguous by the parsimony analysis are considered to predict an equal possibility of mark presence or absence in the fossil record. The accuracy of these predictions was then tested by comparing the character states predicted for the extant taxa by the parsimony analysis to published examples of crocodylian bite marks ascribed to extinct species, particularly *Crocodylus anthropophagus* (Brochu et al., 2010) and *Deinosuchus riograndsensis* (Schwimmer, 2002; Rivera-Sylva et al., 2009).

**Results**

*Bite Mark Identification and Classification*

Presence or absence of particular bite mark types within each sampled taxon is reported in Table 4.1. Scores are present in every sampled taxon, and pits are identified in all but two, *Paleosuchus palpebrosus* and *Paleosuchus trigonatus*. Punctures were less ubiquitous, and were most often created by the physically largest animals sampled (*Alligator mississippiensis, Crocodylus acutus, Crocodylus porosus, Tomistoma schlegelii*). One particularly aggressive, male *A. sinensis* (SAAF 86052) deviated from this generalization though, and created definite punctures on the pig femur presented to him. Punctures were not found in specimens collected from *Crocodylus niloticus* in this survey, but a previous study reported punctures created by members of the species (Njau
Table 4.1

Types of bite marks and modifications caused crocodylians, organized by species.  

<table>
<thead>
<tr>
<th>Species</th>
<th>Pits</th>
<th>Punctures</th>
<th>Scores</th>
<th>Furrows</th>
<th>Bisectons</th>
<th>Trisections</th>
<th>Quadrisections</th>
<th>Fractures</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alligator mississippiensis</em> - American Alligator</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Alligator sinensis</em> - Chinese Alligator</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Caiman crocodilus</em> - Spectacled Caiman</td>
<td>X</td>
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<tr>
<td><em>Caiman latirostris</em> - Broad-snouted Caiman</td>
<td>X</td>
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<tr>
<td><em>Caiman yacare</em> - Yacare Caiman</td>
<td>X</td>
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<tr>
<td><em>Crocodylus acutus</em> - American Crocodile</td>
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<tr>
<td><em>Crocodylus intermedius</em> - Orinoco Crocodile</td>
<td>X</td>
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<tr>
<td><em>Crocodylus johnstoni</em> - Johnston’s/Freshwater Crocodile</td>
<td>X</td>
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<td><em>Crocodylus mindorensis</em> - Philippine Crocodile</td>
<td>X</td>
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<tr>
<td><em>Crocodylus moreletii</em> - Morelet’s Crocodile</td>
<td>X</td>
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<tr>
<td><em>Crocodylus niloticus</em> - Nile Crocodile</td>
<td>X</td>
<td>1</td>
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<tr>
<td><em>Crocodylus novaeguineae</em> - New Guinea Crocodile</td>
<td>X</td>
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<td>X</td>
<td>X</td>
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<tr>
<td><em>Crocodylus porosus</em> - Estuarine/Saltwater Crocodile</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Crocodylus rhombifer</em> - Cuban Crocodile</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Crocodylus siamensis</em> - Siamese Crocodile</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Mecistrops cataphractus</em> - Slender-snouted Crocodile</td>
<td>X</td>
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<tr>
<td><em>Melanosuchus niger</em> - Black Caiman</td>
<td>X</td>
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<tr>
<td><em>Osteolaemus tetraspis</em> - African Dwarf Crocodile</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Paleosuchus palpebrosus</em> - Dwarf Caiman</td>
<td>X</td>
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<tr>
<td><em>Paleosuchus trigonatus</em> - Smooth-fronted Caiman</td>
<td>X</td>
<td>X</td>
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<tr>
<td><em>Tomistoma schlegelii</em> - False Gharial</td>
<td>X</td>
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</table>


and Blumenschine, 2006). Contra Njau and Blumenschine’s (2006) findings, furrows were identified, if only in two taxa: *Alligator mississippiensis* and *Crocodylus novaeguineae*. As with the punctures, this type of mark was caused by particularly large, aggressive animals. Both punctures and furrows were most often present at the proximal
or distal ends of long bone elements, where the bone itself is structurally less dense (Figure 4.2).

Bisected marks were identified in all but seven taxa: *Caiman latirostris*, *Mecistops cataphractus*, *Crocodylus intermedius*, *Crocodylus porosus*, *Crocodylus siamensis*, *Osteolaemus tetraspis*, and *Paleosuchus palpebrosus* (Figure 4.3). However, a previous survey of bite marks made by members of *Crocodylus porosus* tentatively
Figure 4.3

VP-SEM images of bisected and quadrisected marks. Upper left – Bisected score made by SAAF A01025 *A. mississippiensis*. Upper right – Bisected score made by SAAF 89038 *Caiman yacare*. Middle left – Bisected score made by SAAF A04004 *Crocodylus johnstoni*. Middle right – Bisected pit made by SAAF A05006 *Crocodylus novaeguineae*. Lower left – Quadrisected score made by SAAF 88130 *Alligator sinensis*. Lower right – Quadrisected score made by SAAF A04004 *C. johnstoni*. 
Figure 4.4


reported at least one bisected mark (Westaway et al., 2011). A larger scale study of *Crocodylus niloticus* found that bisected marks occur in 10% of marks occurring on 82.5% of all marked bones (Njau and Blumenschine, 2006), and similar percents have since been found among members of *Alligator mississippiensis* as well (Drumheller, unpublished data). It is therefore possible that the specimens collected during both studies
simply reflect examples of the few modified bones expected to still lack bisected marks. However, without a broader survey of the clade to help clarify this issue, the presence or absence of bisectsions in *Crocodylus porosus* is considered to be ambiguous for the purposes of this study.

Multiple subscores were present in a smaller number of taxa, and were only identifiable under magnification in the VP-SEM. Two subscores, forming a trisection, were identified in *Caiman yacare* and *Tomistoma schlegelii*. Three subscores, forming a quadrisection, were found in *Alligator sinensis*, *Crocodylus johnstoni*, *Crocodylus novaeguineae*, and *Osteolaemus tetraspis* (Figure 4.3).

Crushing caused by the impact damage during a biting event was visible under a hand lens, but became even more obvious under the VP-SEM. Further secondary alterations – depressed fractures, fracture lines, and spiral fractures (sensu Byers, 2002) – were often found with marks requiring the most amount of force to create, particularly punctures present on long bone shafts. Depressed fractures occur when the bone surrounding the point of tooth contact collapses under the force of the bite, creating an irregular margin. While these fractures propagate roughly concentrically around the bite mark proper, fracture lines instead radiate outward from the central point of the bite. Spiral fractures were only present in samples taken from *Alligator mississippiensis* (Figure 4.4), but bone breakage, often related to limb loss, has been reported in forensic case studies involving *Alligator mississippiensis*, *Crocodylus acutus*, *Crocodylus niloticus*, and *Crocodylus porosus* (Harding and Wolf, 2006; Sartain and Steele, 2009; Mendieta and Duarte, 2009; Cupal-Magaña et al., 2010). While not found in this survey, spiral fractures has previously been reported in samples taken from a survey of
*Crocodile niloticus* (Njau and Blumenschine, 2006) and in forensic case studies involving *Crocodylus acutus* (Cupal-Magaña et al., 2010). These breaks occur during particularly powerful bites, and propagate diagonally across the long axis of bones (Byers, 2002). All fractures found in this study had pits or punctures associated with the margins of the break.

One unusual mark was found on a sample taken from *C. novaeguineae*: an irregular series of closely spaced scores. The marks were shallower, and more V-shaped in cros section than normal bite marks. Since the animal from which this sample was collected broke a tooth during bite mark collection, this mark may be reflecting the jagged edges of a recently snapped tooth crown (Figure 4.4 D).

**Statistical Analyses of Vital Statistics and Collection Protocols**

The variables related to collection protocol, whether samples were collected on pig femora or cow hind limbs and whether an animal was physically restrained during sample collection or not, were both subjected to a Chi squared test of independence from the presence or absence of subscores in the bite mark samples, with resulting p values of 0.84022 and 0.94817 respectively. Vital statistics given the same statistical treatment yielded equally insignificant results, with sex yielding a p value of 0.93597 and whether the animals was wild caught or captive bred yielding a p value of 0.77902. Measured, continuous variables were compared using a one-way ANOVA. The p values for age, total length, snout-vent length, skull length, and mass are as follows: 0.7178, 0.8905, 0.8848, 0.9437, and 0.7914. Again, none were statistically significant.

In short, none of the variables tested were found to correlate significantly with the
Figure 4.5

Phylogenetic tree showing character states for bite mark characters across Eusuchia. Black lineages indicate subscores are predicted to be present. Red lineages indicate subscores are predicted to be present. Blue lineages indicate the presence or absence of subscores is ambiguous. The left tree addresses single subscores (i.e. bisections). The right tree addresses multiple subscores (trisections and quadrisections).
presence or absence of subscores. Therefore none are interpreted as successful tools for predicting distributions of these types of bite marks in the fossil record.

**Phylogenetic Analysis and Character Mapping**

Bisected marks are predicted to occur throughout the majority of the eusuchian tree. Within Crocodyloidea, the presence or absence of bisected marks was found to be ambiguous in the following taxa: *Crocodylus megarhinus, Australosuchus clarkae, Kambara implexidens, Trilophosuchus rackhami, Quinkana spp, Baru spp, Rimasuchus lloydi, Euthedon arambourgii, Crocodylus pigotti, Voay robustus, and Osteolaemus osborni*. All remaining fossil taxa are unambiguously predicted to have been capable of creating bisected marks (Figure 4.5).

Predictions pertaining to the presence or absence of multiple subscores were less definitive. With the exception of *Eocaiman cavernensis*, whose character state was found to be ambiguous, and *Caiman yacare*, which exhibited multiple subscores in the modern sample, the remaining members of Caimaninae were unambiguously predicted to not create this type of mark. Excluding *Crocodylus johnsoni* and *Crocodylus novaeguineae*, the clade formed by members of the crown *Crocodylus* plus *Mecistops cataphractus* were also predicted to lack the ability to form multiple subscores. All remaining fossil taxa were found to be ambiguous with regards to this character state (Figure 4.5).

Other character states which were mapped in order to explore potential bite mark types included features related to feeding strategies no longer exhibited by extant crocodylians. For example, all members of Pristichampsinae were shown to have laterally compressed teeth (Brochu and Storrs, 2012: Character 79), with *Pristichampsus* itself also exhibiting serrated dentition (Brochu and Storrs, 2012: Character 80), and therefore,
Figure 4.6

Phylogenetic tree showing character states for bite mark characters across Eusuchia. Blue lineages indicate taxa whose alveolar width increases posteriorly in the toothrow. Red lineages indicate taxa whose teeth are laterally compressed, but not serrated. Green lineages indicate taxa whose teeth are both laterally compressed and serrated.
true ziphodonty (Figure 4.6). The members of this clade would therefore be expected to create marks more similar to those made by other ziphodont groups, such as varanids and theropod dinosaurs (D’Amore and Blumenschine, 2009).

Members of Hylaeochampsidae, excluding Alloposuchus precedens, exhibit teeth which increase in diameter posteriorly in the toothrow (Brochu and Storrs, 2012: Character 51), including some species which have the extreme expansion of their penultimate teeth into the ‘anvil’ shape often associated with durophagy (Figure 4.6). While modern, generalist crocodylians do sometimes exhibit durophagous behavior (Milan et al., 2010), none exhibit the dentition of a true, durophagy specialist. As such, beyond the predicted increase in secondary (i.e. crushing) damage to prey items, once again modern crocodylians possibly do not provide the best analogues for predicting the morphology of bite marks made by members of this clade.

**Discussion**

Fossil examples of crocodylian and non-crocodylian crocodyliform bite marks long have been reported in the literature, and more recent publications often discuss the presence or absence of the bisected marks first identified by Njau and Blumenschine (2006). With the patterns of bite mark types reported above in hand, using published fossil case studies to test these phylogenetic predictions becomes possible. The success or failure of this method is discussed on a group by group basis below, with an emphasis on bisected marks.

*Crocodylus anthropophagus*

Njau and Blumenschine’s initial study of crocodylian bite marks was specifically performed in order to address unusual patterns of bite marks present on fossils collected
from the famous hominid site, Olduvai Gorge (2006). The possibility that crocodylians had been active taphonomic agents in the Olduvai environment, even predating on the early hominids living there, had been discussed previously (Davidson and Solomon, 1990), but large-scale actualistic studies had not been performed to verify this interpretation. Njau and Blumenschine’s (2006) survey of *Crocodylus niloticus* feeding traces, including the new bisected marks and hook scores, was fully consistent with the fossil marks present at Olduvai.

At the time of publication, the only crocodylian known from the site was identified as *Crocodylus lloidi*. However, a reanalysis of the Olduvai material lead to the identification of a new species of large, horned crocodylian which was subsequently named *Crocodylus anthropophagus* (Brochu et al., 2010). The crocodylian bite marks identified from the site were consistent with the new species’ size and ecology, and with no other taxa seemingly present at the site, a correlation between marks and specific taxon was made.

As seen in Figure 4.5, *C. anthropophagus* is unambiguously (and accurately) predicted to have been capable of producing bisected marks.

*Deinosuchus riogrindensis*

Schwimmer (2002) identified bite marks on dinosaurian bones, and attributed them to *Deinosuchus riogrindensis* based largely on the ovoid cross-sectional shape and the large size of the traces. At the time, no mention of bisected marks or other traces of a prominent carina was made. It is unclear if this report represents a true absence of bisections, since the study pre-dates the published description of the potentially diagnostic marks (Njau and Blumenschine, 2006), and the provided images do not
provide conclusive evidence one way or the other. At the time, the accuracy of this association in the absence of a more in-depth discussion of the identification process was questioned (Brochu, 2003).

Even after the publication of potentially diagnostic crocodylian bite marks, in the form of those bisections (Njau and Blumenschine, 2006), the record of Deinosuchus feeding traces has not been entirely clear. Large bisected marks were identified on hadrosaurid bones from the Upper Cretaceous of Coahuila, Mexico, which led researchers to point to D. riogranderensis as the potential trace maker (Rivera-Sylva et al., 2009). However, large, round puncture marks on a turtle shell were also ascribed to this species a scant year later, with no mention of bisected structures (Lehman and Wick, 2010). This seems to be a genuine absence of these marks and not an oversight by the authors (Drumheller, pers. obsv).

Why this seeming discrepancy between samples? Even in the large surveys of modern taxa, bisected marks were not found on every single bone. In C. niloticus, the rate of bisections stood at roughly 10% of all marks occurring on 82.5% of all marked bones (Njau and Blumenschine, 2006). Similar rates have been identified in Alligator mississippiensis (Drumheller, unpublished data). It is therefore possible that the current state of the Deinosuchus bite mark literature is essentially suffering from its relatively small sample size, when a larger survey would yield similar rates of mark bisection.

However, it is equally likely that Deinosuchus truly did generate a smaller percentage of bisected marks, which could help differentiate the species from other taxa based on a feature other than mark size. The potential for different rates of bisections to occur in modern crocodylian bite marks has been tentatively explored using samples taken from
Crocodylus porosus (Westaway et al., 2011). The only way to determine which (if either) of these proposed explanations is supported is with the identification and publication of more marks ascribed to D. riograndensis.

For the sake of this study though, the phylogenetic predictions only address presence or absence of bisected marks, not rate. Since one study does identify and provide images of bisected marks associatable with this taxon (Rivera-Sylva et al., 2009), for the purposes of this study, bisections are therefore determined to be ‘present’ in the clade. As such, the marks were again accurately predicted to be present in this taxon (Figure 4.5).

Undescribed Pholidosaur

A fossil rich locality in Texas representing a Cretaceous delta system yielded a new species of crocodyliform and a number of bite marked turtle shells and dinosaurian bones. While the formal description and phylogenetic analysis of the pholidosaur is still pending, an interpretation of the bite marks themselves has been published (Noto et al., 2012). The marks exhibited bisections similar to those identified in modern crocodylians. Mark size and spacing matched the size, shape, and arrangement of teeth in the crocodyliform’s jaw (Figure 4.7 C)

Preliminary analyses have identified the trace maker as a type of pholidosaur (Allen et al., 2011), but without the full published description, inclusion of this taxon in the current phylogenetic analysis is impossible. However, when the data becomes available, the presence of associatable bisected marks from this taxon will project these diagnostic traces far beyond the bounds of the crown group.

Pristichampsus and Other Ziphodont Crocodyliforms
Figure 4.7

Fossil examples of crocodyliform bite marks. A – Utah Museum of Natural History (UMNH) VP 21104 femur with embedded crocodyliform tooth (see Drumheller and Boyd, 2011). B – UMNH VP 21104 scapula with bisected pit (see Drumheller and Boyd, 2011). C – University of Texas Arlington Archosaur Site (UT AAS) T005 turtle shell fragment with undescribed pholidosaur bite marks (see Noto et al., 2012). Photographs used with permission.

Of the taxa included in the phylogenetic analyses, only three exhibit truly ziphodont teeth: *Quinkana* sp., *Pristichampsus vorax*, and *Pristichampsus geiseltalensis*. 
Planocrania hengdongensis and Planocrania datagensis both have laterally compressed, recurved teeth, but no serrations. No modern crocodylian taxa exhibit ziphodonty, which calls the applicability of their bite mark patterns as acceptable analogues into question. Luckily, other taxa do preserve this morphological condition and their feeding traces have been documented in order to explore how this particular type of dentition is reflected in the bite mark record (D’Amore and Blumenschine, 2009). Based on work with Varanus komodoensis, it has been shown that ziphodont teeth leave striations which correlate with their serrations.

Similar marks have been identified in the fossil record. While many have been associated with theropod dinosaurs (D’Amore and Blumenschine, 2009), some seem to be attributable to crocodyliforms. Striated marks were described on a perissodactyl from Middle Eocene localities in Wyoming (Alexander and Burger, 2001). The marked bones were identified within the gut cavity of a specimen of Pristichampsus vorax, and were interpreted as true gut contents. Additionally, some of the bones exhibited striations which were consistent in size and spacing to the denticles found in P. vorax teeth.

Ziphodonty is present in more basal crocodyliform groups as well, and associated bite marks exhibit similar patterns of morphology. Striated marks found on Baurusuchus salgadoensis and Baurusuchus pachecoi, both sebecosuchians from the Cretaceous of Brazil, have been cited as evidence of intraspecific fighting within Baurusuchidae (Avilla et al., 2004; De Vasconcellos and Carvalho, 2010). Striation size and spacing in bite marks found on plesiosaur bones from the Jurassic of England led to their association with the marine crocodyliform Metriorhynchus (Forrest, 2003).

Modern crocodylian bite marks are obviously an inappropriate proxy for marks
made by ziphodont crocodyliforms. Therefore, the reported phylogenetic predictions made based solely on modern taxa are equally inapplicable. However, since the connection between ziphodont teeth and striated bite marks has been established using both actualistic and paleontologic data, characters expressing these conditions may be tapped instead. Phylogenetic predictions of presence or absence of striated bite marks, based on characters related to ziphodonty, are therefore reported in Figure 4.6.

**Durophagous Crocodyliforms**

Modern crocodylians which have a more generalist feeding strategy sometimes exhibit feeding choices and behaviors associated with durophagy. Reports of crocodyliforms regularly feeding on turtles and crabs are quite common, touching on a number of different extant (e.g. Valentine et al., 1972; Thorbjarnarson, 1993) and extinct taxa (Fuentes, 2003; Mead et al., 2006; Steadman et al., 2007). However, no modern species retain the dental adaptations associated with extreme, possibly obligate, durophagy in the fossil record. Additionally, the only study dealing with actualistic traces of durophagous behavior in modern *Paleosuchus palpebrosus* focused on patterns of turtle shell breakage than individual bite marks (Milàn et al., 2010).

One specific ‘nutcracking’ behavior described in *P. palpebrosus* occurs when the turtle is maneuvered onto its side in the crocodylian’s jaws in order to facilitate a crushing bite which breaks apart the carapace and plastron. This feeding strategy has been identified in the fossil record, but it is not diagnostic of any one group (Figure 4.7 C). Positive identification of the actor, a new species of generalist pholidosaur, was instead based on mark size and spacing partnered with the presence of bisected marks (Noto et al., 2012).
A separate feeding behavior, in which some specimens of *P. palpebrosus* attacked the edges of a turtle shell, targeting the slightly more exposed limbs, head, and tail (Milàn et al., 2010), has also been identified in the fossil record, but again, mark association fell to other lines of evidence. Instead, the study attempted to associate the observed bite marks and fracturing to the posterior of the turtle shell by briefly discussing the dental morphology of the crocodylians known from the Eocene of Spain and then ascribing the bite marks to *Asiatosuchus* based on that morphology as well as the association of the remains in the fossil bedding plane (Fuentes, 2003). Though paleobiologically interesting, neither of these behaviors have been sampled widely enough to determine if specific crocodylian clades or morphologies are more prone to exhibit them.

Of the taxa included in the phylogenetic analysis, some members of Hylaeochampsidae exhibit the expanded, anvil-like posterior teeth of truly durophagous crocodyliforms. With no extant crocodylians which exhibit this morphology to sample and no actualistic research on more distantly related, durophagous taxa, such as some chondrichthysans, it is difficult to predict how this feeding ecology might be expressed in the fossil record. However, from a strictly structural and functional point of view, it seems highly likely that any bite marks generated would differ from the patterns made by less specialized groups. As such, these taxa are also considered to be potential exceptions to the phylogenetic predictions made in this analysis (Figure 4.6).

*Other Crocodyliform Studies*

Not all bite marks can be directly associated with a particular species. For example, bisected marks, and even an embedded crocodyliform tooth, were identified in dinosaurian bones from the Kaiparowits Formation of Utah (Drumheller and Boyd,
However, the diversity of crocodyliforms present in this Formation is particularly high (Irmis et al., 2011), and in the absence of serial bite marks, only adults from the physically largest of taxa present could be excluded (Figure 4.7 A and B). Future finds in the area might clarify which species might have been responsible for which bite marks, but without a more definitive association, the results of this study cannot be used in a phylogenetic analysis.

Even when species-level association can be made, many methods of bite mark identification do not lend themselves well to inclusion in a phylogenetic analysis. Mark size and spacing are both potentially useful features for narrowing down potential actors. Mark location on prey bone and geographic association of presumed predator and prey are more problematic methods of identifying trace makers, but are nevertheless often used. However, detailed physical descriptions of the marks themselves are required to identify the diagnostic traits which can be treated as codable characters.

In younger fossil and subfossil assemblages, researchers are often more comfortable associating bite marks with modern taxa known from the site. Bite marks identified on turtle shells in Holocene deposits from the Bahamas were associated with specimens of *Crocodylus rhombifer* found in the same locality (Steadman et al., 2007). Further descriptions of the marks themselves of the methodology used to identify them were not provided, but it seems likely that the association was based on the rough shape of the partially healed marks, which were indicative that the predator had multiple conical teeth.

In slightly older fossil specimens, the general consensus seems to be that more justification is required to associate bite marks with actors. Pleistocene bite marks on a
proboscidean rib from El Salvador were identified as crocodylian based on the conical nature of the predator’s teeth. Interdental spacing was compared in the taxa known to occur in the region, which lead to the exclusion of a number of other taxa in favor of *Crocodylus acutus*, whose fossils had been found in the same assemblage (Cisneros, 2005). Plio-Pleistocene horse and turtle fossils from Costa Rica also bore sets of round punctures, indicating that the trace maker had relatively isodont, conical teeth. However, since the crocodylian material from the site could not be identified beyond the genus level, *Crocodylus*, no attempt to interpret the marks further was made (Mead et al., 2006).

In progressively older deposits, more justification is often given when bite marks are associated with a specific trace maker. However, again, some of the methods used do not mesh well with use in phylogenetic techniques. For example, modern crocodylians are known to participate in violent intraspecific fighting related to access to mates, territory, and other resources. Injuries related to head- and tail-biting behavior are fairly common (e.g. Webb and Manolis, 1983). As such, when bite marks are found in these anatomical locations on fossil crocodylians and their more basal relatives, they are often ascribed to conspecifics. This treatment has been applied to marks identified on the following taxa: *Baurusuchus pacheco* (Avilla et al., 2004), *Baurusuchus salgadoensis* (De Vasconcellos and Carvalho, 2010), *?Brachychamps saaletyi* (Williamson, 1996), *Tilemsisuchus lavocati* (Buffetaut, 1983), and *Toyotamaphimeia machikanensis* (Katsura, 2004).

Based on these studies, this type of intraspecific fighting behavior has been interpreted to be quite ancient. When bolstered with more in-depth descriptions of bite mark features, such as the presence of diagnostic striations (De Vasconcellos and
Carvalho, 2010), tooth spacing within sets of serial marks (Buffetaut, 1983), or physical comparisons to other potential predator’s dentition (Avilla et al., 2004), these argument can be quite convincing. However, when bite marks are interpreted as evidence of intraspecific fighting based solely on the basis of trace location (e.g. Williamson, 1996), more questions often remain. Also, while bite mark location can be useful when identifying specific behaviors such as inertial feeding strategies (Njau and Blumenschine, 2006) or intraspecific fighting, the utility of this characteristic in a phylogenetic framework is tenuous without more study.

*Multiple Subscores*

While this study presents prediction on which sampled taxa should and should not produce bite marks with multiple subscores within a phylogenetic context (Figure 4.6), at the present time, there are no fossil studies with which to test these predictions. Multiple subscores, in the form of trisections and quadrisections, were only visible under high magnification with the use of a VP-SEM. In the existing literature, bite marks are rarely subjected to this level of scrutiny.

The apparent reason for this seeming discrepancy is a general consensus that higher magnification is unnecessary. A blind interanalyst test of correspondence in bone surface modification identification found that a high level of accuracy could be expected with only the use of a 10X hand lens (Blumenschine et al., 1996). Some subsequent bite mark studies have specifically attempted to replicate this studies techniques, from lighting to hand lens magnification (Njau and Blumenschine, 2006; D’Amore and Blumenschine, 2009). However, the goal of the initial study was to differentiate between, for example, bite marks and cut marks, not between bite marks from different sources.
When bite marks are observed using a VP-SEM, interesting results seem to follow. The first example of a crocodylian tooth embedded directly in a bite mark was identified under high magnification (Franzen and Frey, 1993). The current study identified potentially diagnostic bite marks, in the form of trisections and quadrisections, which were only visible in the VP-SEM. Future studies attempting to differentiate bite mark actors at fine taxonomic scales should consider high magnification investigation as a potential source of useful data.

In the meantime, large scale patterns of multiple subscores in crocodylian bite marks remain unclear. The marks may reflect a complexity to crocodylian tooth structure and carina shape which has not been described previously. Then again, they may represent pathological anomalies which do not carry a phylogenetic signal at all. Other archosaurs are known to have teeth which occasionally exhibit split carinae (Erickson, 1995), though not in a manner which would create the marks observed in this study. This aspect of crocodylian bite mark morphology requires further study.

Conclusions

Observing the anatomy, behavior, and ensuing bite marks created by a single taxon and then projecting those observations onto a large and historically diverse clade is potentially problematic. Among related, extant animals with similar tooth morphologies, it has been shown that differences in dietary niche and feeding strategy can still be reflected in bite mark morphology (e.g. Klippel and Synstelien, 2007). Ideally, samples should be taken from multiple different taxa in order to help determine what patterns are, and are not, actually shared across groups. However, the best way to synthesize multiple sources of such data has not been the subject of significant study.
In this instance, patterns of subscore presence or absence in crocodylians did not statistically correlate with any recorded variable related to collection protocol, animal size, age, sex, or origin. Placing the feeding traces into a phylogenetic context did indicate that bisected marks should be present across the entirety of crown Crocodylia, and did successfully predict the presence of these marks in a sampling of published fossil case studies (Njau and Blumenschine, 2006; Rivera-Sylva et al., 2009). Bisected marks are also predicted to occur among more basal groups as well, due to fossil discoveries linking bisected marks to crocodyliforms (Noto et al., 2012). Patterns pertaining to multiple subscores were less definitive, and the need for further research remains.

Treating bite marks types as phylogenetic characters does have limitations – diagnostic bite mark types are not always present on every modified bone in an assemblage, and as actualistic data can only be collected from extant forms, it cannot sample now-extinct behaviors and morphologies. However, even in the absence of actualistic data collected in a phylogenetic framework, phylogeny can still direct when and where more distantly related proxies would be most appropriate to apply. Among crocodyliforms, this is best exemplified by now-extinct clades which exhibited dental adaptations related to ziphodonty and durophagy.

Phylogenies have been utilized as predictive tools in a number of other disciplines. Evolutionary relationships have helped shed light on such disparate subjects as the evolution of parental care in dinosaurs (Tullberg et al., 2002), mating call preference in frogs (Ryan and Rand, 1999), and web building strategies in spiders (Benjamin and Zschokke, 2004; Eberhard et al., 2008). This study indicates that phylogenies have been an underutilized tool for making taphonomic predictions.
APPENDIX A

CHAPTER II. – SPECIMENS AND LANDMARKS


AMNH 9112: 45.694, 14.115; 45.407, 12.967; 44.498, 11.962; 43.684, 10.67; 42.584, 9.761; 40.431, 8.947; 39.282, 8.612; 37.656, 8.182; 35.694, 7.608; 33.732, 7.703; 32.201, 7.943; 30.574, 7.751

AMNH 61563: 49.703, 15.474; 49.594, 14.435; 48.992, 13.396; 47.680, 12.029; 46.258, 10.772; 44.017, 9.678; 42.868, 9.241; 41.337, 8.858; 39.314, 8.038; 37.182, 7.764; 34.995, 7.71; 32.753, 7.874


RWS 11: 20.107, 5.541; 19.977, 5.151; 19.674, 4.762; 19.198, 4.35; 18.678, 4.004;
13.938, 3.03
RWS 12: 18.346, 4.474; 18.228, 4.062; 17.973, 3.669; 17.522, 3.238; 16.972, 2.865;
16.227, 2.59; 15.717, 2.433; 15.108, 2.217; 14.363, 2.001; 13.598, 1.884; 12.872, 1.844;
12.106, 1.825
13.244, 3.336
RWS 14: 24.440, 6.445; 24.323, 5.99; 24.053, 5.586; 23.480, 5.08; 22.840, 4.709;
17.027, 3.85
17.726, 3.488; 17.134, 3.357; 16.454, 3.071; 15.686, 2.874; 14.852, 2.742; 14.063, 2.72;
13.251, 2.764
15.526, 3.511
15.729, 3.485


UF 34788: 36.237, 14.053; 36.125, 13.341; 35.712, 12.554; 34.963, 11.617; 34.176, 10.568; 32.490, 9.856; 31.703, 9.443; 30.653, 9.069; 29.192, 8.656; 27.805, 8.394; 26.419, 8.169; 24.920, 8.132

UF 34886: 43.467, 16.707; 43.180, 15.846; 42.702, 15.032; 41.888, 13.979; 40.835,
32.058, 11.09; 30.558, 11.122
UF 35129: 71.831, 22.075; 71.683, 20.748; 70.847, 19.42; 69.422, 17.749; 67.898, 16.47;
64.997, 14.995; 63.669, 14.651; 61.850, 14.209; 59.834, 13.668; 57.081, 13.373; 55.114,
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UF 38973: 11.450, 6.277; 11.328, 6.014; 11.115, 5.77; 10.811, 5.537; 10.507, 5.304;
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18.057, 6.44; 17.614, 6.302; 17.017, 6.119; 16.359, 5.935; 15.671, 5.828; 14.967, 5.721;
14.203, 5.706


UF 39106: 47.170, 14.721; 46.918, 13.511; 46.111, 12.351; 44.599, 11.192; 43.288, 10.234; 41.171, 9.276; 39.910, 9.074; 38.297, 8.671; 36.331, 8.268; 34.415, 8.117; 32.651, 8.268; 30.534, 8.369


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52.833, 16.145; 50.534, 16.345
UF 43151: 46.514, 18.434; 46.178, 17.191; 45.708, 16.317; 44.632, 15.074; 43.355,
14.099; 41.574, 13.259; 40.532, 12.855; 39.289, 12.385; 37.474, 11.813; 35.793, 11.645;
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19.511, 5.904
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UF 87886: 39.763, 12.76; 39.535, 11.932; 39.221, 11.418; 38.422, 10.619; 37.566, 9.934; 35.739, 9.306; 34.854, 8.963; 33.883, 8.592; 32.570, 8.307; 31.086, 8.164; 29.658, 8.164; 28.031, 8.25

UF 95386: 44.367, 15.892; 44.275, 14.973; 43.861, 13.961; 42.711, 12.858; 41.654, 11.938; 39.861, 11.341; 38.849, 10.881; 37.562, 10.513; 35.953, 9.915; 34.252, 9.64; 32.827, 9.594; 30.988, 9.548


APPENDIX B

CHAPTER III. – BITE MARK TYPES BY SPECIMEN
Table B.1

Chapter 3 – Bite mark types by specimen; associated bones indicated with decimal pointed identification numbers.

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APPENDIX C

CHAPTER IV. – VITAL STATISTICS AND COLLECTION PROTOCOLS FOR SAMPLED SPECIMENS
Chapter 4 – Vital statistics and collection protocols for sampled specimens; abbreviations: Y = yes; N = no; M = male; F = female; C = captive; W = wild; n/a = non-applicable.

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Buckland, W., 1823. Reliquiae diluvianae; or Observations on the organic remains contained in caves, fissures, and diluvial gravel, and on other geological phenomena attesting the action of an universal deluge. London: John Murray.


