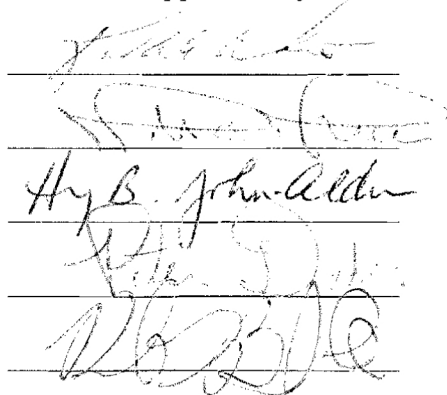A FUNCTIONAL, BEHAVIORAL, AND TAPHONOMIC ANALYSIS OF

ZIPHODONT DENTITION: NOVEL METHODOLOGY FOR THE EVALUATION OF

CARNIVOROUS DINOSAUR FEEDING PALEOECOLOGY.

By

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ABSTRACT OF THE DISSERTATION

A functional, behavioral, and taphonomic analysis of ziphodont dentition: novel

methodology for the evaluation of carnivorous dinosaur feeding paleoecology.

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Research on the feeding dynamics of carnivorous dinosaurs, most which fall

within Theropoda, is based on cranial/limb structure and body dimensions. Significantly

less research has been concerned with dental function. Ichnological and taphonomic

evidence is also used to illustrate feeding ecology, but much is without authentication

through modern experimental evidence. The major goal of this dissertation is to develop

novel techniques to further understand dinosaur carnivory, focusing on the group's

unique ziphodont dentition. Both functionally relevant theropod tooth morphometrics

and experimentation with the Komodo monitor (*Varanus komodoensis*), a living dental

analogue, are used for the first time to draw conclusions about tooth function, feeding

behavior, and tooth mark production.

When defleshing, *V. komodoensis* moves its rostrum so that the teeth are drawn

backward through flesh to section off pieces. Tooth marks reflect this unique behavior.

The majority of marks are scores produced by dragging the tooth tips across bone

surfaces. Half of the marks display curvature that reflects the movement of the rostrum

in an arc, and marks are frequently parallel. There is no bone crushing. Published

accounts of fossil theropod marks indicate similar tooth use, but a stronger bite with less

lateral rostral movement. Tooth serration widths on ziphodont teeth reflect body size in both *V. komodoensis* and theropods allometrically. These serrations can drag along bone surfaces, producing striations. Under ideal circumstances *V. komodoensis* striated tooth marks can accurately reflect the size of the consumer's serrations, and consequently its body size. The body size of a theropod consumer may therefore be determined solely from fossilized striated marks. Variability in the extent of serrations in theropod teeth is linked to the extent of contact the tooth makes with flesh. The tooth region that does not contact unmodified flesh during feeding, defined as the dead-space, does not have serrations. Highly curved teeth have the fewest serrations resulting in the largest dead space. These data also indicate that theropods may have drawn their teeth back through flesh similarly to *V. komodoensis*, defleshing by 'puncture cutting'. All the techniques developed here may be applied to fossil assemblages to answer questions about ziphodont paleoecology.

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CHAPTER 1: Introduction

Reconstructions of Mesozoic ecosystems, with their unique fauna of immense

Dinosauria, are of considerable interest to the paleontological community.   Studies

using several techniques have yielded significant paleoenvironmental and paleoecological

information from Mesozoic assemblages. For example, studies have investigated aspects

such as dinosaur habit preference (Dodson, 1971; Dodson et al, 1980), relative

abundances (Bakker, 1980), predator/prey ratios (Lockley and Hunt, 1995), and

environmental conditions during death and accumulation (Rogers, 1990; Sander, 1992;

Holtz & Barberena, 1994; Schwartz & Gillette, 1994; Fiorillo et al., 2000; Rogers et al.,

2001). Another major component of Mesozoic paleoecology is the reconstruction of

trophic interactions between higher-level consumers and their prey. Establishing these

connections is essential in the reconstruction of food webs in any ecological system

(Morin, 1999; references within). Because these interactions cannot be observed in

extinct systems, "the paleoecology of carnivory must be recognized by circumstantial

evidence" (Fastovsky and Smith, 2004:620). Therefore, indirect evidence of trophic

interactions must be solely relied on. This is made even more difficult by the fact that

carnivorous dinosaurs, most of which belong to Theropoda, are two orders of magnitude

less common than their herbivorous counterparts (Bakker, 1980; Farlow, 1993).

Consequently, a wide range of techniques have been recommended to reconstruct

predatory dinosaur feeding.

The major goal of this dissertation is to develop novel techniques to further

elucidate upon carnivorous dinosaur feeding dynamics. This introduction presents the

'state of the art' of reconstructing predatory dinosaur feeding paleoecology, and how the research in this dissertation can build upon it. First, the literature is reviewed and the methods and conclusions drawn involving carnivorous dinosaur feeding dynamics are outlined. Studies reviewed investigate carnivorous basal saurischian and theropod functional morphology, inferred feeding behaviors, and trophic paleoecology. For the purposes of brevity, I focus on morphological and behavioral evidence and do not investigate inferences derived from general paleoenvironmental reconstruction. I then discuss the areas where more work should be done, and elaborate upon how the techniques developed in this dissertation may be used to answer unexplored questions.

LITERATURE REVIEW

<u>Body size and general morphology</u>

Because dinosaurs possess record-breaking sizes as far as terrestrial vertebrates

are concerned, carnivory is frequently approached from the perspective of relative body

size. Carnivorous dinosaurs display a limited number of morphotypes believed to

possess distinctive feeding characteristics, and may be separated into morphotypes based

on size and cranial and limb proportions (Fastovsky and Smith, 2004). The largest

morphotype, consisting of tyrannosaurids, carcharadontosaurids, etc., has large heads and

small forelimbs. The running speed of this morphotype is called into question; some

argue that they were fast (Larson, 1997), but many say that their large bodies could not

withstand the stress produced at high speeds (Farlow et al., 1995). Speed negatively

correlates with estimated mass based on computer models (Seller and Manning, 2007),

suggesting that this morphotype consists of either partial or obligate scavengers (Horner

and Lessem, 1993; Horner 1994). Prey choice was affected by mass as well. Because

tyrannosaurids were large, they probably fed on large prey (Holtz, 2004). Consequently,

as tyrannosaurids grew in size during their lifetime they filled many different niches

(Foster et al. 2001). Currie (2000) instead proposes that *Albertosaurus* incorporated pack

hunting with a division of labor based on size. Meers (2002) determined a high bite force

in this group also based on their immense size.

The next largest morphotype, consisting of medium sized carnosaurs and

ceratosaurs, are considered to be mostly hunters based on their size relative to potential

prey items. Because much larger herbivorous taxa (i.e. sauropods) lived along side them,

researchers assert they most likely ate prey larger than themselves (Molnar and Farlow,

1990; Bakker, 1998). Because of this size difference, Paul (1998) stated that *Allosaurus*-like predators may have fed on sauropods without killing them. This feeding methodology resulted in the trend toward a larger predator/prey size ratio seen in the Cretaceous. The next size down consisting of herreresaurids, dromeaosaurids, and troodontids are also considered to be high energy predators who, based on their weaponry and hypothesized pack hunting behavior, fed on larger prey such as sauropods and ornithopods (Maxwell and Ostrom, 1995). Individuals with this body type may have allowed the first basal saurischians to form a separate niche from the co-occurring crurotarsans (Benton, 1983; Langer, 2004). The smallest size morphotype consists of gracile, long limbed species. Because of their size, they are believed to have focused on lepidosaur, therapsid, and insect prey (Fastovsky and Smith, 2004).

Skeletal Functional Morphology

Tail and appendicular skeleton: The functional morphology of the appendages and tail are usually approached from the standpoint of hunting ability. Because the majority of carnivorous dinosaurs are bipedal, the forelimbs are free from locomotor obligations and may be used for prey acquisition. This advantage may have even selected for a bipedal gate in early Dinosauria (Sereno, 1993). Long, powerfully built forelimbs of many carnosaurs, ceratosaurs, and herrerisaurids were probably used in prey handling (Ostrom, 1969a; Sereno, 1993; Holtz, 2002). Conversely, the reduced forelimbs of tyrannosaurids and abelisaurids indicate a trend toward a prey acquisition method with their jaws (Holtz, 2004; Tykoski and Rowe, 2004). The long, slender forelimb and manus, distinctly flexible wrist, large curved unguals, and potentially opposable first digit are considered to be major weapons in a dromaeosaurid's hunting arsenal (Ostrom 1969a,

1969b, 1994). Curved unguals also show carnivory in oviraptorids (Currie et al., 1993), but a lack of curvature combined with limited dexterity argues against vertebrate predation in ornithomimids (Nicholls and Russell, 1985). Spinosaurids may have used their large ungual to acquire fish (Charig and Milner, 1986) or disembowel carcasses while scavenging (Kitchener, 1987). Therizinosaur unguals, with their unique, elongate morphology, have been suggested to indicate a range of functions including piscivory, insectivory, and herbivory (Rozhdestvensky, 1970; Barsbold and Perle, 1980; Paul 1984; Russell and Russell, 1993).

The tail, pelvis, and hind limb have also been used to speculate about carnivorous behavior, usually from the perspective of cursorial pursuit predation. Herreresaurids and many smaller theropods have incorporated elongate caudal prezygopophyses to stiffen their tail. This may have made the animals more gracile, increasing running and leaping ability (Ostrom 1969a; Sereno, 1993). A high tibia to femur length ratio has been argued as a sign of speed, suggesting dromaeosaurids chased and leapt on prey (Fastovsky and Smith, 2004). This line of reasoning argues against speedy pursuit in tyrannosaurids.

Because of their enlarged second pedial ungual, the pes is believed to contribute directly to prey acquisition in a dromaeosaurids . This digit's function as a killing weapon is unanimously agreed upon (Ostrom, 1969b). Originally thought to be used as a slashing/disemboweling weapon, these claws have been suggested by recent studies to help dromaeosaurids 'hook and climb' onto prey (Manning et al., 2006). Although this enlarged claw is apparent in troodontids, it is smaller by comparison and has resulted in speculation as far as its use (Osmolska, 1982).

Cranium and manidible: Food manipulation, and most likely acquisition, was facilitated by the head structures of the predator. Cranial studies have used a number of techniques to determine the structural integrity of the skull and what that indicates about the limits of potential behaviors. Busbey (1995) found the high lateral walls of the theropod cranium make the skull less susceptible to dorsoventral bending, so strong vertical forces may be applied. Using linear plane frame models, Molnar (1998) concluded that this allows for high bite forces and lateral torsion in *Tyrannosaurus*. Henderson (1998) found that differences between the orientations of the certain cranial bones in Jurassic co-occurring theropods to indicate differences in bite force. The inclination of the *Allosaurus* quadrate would allow for a skull resistant to breakage at a wide gape (Bakker, 1998; Henderson, 1998).

Fenestration, or openings within the skull, influence function because the bony bars between the fenestra perform a dual function of muscle attachment and structural support. Temporal bar structure is much thicker in tyrannosaurids than most other large theropods (Molnar, 1998), indicating a sturdy skull with a strong bite. Henderson (2002) determined that smaller, more vertical oriented, elliptical orbits reflected resistance to bending, and resulted in stronger bite forces in tyrannosaurids and abelisaurids. Finite element analysis indicates *Allosaurus* had a very lightly built skull, but could resist extremely large tensional and compressional forces (Rayfield et al, 2001). Bar thickness may be linked with muscular attachment, and indicate weak musculature and low bite force in *Allosaurus*. Consequently, *Allosaurus* may have not used a strong bite but a running impact with a wide gape to secure prey.

The degree of joint fusion directly relates to the overall strength of the skull. The nasals are heavily built in all theropods, but in tyrannosaurids and abelisaurids they are transversely arched and fused along the midline. These act as compressional members, transmitting forces and greatly reinforcing the snout against breakage (Molnar, 1998; Snively et al., 2006). Unfused joints can result in variable degrees of movement. In *Tyrannosaurus*, akinetic abutted joints occur where force of a bite would be strongest (Russell, 1970; Bakker, 1986; Molnar, 1998). Alternatively, Rayfield (2004) concluded that mobility in these cranial joints allowed for shock absorption during biting and pulling.   Rowe & Gauthier (1990) and Wells (1984) assert that *Dilophosaurus* cranial joints allowed for passive movement within the skull. They saw these same sutures as a weakness that may have confined it to a scavenging niche.

Cranial kinesis, the mobility of cranial elements (Versluys, 1910), are often considered to be functionally significant. This condition is usually attributed to prey acquisition and manipulation as seen in several kinetic extant species, including birds (Bock, 1964) and lepidosaurs (Frazzetta, 1962; Condon, 1987; Herrel et al., 1999). A kinetic condition in fossils cannot be observed, but is estimated by the degree of cranial suturing. This has resulted in many contradictory claims about the theropod kinetic condition. Versluys (1910) concluded *Allosaurus* had a mesokinetic skull consisting of three kinetic regions (see also Matthew & Brown, 1922; Madsen, 1976). Iordansky (1990) argued for a prokinetic condition in *Ceratosaurus*. Conversely, Bakker (1986) and Wells (1984) both argued against kinesis in the non-interdigitating sutures of ceratosaurs. Mazzetta et al. (1998) proposed a highly kinetic skull in *Carnotaurus*, resulting in a five-joint crank system like in modern Varanidae (see also Rowe &

Gauthier, 1990). Frazzetta & Kardong (2002) also asserted that the cranial kinesis in *Allosaurus* is similar to that of extant squamates. Bakker (1986) speculated that *Coelophysis* could rotate its muzzle to remove flesh, but independent of a crank system.

The cranial musculature has been thoroughly analyzed in a variety of extant vertebrates (examples include Maynard Smith & Savage, 1959; Iordansky, 1964; Schumacher, 1973; Cleuren & DeVree, 1992, 2000; Schwenk, 2000), and has successfully been correlated to feeding behaviors. The majority of the adductor muscles in theropods are believed to be located postorbitally, therefore a wide postorbital skull was correlated with large muscle bellies and attachments (Van Valkenburgh & Ruff, 1987). *Tyrannosaurus* cranial morphology indicates large musculature for a strong, solid bite (Molnar & Farlow, 1990: Meers, 2002). Conversely, *Allosaurus,* and *Ceratosaurus* both tend to possess narrow postorbital regions, which may indicate quick slashing bites as seen in modern canids (Henderson, 1998).

Certain theropod taxa deviate markedly from the typical, deep-snouted rostral morphotype. The elongate spinosaurid skull, with reduced fenestration, a terminal rosette, and a rudimentary secondary palette, superficially resembles a crocodylian rostrum and may indicate a piscivorous niche (Charig and Milner, 1986; Holtz, 1998). Finite element analysis further corroborates this, displaying mechanical similarities between spinosaurids and the piscivorous *Gavialis* (Rayfield et al., 2007). The edentulous, oviraptorid beak has been suggested to facilitate a diet of eggs (Currie et al., 1993), and plants (Smith, 1992). Although hard-shelled mollusks are also proposed (Barsbold, 1983), the highly pneumatic skull suggests against durophagy (Currie, 1987).

The mandible is also considered from the standpoint of strength and kinesis. In both *Tyrannosaurus* and *Majungasaurus* reinforced mandibles functioning to increase resistance for a strong bite convergently evolved. Therrien et al. (2005) used linear models to determine that relative bite forces are directly related to the mandible resisting to bending loads. Sereno & Novas (1993) described an intra-mandibular joint in herrerasaurids that allowed for kinetic movement, and likened this to modern varanoids. Conversely, Bakker (1986) asserted that *Ceratosaurus* possessed a laterally bending intramandibular joint. This allowed for expansion of the gullet, resulting in the active swallowing of large prey items.

Bakker (1998) states that additional modifications in the neck musculature allow for a very large gape when attacking prey. Snively and Russell (2007) found tyrannosaurid neck musculature conforms to immense dorso-flexion resulting in a powerful shake and puncture. Conversely, ceratosaurids and carnosaurs reflect a more ventro-flexion oriented weaker bite, supporting a slashing behavior.

Dentition: Theropod dentition is described as ziphodont and is characterized by laterally compressed, curved, serrated teeth (Langston 1975; Prasad and Lapparent de Broin 2002). This condition assumes carnivory in Theropoda (Holtz et al., 2004), and has occurred in several other tetrapod taxa independently (Table 1.1). Farlow et al. (1991) described a range of theropod and other ziphodont teeth using Euclidean measurements, and noted convergence in tooth structure across most of the sample. Theropod teeth are multipurpose structures used for killing prey, cutting flesh, and occasionally breaking bone. *Tyrannosaurus* teeth are unusually stout indicating high resistance to bending forces and breakage, potentially against hard materials such as

bone. This condition increased with age, indicating a shift from flesh specialization toward a bone modifying niche (Carr, 1999).

Tooth studies focused on ecological function has been the topic of only a few species, and are rarely quantitative in nature. *Allosaurus'* laterally flattened teeth would be better at a slashing bite, and *Tyrannosaurus* widened teeth are better built for penetration of cortical bone and dermal armor (Rayfield et al. 2001; Meers, 2002). By possessing stouter teeth, certain Jurassic theropods exhibited selection towards maximizing tooth strength, resulting in niche separation (Henderson, 1998). The degree to which the upper and lower tooth rows occlude also indicates where forces are concentrated during biting. The lower tooth rows in *Tyrannosaurus* are more medial in relation to the upper as opposed to most theropods, allowing them to crack rigid objects such as bone (Meers, 2002). A degree of heterodonty is apparent in tyrannosaurids, as indicated by the 'D-shaped', mesially positioned teeth (Molnar, 1978; Holtz, 2004; Smith, 2005). The elongate conical teeth of spinosaurids suggest piscivory (Farlow et al., 1991). The deviation from the typical ziphodont morphotype in *Eoraptor* and *Alwalkeria* to a heterodont, more basal sauropodomorph-like dental morphotype may indicate a shift to omnivory (Langer, 2004)

The serrations on theropod teeth, known as denticles, increase allometrically in size relative to the size of the tooth (Chandler, 1990; Farlow et al., 1991; Smith et al., 2005). Chandler (1990) suggests that ziphodont teeth are designed to cut by a combination of puncturing and drawing the denticulate margins through flesh. According to Farlow et al. (1991) denticle size appears to be regulated by the potential for binding with flesh. Abler (1992) experimented with tooth performance in tyrannosaurids, and

found that the primary function of denticles is to assist the tooth in completing a downward puncture. *Troodon* deviates from this allometric trend by having relatively large denticles, which may indicate a partially herbivorous niche (Holtz et al. 1998).

Tooth wear has also yielded functional and behavioral conclusions. Chandler (1990) found there was more wear apparent on the tip, or apex, than on the denticles in most theropod taxa, indicating that the apical region is receiving the initial resistance from food. Wear surfaces on shed tyrannosaurid teeth illustrate that damage occurred mostly on the apex (Farlow & Brinkman, 1994: Jacobsen, 1996; Schubert and Ungar, 2005). These wear facets suggest that deep bites were made into both flesh and bone, which resulted in wear. Bite force may have exceeded tooth strength due to the repeat occurrence of breakage.

Varanid lizards, and the Komodo monitor (*Varanus komodoensis*) in particular, have ziphodont teeth considered to be most similar to those of theropods (Auffenberg, 1978, 1981; Paul, 1988). Excavators have actually confused isolated large varanid teeth for archosaur teeth (Molnar 2004). Due to these similarities alone, many authors have assumed that theropods share a similar feeding style with *V. komodoensis*. Molnar & Farlow (1990) noted major similarities in relative tooth height, and hypothesized similar defleshing methods. Modeling of *Allosaurus* skulls and teeth suggested that attacks on prey were similar to *V. komodoensis* (Busbey, 1995: Rayfield et al., 2001; 2002). The base lengths of *V. komodoensis* denticles are similar to those expected of theropod teeth of comparable sizes (Farlow et al., 1991), perhaps indicating similarities in feeding behavior (Abler, 1992; Farlow & Brinkman, 1994).

Ichnology and Taphonomy

Traces on Mesozoic fossils are often considered to be tooth marks by researchers, and numerous paleoecological conclusions have been postulated based on them. Consumer identification is often made based on tooth marks, specifying *Albertosaurus* (Dodson, 1971; Jacobsen and Ryan, 1999) *Allosaurus* (Matthew, 1908; Colbert, 1961; Farlow, 1976; Hunt et al., 1994; Bakker et al., 1997; Carpenter et al., 2005), *Daspletosaurus* (Fowler & Sullivan 2006), *Deinonychus* (Gignac et al. 2007), *Majungasaurus* (Rogers et al., 2003), *Saurornitholestes* (Currie et al. 1990; Currie and Jacobsen; 1995; Jacobsen 1995, 1997; Jacobsen and Ryan, 1999), and *Tyrannosaurus* (Erickson and Olson 1996) as perpetrators. Conclusions have also been made concerning food processing behavior. Tyrannosaurid mark morphology supports the 'puncture and pull' method (Erickson and Olson 1996), others indicate 'nipping' meat off bones (Chure et al. 1998), and most marks indicate a 'backwards' motion of theropod teeth (Jacobsen, 1995). There is no evidence to suggest gnawing or bone crushing in theropods, despite stout teeth of tyrannosaurids and their hypothesized role in bone breakage, and mark morphology reflects a similar feeding technique to that of *V. komodoensis* (Fiorillo 1991a; Jacobsen 1995, 1998; Erickson and Olson 1996).

Higher level behavioral conclusions have also been made from these traces, including perimortem, intraspecific aggression based on healing (Sereno and Novas 1993; Tanke and Currie 1995, 1998; Carpenter 1998), parental behavior (Bakker, 1998), scavenging (Jensen 1968; Hunt et al. 1994; Chure et al. 1998; Jacobsen and Ryan 1999; Fowler & Sullivan 2006), and even cannibalism (Rogers et al. 2003). Environmental

factors, such as drought (Varricchio 1995) or low prey availability (Jacobsen 1995, 1997, 1998), have also been hypothesized.

Tooth marks have also been used to determine bite forces. *Tyrannosaurus* tooth replicas were produced and used to penetrate bovine ilia. The results showed that *Tyrannosaurus* had a bite force larger than any extant taxon recorded (Erickson et al., 1996). The bite force of *Deinonychus* was also determined from marks on a *Tenontosaurus* bone (Gignac et al. 2007).

Due to continuous tooth replacement in Archosauria, shed teeth are more likely to be found around a carcass because feeding can dislodge loose teeth (Fiorillo, 1991). The shed tooth then becomes direct evidence of trophic interactions. Shed teeth suggest large, Jurassic theropods fed on sauropod carcasses (Matthew, 1908; Buffetaut & Suteethorn, 1989) and *Deinonychus* hunted *Tenontosaurus* in packs (Maxwell and Ostrom, 1995). *Liliensternus'* shed teeth illustrated scavenging on mired prosauropod carcasses (Sander, 1992). Last, tyrannosaurid shed teeth in a mass death assemblage strongly indicated the scavenging on the large grouping of carcasses (Horner and Lessem, 1994).

Fossilized gut contents provide excellent evidence of trophic behavior. Etched fish scales in addition to some ornithischian remains indicate that spinosaurids may have been at least partially piscivorous (Charig and Milner, 1987). Lepidosaur remains have been found in *Compsognathus* (Ostrom, 1978), rhynchosaurs remains were found in *Herreresaurus* (Novas, 1997), and mammalian remains were found in *Sinosauropteryx* (Fastovsky and Smith, 2004). Coprolites have also given researchers insights as to the diet and digestive process of theropods. The most notable example is the large coprolite found from a tyrannosaur (Chin et al., 1998). The large amount of bone fragments within

the coprolite suggest a significant degree of bone processing prior to ingestion, despite

supposed lack of bones broken by feeding.

DISCUSSION

The reliability and focus of dinosaur carnivory studies:

There is an unevenness in the degree to which paleoecologically relevant questions about dinosaur carnivory have been investigated. As far as structural studies of skeletal features relevant to feeding are concerned, the theropod cranium has received the most attention. In addition, the number of different approaches and analytical techniques used are more diverse than any other skeletal region. The use of principles such as compression, tension, stress, and strain, which are well understood from both engineering and biomechanical perspectives, have yielded many reliable conclusions. Simplified linear models, geometric morphometrics, and complex finite element analyses have all been used. Also, both qualitative and quantitative analyses of pneumatization, joint structuring, and fenestration have been incorporated to give a clearer picture of carnivorous dinosaur cranial mechanics.

Not all methods used to investigate cranial mechanics are as rigorous as those mentioned above. All reconstructions of theropod musculature are based solely on skeletal structure and analogy with modern archosaurs (Iordansky, 1973; Rayfield et al, 2001). Large open spaces are traditionally considered to be area for muscles, but Witmer (1997) later indicated this was false concerning the antorbital fenestra. In addition not all muscle scars are easily detected, or differentiated from one another, due to preservation. Even with well preserved scarring, the muscle belly size is still unknown. *Allosaurus'* weak bite force based on muscle estimates does not match the strength of the skull. This discrepancy may simply be the result of underestimating musculature.

Even more problematic are conclusions drawn from joint structure and kinematics. The many contradictions observed may result from a low level of understanding of joint function in theropods. Due to the mineralized nature of fossils, there is no way of knowing the degree of joint mobility (Rieppel & Gronowski, 1980). The degree of contact or suturing between the cranial bone elements is also not a reliable indicator of active kinesis (for examples in Varanidae see Smith, 1980; 1982). Last, the mechanical implications of kinesis are also uncertain. Although many authors claim that kinesis weakens the skull in both structure and bite force, it has also been argued to increase bite force in lizards (Smith, 1980).

It is obvious that cranial function has received the majority of attention, and from the most analytical directions. The wealth of techniques used on the cranium should be applied to other skeletal structures, but this is unfortunately not the case. Concerning tooth function, only limited Euclidean morphometrics have been used and there has been only one mechanical model. Theropod tooth morphometric studies tend to focus primarily on the description and/or taxonomic identification of isolated teeth, and do not approach dentition from the standpoint of function (Currie et al., 1990; Molnar, 1998; Sadlier and Chapman, 1999; Sankey et al. 2002; Carr and Williamson, 2004; Smith 2005; 2007; Smith et al. 2005). Most functional conclusions based on tooth morphology are qualitative. Although commonly compared with theropods, *V. komodoensis'* tooth morphometrics has never been rigorously investigated and directly compared to theropods. In addition, none of the researchers using *V. komodoensis* as a behavioral analogue have actually observed living individuals. Instead, they simply cite Auffenberg's (1981) seminal volume. A similar problem exists concerning limb

morphology. Simple comparative lengths of long bones provide the most in depth look into limb function. Only one mechanical model has been produced of the frequently noted dromeaosaurid pedal ungual (Manning et al., 2006). Although many behavioral conclusions have been developed from the forelimbs, no functional studies have been conducted to determine capabilities of the forelimb in the context of prey capture and handling.

Using size to determine trophic interactions is commonplace in dinosaur carnivory, but these conclusions are usually not based on rigorous analyses. Aside from Seller and Manning's (2007) computer models, most studies of size have been qualitative. In addition, the trophic interactions stated are not substantiated by any evidence. It has been often concluded that larger size equals larger prey, but there is no direct evidence to suggest this. This relationship also does not always occur in modern systems (examples in Morin, 1999). There is also a double standard; tyrannosaurids supposedly ate larger prey as they became larger, but most taxa smaller than tyrannosaurids also ate larger prey by pack hunting or non-lethal attacks. Very little consideration is given to the idea that small and young prey individuals were primary targets of these large predators. Last, the large size of tyrannosaurids may not have restricted them to scavenging, but to hunting large, co-occurring prey species.

Tooth marks make for effective evidence of trophic interactions because they are a direct link between consumers and their prey items (Blumenschine et al., 1996; Pobiner & Blumenschine, 2003). Unfortunately, the nature of ziphodont tooth marks is poorly understood at present, and many conclusions remain unsubstantiated. There are no conclusive data to indicate whether or not these taphonomic traces were actually

produced by a dinosaur consumer, as opposed to diagenesis, trampling, etc. Defleshing behavior has also been drawn from these marks, yet a link between this methodology and mark morphology has never been tested. Bite force based on tooth marks is based upon certain assumptions that may not hold true. For example, the assumption is made that bovine ilia have similar histological structure as *Triceratops* ilia. Mineralization may not allow this judgment to be made accurately, and bone density variation can alter tooth mark morphology (Selvaggio & Wilder, 2001: Dominguez-Rodrigo & Piqeras, 2003).

Although gut contents and coprolites make for exceptionally reliable indicators of trophic interactions, they are very rare. Shed teeth are also reliable taphonomic indicators because they provide direct evidence of consumption of a carcass. It should be noted though that these teeth only have significance if; 1) they can be shown to be autochthonous, 2) they can be properly identified, 3) they did not fall off during an activity other than feeding. Also I am in agreement with Brinkman et al. (1998) that an abundance of teeth may suggest group feeding, but does not necessarily indicate cooperative hunting.

A justification for this research

As stated above, the major goal of this dissertation's research is to develop novel techniques to further elaborate upon carnivorous dinosaur feeding dynamics. Because of the unevenness in both the attention to the systems studied and the techniques used, there are many approaches that can be taken to further understand the feeding dynamics of carnivorous dinosaurs. This dissertation uses novel approaches from functional, behavioral, and taphonomic standpoints, to elaborate upon the more poorly studied aspects of this discipline.

Because so little has been done with theropod dentition, the function and behavior linked to ziphodont dentition is the major underlying thread of this study. Most morphometric studies of theropod teeth measure traits that are relevant to the identification of isolated teeth in sediment. Here I measure more functionally significant traits never investigated before. These include the orientation of the tooth apex that is relevant to puncturing flesh, and the degree of denticulation that dictates a tooth's ability to cut through flesh. I also consider a tooth's position along the dental arcade and how this affects function. Most studies attempting to understand theropod tooth morphometrics are limited to Euclidean distances, or straight-line measurements between points on a tooth. I instead use landmark based geometric morphometric software (Zeilditch et al., 2004). This method factors in all the information in the distances between morphologically relevant structures, and not just certain distances with preconceived importance. This can also eliminate compounding factors such as size from the variance if desired. This also allows for ordination techniques to rigorously compare the teeth to one another.

This is the first study to incorporate actualistic feeding, or experimentation on a living analogue, to better understand the feeding behavior linked to ziphodonty. Actualistic experimentation with *Alligator* has been successfully conducted to address bite force and skull strength (Erickson et al., 2006). Estimations of theropod bite forces have been directly compared to this data to yield behaviorally relevant conclusions (Rayfield, 2004; Therrien et al., 2005; Rayfield et al., 2007). Along the same line of reasoning, this dissertation uses *V. komodoensis* as a behavioral analogue for theropods based on its dental similarities. I fed live *V. komodoensis* specimens to evaluate the

function and behaviors linked with teeth first hand, as opposed to speculating based simply on morphology.

In addition to general feeding behaviors, this actualistic experimentation also addresses the functional implications of tooth marks. Actualistic feeding experiments have been conducted with a wide range of non-ziphodont models, including living crocodilians (Njau & Blumenschine, 2006) and mammalian carnivores such as hyenas (Binford et al., 1988: Blumenschine, 1986; Marean et al, 1992), lions (Dominguez-Rodrigo, 1999, 2001; Dominguez-Rodrigo & Piqueras, 2003), leopards (Cavallo & Blumenschine, 1989), and canids (Munson, 2000; Munson & Garniewicz, 2003). These have proved to be effective in yielding reliable tooth markings for comparison with archeological fossil assemblages. Conducting a feeding experiment with *V. komodoensis,* and analyzing the remains will clarify many ziphodont tooth mark characters and the behaviors that caused them.

Last, much speculation about trophic interaction is based on body size, but there is no basis for most conclusions. If body size is going to be used as a criterion for establishing predator/prey interactions, it is crucial to have a well developed method to link a certain size consumer with a prey item. I develop a method for determining the size of a predator based on the tooth marks it leaves on bones. Researchers have asserted that the size of the denticles on a ziphodont tooth may be transcribed to a bone surface during the production of a tooth mark (Jacobsen, 1995; Rogers et al., 2003). I not only test this using actualistic experimentation with *V. komodoensis*, but also link denticle size in ziphodont carnivores with body size. This method can be applied to fossil assemblages to determine the size of the perpetrator.

Table 1.1: Selected accounts of ziphodont tetrapod taxa across time in alphabetical order.

Taxon	Reference
"Araripesuchus" wegeneri	Prasad and Lapparent de Broin, 2002
Archosauria	Benton, 2004
Dimetrodon sp.	Farlow, 1991
Euparkeria capensis	Senter, 2003
Hamadasuchus rebouli	Prasad and Lapparent de Broin, 2002
Iberosuchus sp.	Prasad and Lapparent de Broin, 2002
Mahajangasuchus	Prasad and Lapparent de Broin, 2002
Megalania prisca	Molnar
Ornithosuchus	Farlow, 1991
"Phytosaurs"	Farlow, 1991
Pristichampsus sp.	Langston, 1975
	Prasad and Lapparent de Broin, 2002
"Rausuchians"	Farlow, 1991
Sebecus sp.	Prasad and Lapparent de Broin, 2002
Theropoda	Currie and Carpenter, 2000
	Currie et al., 1991
	Farlow, 1991
	Sankey et al., 2002
	Smith et al., 2005
	Smith et al., 2007
	Smith, 2005
	Sweetman, 2004
	Weishampel et al. 2004
Varanidae	Farlow et al., 1991
Varanus komodoensis	Auffenberg, 1981

CHAPTER 2: Komodo monitor (*Varanus komodoensis*) feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology.

ABSTRACT

Most functional interpretations of ziphodont dentition are based on limited morphometric, behavioral, and taphonomic studies, but few are based on controlled observations of a modern ziphodont consumer. The purpose of this study is to determine through controlled feeding observations if the behaviors indicative of a ziphodont consumer are reflected by tooth marks left on bone surfaces by *Varanus komodoensis*, the Komodo monitor. We document feeding behavior, expand upon dental function, and correlate these aspects to tooth mark production. We also discuss the significance and limits of applying these data to fossil assemblages.

Goat carcasses were fed to eleven captive individuals. *V. komodoensis* modifies bone surfaces extensively. Individuals exhibit a 'medial-caudal arc' head movement when defleshing, followed by inertial swallowing. Bone crushing was not observed. The vast majority of tooth marks are scores, with pits being significantly less common. Tooth furrows and punctures are rare. 'Edge marks' are produced on flat elements. Marks are elongate and narrow, with variable lengths and curvature. Over one-third of the marks occur within parallel clusters. Striations are evident on five percent of all marks

Both feeding behavior and tooth marks indicate that ziphodont teeth are ideal for defleshing by being drawn through a carcass. Teeth are poorly built for crushing, and within-bone nutrients are acquired through swallowing. Mark production is a by-product

of the tooth movement during the flesh removal process. Scores are the consequence of apical dragging. Edge marks and striated scores result respectively from distal and mesial carinae contact. Mark curvature is the consequence of arcing motions of the head. Parallel clusters may result from repetitive defleshing strokes, and/or multiple tooth contacts during a stroke.

When applied to fossil assemblages, functional, behavioral, and taphonomic interpretations may be made. When provisionally applied to theropod tooth marks, similar tooth function and defleshing behavior with little bone crushing is apparent. Differences occur concerning mark frequency and curvature, relating potentially to taphonomic biases and rostral motion, respectively.

INTRODUCTION

Throughout history, certain groups of tetrapods possessed a unique dentition known as ziphodont. Meaning 'sword tooth', it is characterized by labio-lingually compressed, curved, serrated teeth. These serrations rest on carinae along each margin, and are referred to as denticles (Langston, 1975; Prasad and Lapparent de Broin, 2002; Molnar, 2004). These attributes occur in varying degrees among these different taxa (Farlow et al., 1991; Smith et al., 2005). The term ziphodonty was first coined by O.C. Marsh as a characteristic of the Eocene crocodilian *Pristichampsus vorax* (Langston, 1975). Ziphodonty is a synapomorphy of Archosauria (Benton, 2004), and although it has occurred in several Cenozoic crocodilians, it is predominantly found in Mesozoic taxa. This includes Theropoda, the majority of Crurotarsi, and basal Archosauria (Farlow et al., 1991; Senter, 2003; Benton, 2004; Holtz, 2004; Smith et al., 2005). The Permian pelycosaur *Dimetrodon* also possessed ziphodont characters. Within modern taxa, ziphodonty is rare and is not represented by any modern archosaur or synapsid taxa. It only occurs in certain members of the squamate family Varanidae (Auffenberg, 1981). These teeth are morphologically very similar to their extinct counterparts, and excavators have confused isolated teeth of ziphodont crocodilians for large varanid teeth (Molnar, 2004). The teeth of modern crocodilians and the canines of mammalian carnivores are robust and conical, and do not have denticles (Prasad and Lapparent de Broin, 2002). Although several species of shark and saber-tooth cats possessed denticulate teeth, we do not consider them ziphodont based on size and/or shape differences (Akersten, 1985; Farlow et al., 1991).

Varanids are the only extant ziphodont representatives, and although many feeding studies have investigated the kinetic varanid cranium (Frazzetta, 1962; Bolt & Ewer, 1964; Smith, 1982; Smith & Hylander, 1985; Condon, 1987), only a few studies have actually investigated dental structure, function, and consequential feeding behaviors. Rieppel (1979) hypothesized that the highly curved teeth of *Varanus salvator* are effective because cranial kinesis reorients the tips, or apices, to contact prey first. The most in-depth accounts of varanid feeding behavior and dental function are in Auffenberg's (1972, 1978, 1981) seminal volumes. He discusses the feeding dynamics of *V. komodoensis*, the Komodo monitor or Ora, based on observations in a natural setting (see also Burden, 1928). When feeding on a carcass, *V. komodoensis'* mouth is moved forward and to the side over a portion of the carcass, and repetitively drawn back in an arcing motion. The ziphodont teeth are positioned along the margin of the rounded rostrum. The margin of the tooth row appears convex from the lateral perspective, and all teeth function in unison like one "curved scalpel blade" (Auffenberg, 1981:210) (Figure 2.1). When defleshing occurs, a back tooth makes initial contact and the longer, front teeth sequentially cut deeper than the previous tooth.

Concerning extinct ziphodont representatives, several approaches have been used to determine dental function. A small number of morphometric studies, mainly of theropods, investigate this. Farlow et al. (1991) speculated on the function of denticulated teeth by applying serrate cutting mechanics of metal blades as outlined by Frazzetta (1988). Abler (1992) experimented with denticulated tooth performance in tyrannosaurids, and examined the forces involved in cutting and puncturing flesh. These exceptions aside, morphometric studies of ziphodonts tend to focus solely on the

taxonomic identification of isolated teeth (Chandler, 1990; Currie et al., 1990; Holtz et al., 1998; Molnar, 1998; Sankey et al., 2002; Smith, 2005, 2007; Smith et al., 2005).

Several conclusions about tooth use are also drawn from the investigations of *V. komodoensis* discussed above. The teeth and skull morphology of large theropods suggests similar food processing to *V. komodoensis* (Paul, 1988; Molnar and Farlow, 1990; Rayfield et al., 2001). Several researchers propose that theropods may have cultivated bacteria between denticles (Abler, 1992; Carpenter, 1998), as was once believed for *V. komodoensis*. Certain basal archosaurs may have been active predators based on dental similarities (Senter, 2003). Ziphodont crocodilians are thought to have had feeding behavior similar to *V. komodoensis* due to their similar tooth and rostrum morphology (Busbey, 1995). Theropod neck mobility supports a *V. komodoensis*-like feeding model for several large taxa (Snively and Russell, 2007).

Alternatively, taphonomic approaches to reconstructing extinct ziphodont behavior have gained increased attention in recent years. One such approach is the examination of modifications to bone surfaces by teeth of a consumer, such as a feeding predator or scavenger. These taphonomic traces are especially useful because they directly link consumers to the formation of fossil bone assemblages (Brain, 1981; Gifford, 1981; Blumenschine et al., 1996; Erickson, 1999; Kowalewski, 2002; Pobiner & Blumenschine, 2003). Bone surface modifications ascribed to ziphodont tooth marks have been identified in many assemblages (Table 2.1). From these, many behavioral reconstructions have been developed. Concerning tooth function and feeding behavior, theropod tooth marks have a morphology and frequency that is argued to reflect a similar feeding technique, and consequently similar tooth function, to that of *V. komodoensis*.

Specifically, these marks display teeth being drawn back through flesh and a lack of bone gnawing (Fiorillo, 1991a; Jacobsen, 1995, 1998; Erickson and Olson, 1996).

Unfortunately, the nature of modern ziphodont varanid studies makes them inadequate for drawing in-depth conclusions on the nature of ziphodont function. Although groundbreaking, Auffenberg's studies do not provide a controlled setting in which *V. komodoensis*, or any of its congenerics, are used as a model for ziphodont function. The majority of the aforementioned conclusions about ziphodont archosaurs rely on Auffenberg (1981) as the sole reference to support their conclusions even though dental function was not his major focus. Virtually no studies have been conducted on the feeding behavior of either wild or captive *V. komodoensis* individuals since. In fact, none of the paleontological studies addressing *V. komodoensis* dentition and behavior as analogues for ziphodont archosaurs have involved observations made on live individuals.

Along the same line of reasoning, prior conclusions based on taphonomic traces are also inadequate for drawing strong functional/behavioral conclusions. Although many intriguing ideas have been prompted by these Mesozoic traces (Table 2.1), none have been based on traces produced by extant ziphodont carnivores in a controlled setting. Such actualistic, or neotaphonomic, studies have been conducted on a wide range of modern non-ziphodont carnivores, yielding reliable data on tooth mark morphology that has been applied successfully to Stone Age archaeological assemblages. Consumers observed actualistically include Crocodylia (Njau and Blumenschine, 2006; Drumheller, 2007) and various mammalian carnivores such as hyenas, lions, leopards, and wild and domestic canids (Binford, 1981; Binford et al., 1988; Blumenschine, 1986, 1988, 1995; Blumenschine and Selvaggio, 1988; Marean and Spencer, 1991; Marean et al., 1992;

Blumenschine and Marean, 1993; Capaldo, 1997; Dominguez-Rodrigo, 1999, 2001;

Munson, 2000; Dominguez-Rodrigo and Piqueras, 2003; Munson and Garniewicz, 2003;

Pobiner, 2006). Although the lack of ziphodont actualism has been attributed to a paucity

of suitable modern analogues (Hunt et al., 1994), the morphologically similar varanids

have never been studied in this context (D'Amore, 2005). As a result, there is no

experimental evidence to indicate what taphonomic characters are indicative of ziphodont

feeding, and if these characters actually reveal meaningful information concerning

ziphodont behavior or tooth function. This casts doubt on prior interpretations drawn

from fossil examples of these marks. The tooth mark models developed from modern

mammals and crocodilians are unsuitable substitutes, given differences in tooth, jaw, and

cranial morphology between them and most ziphodont taxa (Busbey, 1995; Van

Valkenburgh and Molnar, 2002).

The purpose of this study is to determine what behaviors are indicative of

ziphodont dentition, and if these behaviors are represented in tooth marks left on bone

surfaces. In order to achieve this goal, two aspects must be explored. First, one must

have a thorough understanding of feeding behavior and consequently dental function.

Second, tooth marks on bone surfaces produced by a ziphodont consumer, ideally under

controlled circumstances, must be evaluated in reference to these behaviors. As stated

above, neither of these concepts has been adequately explored to the point where a

reliable comparison can be made. The only way to rectify this is through an actualistic

investigation of a modern ziphodont representative. This is achieved through controlled

feeding experiments with captive *V. komodoensis* individuals. General behavioral trends

observed during these feedings are reported on, building and expanding upon the

descriptions of previous researchers and evaluating dental function. I observe and categorize bone surface modifications produced during these controlled feedings, describing for the first time *V. komodoensis* feeding traces. I then discuss how these tooth marks represent ziphodont behavior and dental function. Last, I elaborate upon the potential significance and analytical limits of utilizing actualistically derived tooth marks for the purposes of behavioral and functional interpretation of fossil assemblages modified by ziphodont consumers, using theropods as an example.

METHODS

        Varanus komodoensis is the best living example of a ziphodont consumer as well as the most suitable dental analogue to most extinct ziphodont consumers, based on its size and ziphodont characters.   Not all varanids are ziphodont or even ziphodont-like, with many having bulbous or molarform teeth. Out of the several examples of ziphodont varanids, most notably *V. salvator* and *V. varius* (Auffenberg, 1981; personal observation), *V. komodoensis* is considered to be the 'most' ziphodont. *V. komodoensis* teeth are strongly curved, and no other extant reptile has teeth that are as laterally compressed (Burden, 1928; Auffenberg, 1981). Its large size results in more easily visible tooth mark characteristics. It is also most commonly compared to extinct Mesozoic taxa (see INTRODUCTION). The tooth morphology of this species and its extinct counterparts is very similar, especially between teeth of similar sizes (Farlow et al., 1991). *V. komodoensis* has been compared with large Mesozoic predators for other reasons as well, such as its large body size, cranial structuring and kinesis, predator/prey ratio, hunting tactics, and thermoregulatory abilities (McNab and Auffenberg, 1976; Bakker, 1980, 1986; Hotton, 1980; Farlow, 1983; Busbey, 1995; Valkenburgh and Molnar, 2002; Frazzetta and Kardong, 2002).

        Controlled feeding studies were conducted with eleven *V. komodoensis* individuals at two locations: the Miami Metrozoo in Miami, Florida, and the Denver Zoo in Denver, Colorado (Table 2.2). Only adults were sampled because *V. komodoensis* feeding habits change ontogenetically. Juveniles occupy an arboreal feeding niche. As the size of an individual increases, a larger portion of its life is spent on the ground. The prey items selected change as well, with smaller individuals consuming more rodents and

insects. The feeding methods employed by immature individuals may also be different (Auffenberg, 1981).

Carcass Preparation

Each *V. komodoensis* individual was fed a skinless portion of fresh, USDA approved Australian goat (*Capra hircus*), referred to here as a 'carcass portion'. These carcasses portions were obtained from a local butcher by the commissary of the housing zoo, and meat from one location was unable to be used at another. All carcass portions bore unmodified flesh and bones except for the caudal-most ribs having being sawn off distally, and the vertebral and sternal elements halved mid-sagittally. The butcher also produced a small number of marks other than those associated with the sectioning process on two carcasses. The location of these modifications was noted. All butchery marks were easily distinguished from tooth scores using the system outlined in Blumenschine et al. (1996).

Although it would be ideal for all introduced carcass portions to have identical skeletal composition, the only available carcasses were artificially sectioned from different body regions. Three carcass portion types were available. 'Upper forequarter' portions contain vertebrae from the axis to the fifth or sixth thoracic vertebrae, ribs one through five or six, the scapula and the proximal most portion of the humerus. 'Thoracic/lumbar' portions consist of thoracic vertebrae and ribs six through thirteen, as well as lumbar vertebrae one through six. Last, the 'upper hindquarter' portions contain the sacral vertebrae, usually one or two caudal vertebrae, an innominate, femur, patella, and the proximal portion of the tibia. All of these had been sectioned along the midline through the vertebral elements into left and right sides.

The masses of all carcass portions used ranged from .82 to above 4.16 kg directly prior to introduction. Because this large range of sizes was all that was available, we elected to maximize mark production and introduce carcasses to individuals based on their ability to remove enough flesh to make bone-tooth contact before becoming sated. This was judged based on the size of carcass portions available at a specific location, coupled with an individual's mass, age, and prior knowledge of that animal's feeding habits and disposition (based on input from the particular zoo's staff). For example, large individuals usually consume the most flesh, but significantly older individuals tended to eat more slowly and lose interest in the carcass portion more quickly (D'Amore, personal observation). On the other hand, younger individuals were timid about engaging with the carcass at the Denver Zoo, but more eager at Miami Metro. Excess flesh was also removed by the researcher prior to feeding in certain instances based on these specifications. Caution was used to ensure that the butchering tool did not make contact with bones.

Feeding Trials:

Fourteen feeding trials were conducted in the *V. komodoensis* individual's normal enclosure under the supervision of a zookeeper. Only one individual was in the enclosure the entire time the carcass portion was available to them. Each carcass portion was weighed before introduction and after retrieval to see how much flesh was consumed. A single carcass portion was placed on the floor of the enclosure and tethered with a rope to ensure the safety of the animal and researcher when retrieving the remains. The tether also served to prevent any feeding individual from moving the carcass portion a significant distance away from the researcher or out of the field of view. Individuals

appeared to react to the tethered carcass portionas though it was fixed. This increased the willingness of individual to remove flesh from the carcass portion and deterred it from attempting to swallow it whole. *V. komodoensis* usually did not directly engage the tether, but on two occasions the rope was either smelled or bitten. When individuals lost interest in feeding, the researcher would lightly tug on the tether to renew interest. The trial was considered complete when the individual no long interacted with the carcass portion or at the request of the zoo staff.

Carcass Processing:

After collection, the carcass portion was boiled whole in water with a small amount of non-enzymatic laundry detergent, following Blumenschine (1988). This allowed remaining flesh to be peeled either by hand or with the aid of a blunt wooden knife so as to avoid marking bone surfaces. Further cycles of simmering and rinsing were performed to remove ligaments, cartilage, and grease. Upon drying, all skeletal elements were labeled.

All elements were examined for surface marks following procedures described in Blumenschine et al. (1996). Marks were viewed under a 100-watt light bulb with a 10x hand lens. Rotating the element during evaluation and changing the angle of incident light on bone surfaces allowed for shadows to better expose the indentations of inconspicuous marks, which might otherwise be missed. Almost all marks were subsequently examined under a dissecting microscope to allow for more accurate evaluation of certain characteristics. Finally, all elements were photographed, and all tooth marks were labeled on the photograph and numbered. Six characteristics recorded for each mark are described below.

Tooth Mark Characteristics:

Classification: I use an expanded version of Binford's (1981) terminology to describe tooth marks, which is the standard used in the vast majority of studies in mammalian taphonomy (see INTRODUCTION). Binford defined four types of tooth marks, all of which are produced by *V. komodoensis*. 'Punctures' are marks where thin cortical bone collapses under the pressure of the tooth, exposing cancellous bone beneath. Punctures through thick cortical bone lacking underlying cancellous bone were not observed for *V. komodoensis*. 'Pits' occurred if the pressure is not strong enough to collapse the bone but still leaves a sub-circular to polygonal trace at the point of tooth contact. 'Furrows' are linearly extended punctures. The initial impact exposes cancellous bone and extends past the point of initial contact. Similarly, a 'score' is a linearly extended pit caused by dragging of a tooth along the surface of the bone after initial contact.

Other types of modifications were also observed. In twelve instances, scores and pits terminated in a 'chip', defined here as the negative scar remaining after a tooth had chipped-off a small flake of bone, usually along the edge of a process. Fracturing, the cracking or breaking off of substantial portion of bone, was extremely rare with small fractures occurring only six times. We also define a new type of tooth mark, labeled 'edge marks'. These marks are defined by a characteristic V-shaped cross-section, a relatively short length, and positioning along the thin edges of bone elements. These are usually found on flat bones or processes, such as ribs and vertebral processes.

Striations: Any furrow, score, or edge mark that possesses striations was noted. Striations are potentially the result of denticulated carinae or another undulating surface dragging across the bone (Jacobsen, 1995, 2001; Rogers et al., 2003), and may not result

from the strictly downward pressure that causes pitting or puncturing. Striations are any grouping of parallel or sub-parallel indentations in close proximity thought to form from one action that run along the whole or a portion of the length of a mark. These striations are usually visible only with a hand lens or a dissecting microscope and may be regularly or irregularly spaced. All striations are included as one mark.

Morphometrics: Several quantitative values were taken for each tooth mark. Length is the longest dimension of the mark. For curved scores, length is the straight-line distance from one end point of the mark to the other end point. Width is perpendicular to the length, and the distance across the actual modification at its widest point   Digital calipers were used to measure all dimensions over 1.5 millimeters to the hundredth mm. All dimensions less than 1.5 mm were measured using a dissecting microscope (20x) with an ocular scale bar to the nearest .053 mm. Less than 2% of all marks were too faint to accurately measure the width and/or length. Lengths and widths were plotted in inter-quartile ranges in order to eliminate outliers from representation.

Curvature: Five categories of mark curvature were recorded for scores, furrows, and edge marks. Pits and punctures are not elongate, and therefore have no curvature. 'Bending' or 'bowing' along the length of a mark will reorient one end of the mark length at an angle to the opposite end. Curvature is measured by comparing the relative angle of these ends (Figure 2.2). If there is no bowing or bending, the mark is considered 'straight'. If the mark bends at more then one point along its length, it is considered 'sinuous'. Marks with a single curve fall into three major categories based on their curvature; <45°, 45°-90°, >90°. This last category is labeled 'hook scores' by Njau and

Blumenschine (2006). Because these groups are very broad, the use of a protractor or similar tool was not deemed necessary.

Parallel Clusters: Any grouping of two or more tooth scores, furrows, or edge marks on a single bone element that are parallel may form a 'parallel cluster' (Figure 2.2). Marks must be next to one another and are only considered parallel if they occur on a similar area of the bone surface (i.e. a mark on the medial surface of a rib cannot be considered parallel to a mark on the lateral surface). Marks with different lengths and curvatures may be parallel. Two marks are considered parallel only if the portion of one mark that runs alongside the other is parallel to it.

Element: This is the skeletal element on which each mark is located. Because goat carcasses are halved mid-sagittally, there is never more than one of each type of element for a given carcass portion (e.g. there is no left versus right 10th rib). The position of marks on the skeletal element is not considered here. Elements considered to be in close proximity to a 'substantial' portion of boneless flesh were specified. Quantity of flesh was not directly measured, but based on observation and accounts in the literature (Frandson, 1974). Elements that are positioned near large muscle bellies were distinguished. Specified muscle groups in the upper forequarter were the proximal *m. trapezius, m. brachiocephalicus, m. deltoideus,* and *m. triceps brachii.* The thoracic/lumbar elements considered were those adjacent to the portion of the *m. obliquus externus* and *internus* that is not flush against the ribs. Last, the upper hindquarter elements were those adjacent to the *m. biceps femoris, m. gluteus medius,* and *m. tensor fasciae latae.* A student's t-test was conducted to determine if these elements had a significant amount of difference in mark number than the remainder of elements.

<u>Recording and Behavior Analysis:</u>

Nine of the fourteen feeding bouts were recorded using a hand held digital camera. The remaining bouts could not be recorded due to the nature of the enclosure or the individual's unwillingness to feed with observers present. Out of these nine, eight were used in the following analysis. Because of the consistency in *V. komodoensis* behavior witnessed, we do not feel that this sample excludes any significant behaviors. Although attempts were made to be consistent and record all behaviors, the camera was stopped a total of 13 times in order to replace film, or reposition or remove the carcass portion because flesh had been removed to the point where underlying bones may have been swallowed. These pieces were removed and the carcass portion was reintroduced. In only one instance did the carcass portion have to be forcefully removed because the *V. komodoensis* was pulling it out of view. Regurgitation occurred only twice.

The film was reviewed and all behaviors witnessed during controlled feeding trails were noted. Only the major behaviors associated with *V. komodoensis* carcass consumption are described here. Particular attention was paid to the part of the carcass portion on which *V. komodoensis* individuals were feeding in a way that may have resulted bone-tooth contact. Marks were later referred back to these observations. The frequency or duration of behaviors were not quantified and, although important, are beyond the scope of this study.

<u>Tooth description nomenclature:</u>

Because there is no standardized nomenclature for the description of ziphodont teeth (Smith and Dodson, 2003; Sweetman, 2004), I use the nomenclature proposed by

Smith and Dodson (2003); mesial, towards the premaxillary and mandibular symphyses; distal, away from the premaxillary and mandibular symphyses; lingual, towards the tongue; labial, towards the lips; apical, towards the tip of the tooth/the apex; basal, towards the base of the tooth/where the tooth meets the host bone; carina, the denticulated mesial/distal region; substrate, the material that the tooth modifies. The direction of tooth movement through the substrate is defined by the leading carina. For example, a tooth that is 'drawn distally' is describing the host bone moving the tooth so that it is leading with the distal carina. This is movement relative to the substrate, and *not* the movement of the tooth relative to any other skeletal elements.

RESULTS

V. komodoensis individuals fed on the introduced carcass portions during all fourteen feeding trials. The duration of the feeding trials was between 32 to 105 minutes with a median of about 66 minutes (Table 2.3). The rate of *V. komodoensis* flesh removal ranged from about 1.5g/min to over 13 g/min. All skeletal elements were retrieved from the artificial carcass portions in all trials except for one. In this instance, the carcass portion was torn from the tether and swallowed before retrieval was possible. Because no skeletal elements were recovered in this instance, it is excluded from further consideration.

Observed Feeding Behaviors:

The feeding technique observed here by *V. komodoensis* supports that reported by both Burden (1928) and Auffenberg (1978, 1981). After the introduction of a carcass portion into an enclosure, all *V. komodoensis* individuals exhibit some sort of exploratory behavior prior to consumption.   Individuals would lower the head and either circle the carcass portion or walk directly towards it. Tongue flicking either in the direction of or directly on the carcass portion would often occur.   Individuals would also rub their rostrum back and forth on the carcass portion. Small initial bites were occasionally made involving a slight opening of the mouth.

Defleshing behavior is the most commonly observed and distinctive aspect of *V. komodoensis* feeding behavior. Defleshing is defined as any behavior that removes meat without attempting to swallow the carcass whole (Figure 2.3). As mentioned previously by Auffenberg (1981), the jaws are opened and the head is moved forward and faced laterally. This positions the head at a more perpendicular angle in relation to the body.

The jaw is then closed and the rostrum is pulled back in an arcing motion, repositioning it so it is parallel to the mid-sagittal plane of the rest of the body. This results in the head being medial and caudal to where it started. This 'medial-caudal arc' motion usually conforms to the margin of the rounded rostrum of *V. komodoensis*, also noted by Auffenberg (1981). We refer to a single such motion as a defleshing stroke. During a stroke, the direction of head movement starts off mostly medial relative to the body's mid-line, but eventually transitions to being almost exclusively caudal. The mouth is then reopened and repositioned for the next stroke, usually over the same location. Defleshing strokes may be repeated several times, either consecutively towards one side or alternating between two sides. These movements were either slow and methodical, or quick and violent. The intensity of these movements was usually consistent for any given individual.   Strokes may be accompanied by straightening of the forelimbs resulting in a cranial-caudal 'rocking' motion of the body when repeated. In certain instances, *V. komodoensis* applied significant tension to the tether by jerking its head back, accompanied by stepping backward with both the fore and hind limbs. If lateral movements of the head were quick, the carcass portion may be tossed from side to side.

Once a section of the carcass portion is successfully removed, it is swallowed via inertial feeding (Gans, 1961, 1969; Auffenberg, 1981), where the head is elevated and shifted forward after the food item is released by the jaws, repositioning it further into the mouth. A high salivation rate and a kinetic mandible further assist this process. Kinetic movements expanding the mandibles and hyoid area almost always accompany this behavior. Although *V. komodoensis* is not a lingual feeder, its tongue is used constantly to remove meat remaining on the rostrum after swallowing.

Inertial feeding is also witnessed when the individual attempts to swallow the carcass portion whole. At first, a piece of the carcass portion is usually bitten and the head may be elevated to provide inertia, or the individual may press the carcass against the floor or wall of the enclosure to advance it into the mouth with lateral head movements. Although only briefly noted by Auffenberg (1981), I saw this latter behavior often in certain individuals. When the carcass portion was elevated, several quick jerking head movements followed to help 'force' the large item down. Attempts made to swallow the entire carcass portion were unsuccessful due to its size and tethering, such that it was regurgitated after partial ingestion.

In sum, a typical feeding series observed among all *V. komodoensis* can be specified, varying only in the intensity and frequency of behaviors among individuals. Exploratory behavior always occurs first, and is followed by defleshing and the inertial swallowing. This series is repeated throughout the feeding bout, usually after a brief pause in between. Areas of the carcass fed on first tend to bear large portions of intact, boneless flesh. Attempts to swallow the carcass whole start at the end most easily fit into the mouth, and occurred in only three trials, persisting for several minutes. Few behaviors deviate for those outlined above. Contact between the carcass and the manus occurs rarely, lasting only a few seconds, and altering the position of the carcass minimally. Although the general defleshing model proposed by Auffenberg (1981) is supported, it was difficult to tell whether or not amphikinesis occurred, or if it had any influence on feeding mechanics.

Certain areas of each carcass portion received the most attention in the form of defleshing and swallowing behaviors. For the upper forequarter portions, the dorsal-

/cranial-most area received the most attention, whereas the area containing the caudal thoracic vertebrae was fed on the least. Thoracic/lumbar portions were consumed in the caudal-most thoracic and lumbar areas, with the central thoracic area receiving the least attention. For the upper hindquarter portions, the entire pelvic and limb areas received large amounts of attention, but the sacral/caudal vertebrae were usually ignored.

At no time did *V. komodoensis* attempt to disarticulate joints, or gnaw or fracture bone. Disarticulation did occur occasionally, but this was a consequence of defleshing. These trends were witnessed regardless of the type of carcass. Bone-tooth contact does not appear to be intentional. Although contact was made (and could even be heard at times), extensive contact was avoided. On several occasions when defleshing, the *V. komodoensis'* teeth were caught on a small bone such as a rib or vertebral spine. Instead of attempting to break through the obstruction, the individual usually would quickly yet gently draw its head rostrally to dislodge its tooth. No tooth breakage was observed.

Tooth Mark Description:

A total of 1024 tooth marks produced by *V. komodoensis* are found on 71 of the recovered bone elements (Table 2.3 and Figure 2.4). The remaining 153 elements, or over two-thirds of the total sample, are unmodified. The number of marks produced during each feeding trial range from 0 to 330, with a median value of 40. As expected, carcass portions that tended to have more tooth marks also had a higher number of marked elements. The majority (81%) of tooth marks produced by *V. komodoensis* are scores (Figure 2.5); few are pits (8%) (Figure 2.6), while punctures and furrows are rare (<1.5% each). Edge marks make up fewer than 7% of all marks. 5% of all marks display striations (Figure 2.7). The majority of these striated marks are scores, but seven edge

marks and one furrow also display striations (Figure 2.8). Like pits and scores produced

by mammalian carnivores, internal surfaces show crushing of fibro-lamellar cortical

bone, at least on specimens from which all grease had been removed during cleaning.

There does not appear to be any relationship between the total mass of flesh removed

from the carcass portion and the number of tooth marks produced.

Typical *V. komodoensis* tooth marks are narrow, but many have variable lengths.

The vast majority of all pits and scores are under 1mm wide. In all cases median lengths

and widths are smaller than averages, indicating an increased frequency at the lower

values (Table 2.4). Pits and scores have similar median widths but punctures and

furrows, both penetrating cancellous bone, are three times wider. Lengths are much more

variable. Pits are the shortest marks observed: all are under 5 mm and the majority is

under 1 mm. Scores have less limited lengths with over half between 1-4 mm. Median

score and furrow lengths are over 5 times greater than widths, whereas pits and punctures

have a median length only slightly over twice the width. Edge marks have median widths

and inter-quartile ranges greater than those of scores but are substantially shorter (Figure

2.8). The largest mark overall, a score, is over 10 times wider and nine times longer than

average. Such large marks are quite rare. When looked at separately, scores possessing

striations have a median length similar to those without, but are 60% wider.

V. komodoensis also produces parallel clusters at a moderate rate. Of all the marks

present, 32% are within a parallel cluster with at least one other mark, producing 91

clusters. 34 of the 71 marked bone elements have at least one cluster of parallel marks,

with a maximum number of nine (Figure 2.9). Half of all of these elements have only

one cluster of parallel marks, and only four elements have five or more clusters. The

maximum number of parallel marks within these clusters is 17, but the modal value is two. The majority of these marks are scores. We approximated the maximum distance between marks in a cluster to be under 1 cm in the vast majority of cases.

Under half (45.9%) of 922 marks for which curvature was measured are straight. Over 30% curve <45°, and 10% curve between 45°and 90°. Scores, furrows, and edge marks are included in all these categories. Sinuous scores are rare (3.1%) and do not include furrows. Only three scores are 'hooks scores', curving more than 90°.

For the frequency of *V. komodoensis* tooth marks on certain elements types, there was a significant difference in mark number found on elements with a 'substantial' amount of proximal flesh according to the t-test (Table 2.5). The test returned a p value of below .00002. The elements bearing or in close proximity to 'substantial' amounts of flesh have an average of 8.6 marks per element type, as opposed to the remainder that have an average of 1.3 marks. Only a few elements not adjacent to a 'substantial' amount of meat had a noticeably high number of marks. These were the axis in the cervical/thoracic section and the cranial most thoracic vertebrae and rib on the thoracic lumbar sections. On the upper forequarter portions, the scapula bears the highest average number (24) of tooth marks, followed by the first rib, first thoracic vertebra, and the humerus. With the exception of the atlas, all cervical vertebrae have a moderate number of tooth marks along the column. For the upper hindquarter portions, the three largest elements are heavily marked, with the femur also having over 24 marks/element. For the thoracic/lumbar portion, the most heavily tooth-marked rib is the caudal-most (rib 13). With the exception of lumbar vertebra 6, the cranial-most (thoracic vertebra 5) and caudal-most (lumbar vertebra 5) are most frequently tooth-marked, with progressively

lower numbers of marks occurring toward the central vertebrae of this carcass type. It should be noted that these elements were in areas that received the most attention in the form of defleshing behaviors during feedings. Although scores and pits appeared on almost all element types marked, edge marks were only found on ribs and vertebrae and were absent on the appendicular skeleton.

We were unable to determine which tooth row, the upper or lower, modified tooth surfaces for two main reasons. First, most bones with extensive modifications had marks on several sides, making it difficult to rule out one row. Many elements had edge marks on the edges of flat surfaces, which could have been produced by either row. Second, the carcass portion was flipped over frequently during almost all trials, making a single bone surface accessible for potential tooth contact by either tooth row. Individuals fed on certain areas regardless of carcass portion orientation.

DISCUSSION

Varanus komodoensis feeding behavior and tooth function

The feeding methods discussed above support accounts of previous authors (Burden, 1928; Auffenberg, 1981), but there are certain inferences that may be derived from this behavior that have not been proposed. *V. komodoensis* shows a consistent set of behaviors when feeding. Due to the uniform nature of these behaviors in our sample, I suggest that they are typical for the vast majority of *V. komodoensis* individuals, both wild and captive.

Defleshing behavior moves the head in a repetitive, 'back and forth' motion, but I assert that defleshing is strictly unidirectional. As first discussed by Auffenberg (1981) and expanded upon here, ziphodont teeth function best when drawn distally. When *V. komodoensis* feeds, the teeth only contact and cut through flesh when drawn distally during the medial-caudal movement. Once the teeth have been drawn distally, they are withdrawn. No cutting occurs when the rostrum is then brought forward (rostro-lateral) over the carcass for a subsequent stroke. The teeth are usually reintroduced where the previous stroke started, allowing for the teeth to cut deeper with each stroke. This process is repeated until the flesh is entirely cut or the teeth are impeded by a hard substrate such as bone.

Flesh is cut with one side of the rostrum at a time. The arcing motion of the rostrum during defleshing moves the teeth on one side of the rostrum a large distance in an arcing direction (Figure 2.3). This arcing motion conforms to the rounded shape of the rostrum to ensure that the teeth on this side follow one another through flesh (Auffenberg 1981). The teeth on the opposite side move a shorter distance and not in

such a way as to cut efficiently. The teeth moving along the arc are the only ones that cut during defleshing. If teeth from both sides cut simultaneously, it would be unnecessary for individuals to alternate the orientation of the rostrum during defleshing, which was commonly seen. This also implies that only one side of the rostrum would produce markings during a particular stroke.

As noted by previous authors, *V. komodoensis'* tooth function is specialized for flesh removal (Burden, 1924; Auffenberg, 1978, 1981). Ziphodonty is ideally structured for distal movement through flesh, facilitated in this case by medial-caudal defleshing. Because the teeth are drawn distally, the highly curved teeth contacts the carcass apex first. This results in axial loading and the best chance for puncturing skin or flesh (Rieppel, 1979). Lateral flattening and the denticulated carinae result in less resistance, allowing for the tooth to move distally through the substrate more efficiently (Frazzetta, 1988). Although these teeth are optimal for cutting soft material, the ziphodont teeth of *V. komodoensis* are poorly built for bone crushing. The direct downward force necessary for bone crushing on a laterally compressed, curved tooth would not allow for axial loading, resulting in potential tooth breakage (Rieppel, 1979). *V. komodoensis'* lack of gnathic and dental morphologies suitable for bone breakage and oral extraction of within-bone nutrients is reflected in its avoidance of extensive contact with bone surfaces. Finite element modeling data as well as direct measurements indicates that *V. komodoensis* has an uncharacteristically low bite force for an animal its size (Moreno et al., 2007, 2008), further impeding any bone breaking ability.

Although all individuals sampled used defleshing methods, we assert they would all swallow the carcass portion whole if possible. Our observations showed that

defleshing behaviors result in subsequent size reduction and disarticulation. Defleshing

proceeds until the individual determines the size of the carcass portion is sufficiently

reduced to swallow. Elevating the carcass portion or pressing it against a fixed the

substrate are two ways of achieving the same end: moving the carcass portion or large

section of it down the gullet without lingual assistance. This method explains how *V.*

komodoensis can obtain bone and within-bone nutrients while avoiding the need for

crushing or gnawing dental adaptations. The prey bones, their contents, and the adjacent

tough soft tissues (e.g., ligaments, cartilage) are all swallowed whole and digested. This

method also allows for a relatively small amount of wastage when compared to other

modern carnivores (Auffenberg, 1978, 1981).

Varanus komodoensis tooth mark production:

Results show that the ziphodont teeth of *V. komodoensis* modify bone surfaces

frequently. Most marks may be inconspicuous due to their small size and shallowness,

but are unambiguously present upon inspection using our methodology. Narrow scores of

variable length and curvature are most commonly produced, often within parallel

clusters. Pits are substantially less common. Wide scores, furrows, and punctures are

rare, with few modifications entering cancellous bone and none penetrating compact

bone. Edge marks are restricted to ribs and vertebrae. Striated marks occur, although

uncommonly.

Tooth mark production by *V. komodoensis* reflects feeding behavior and dental

function, specifically the distal drawing of curved teeth through the substrate facilitated

by the medial-caudal arc. These behaviors are reflected best in the dominance of tooth

scores, as well as their distinct morphology. Because the defleshing strokes draw the

tooth teeth distally into the fleshy substrate, the apices are the first to make contact and are dragged along the bone surface, resulting in a score (Figure 2.10). The width of a score is limited by the width of the apex, which is narrow for all teeth in the arcade. Because they are the majority of marks and are found on all marked element types, the shape of a particular element does not appear to affect score production. The apex may be dragged across the surface of an element whether it is rounded or flat.

Pits are formed in a similar manner to scores. The fact that pits are also found on most marked element types, coupled with the fact that their average width and inter-quartile width ranges are so similar to those of scores, lends support to this (Figure 2.8). Pits result from similar apical contact without subsequent dragging across the bone surface. The apex also limits the pit's width to those similar to scores. They are much rarer than scores because the primary feeding method of *V. komodoensis* involves the drawing of teeth. If a tooth punctures flesh enough to contact bone but is not drawn distally, the cutting function of ziphodont teeth is not achieved. Pits are therefore infrequent because the behavior that produces them does not result in flesh removal. Unlike assemblages accumulated by mammal carnivory, pits are not the result of gnawing.

Striations on scores and furrows result from contact between the mesial carina and the bone surface during mark production. The curvature of a typical tooth positions the mesial carina in such a way that the denticles are allowed unobstructed access to bone surface (Figure 2.1). Outside of edge mark production (below), it is difficult to envision the denticles of the distal carina contacting and dragging across bone surfaces due to the concave form of the distal carina and the linear arrangement of teeth in the arcade. In

order for striations to form from the dragging of denticles, the carina needs to be reoriented so movement of the tooth through the substrate is lateral (in the labial/lingual direction) as opposed to the typical distal direction (Figure 2.10). This moves the tooth perpendicular to the denticulated carinae. This would be possible during the beginning of a defleshing stroke when rostral movement is more medial (Figure 2.3), because this motion would be perpendicular to the carinae of most teeth. If contact is made at this point, these denticles are dragged across the surface resulting in a striated tooth mark. The large width of these marks is because the elongate mesial carina contacts more bone surface area than the apex typically does. The direction of tooth movement may be reoriented back in the distal direction during mark production as well. This explains why striations may occur on only a portion of the mark.   Striation production is discussed in more detail in Chapter 3.

Similar to scores, edge marks reflect distal tooth movement. Alternatively, they are formed not by the tooth apex, but rather by the distal carina (Figure 2.10).   This makes them unique to ziphodont consumers.   During a defleshing stroke, the distal drawing of a tooth may cause the distal carina to make contact with a process or flattened edge of an element. The carina wedges into the bone surface. The short length of these marks reflects the length of the portion of this carina that makes contact with the bone edge, which is dictated by the thin size of the bone edge itself. There is little room for the distal dragging of the tooth, so the length of the mark does not increase much before the tooth is dislodged. Similar to scores and furrows, striations on edge marks may also result from lateral motion of the tooth, but are the result of the distal carina.   This limited lateral motion may result from the tooth sliding across the bone surface when initial

contact is made, or from behaviors intended to dislodge a wedged tooth. Unlike scores and pits, edge marks are the only commonly formed mark exclusive to certain element types. The edges of rib shafts and vertebral spines both possess long, flattened regions ideal for edge mark production. Conversely, the large, rounded contours of limb bones make them unlikely candidates for edge mark accumulation.

The substantial number of curved tooth marks results from the positioning of teeth along the margin of the *V. komodoensis'* wide, rounded rostrum, in combination with the arcing medial-caudal defleshing strokes seen. The arcing motion of defleshing strokes moves the teeth along an arcing track that corresponds with the curvature of the rostrum. If the apex is dragged along the bone surface throughout this motion, the result will be a curved score. Straight marks are the result of abbreviated contact or contact at the end of a stroke when motion is primarily caudal.

I propose two hypotheses for the production of parallel clusters, both involving deviations in tooth position at the point of bone-tooth contact when defleshing. The first is that several teeth in a particular tooth row contact a bone surface during one motion, resulting in parallel marks. Jacobsen (1995) first suggested this for theropod parallel marks. Because the *V. komodoensis* defleshing arc moves teeth into fleshy substrate in sequence, each tooth should theoretically enter in the same place during a single stroke (Auffenberg, 1981) and produce overlapping marks. In practice though, slight differences in the tooth position when entering the substrate may result in parallel, as opposed to overlapping, marks. The second hypothesis is that the repetition of defleshing strokes to detach a single morsel results in sequential parallel mark production. *V. komodoensis* will repeat a defleshing stroke over one area many times in order to remove

flesh. The strokes could deviate in position slightly, resulting in tooth mark locations being adjacent to one another. Since the motions of consecutive strokes are so similar, teeth would move in the same direction, resulting in marks of a similar orientation.

We could not test these hypotheses using feeding footage. There is no evidence to indicate if these two methods would result in different mark morphology and, if so, what these differences would be. Both methods involve the dragging of apices across bone surfaces, which is the major component in score production. It should also be noted that parallel clusters produce marks very close to one another, usually within 1 cm maximum. For parallel marks such as these to form during one defleshing stroke, only a slight irregularity in the arcing motion would be necessary to cause the teeth to move out of position enough to produce marks this distance apart. For parallel marks to form due to repetitive strokes, rostral position would deviate less than a centimeter from stroke to stroke. The variation in head movement that would facilitate either positional deviation would be very difficult to detect using our filming methods.

Carcass swallowing behavior also induces tooth mark production, though apparently rarely. In one unsuccessful attempt by a *V. komodoensis* to swallow an entire carcass portion, the rostrum was positioned at the distal femur. The individual then displayed repetitive defleshing strokes, perhaps to unsuccessfully manipulate the innominate into the mouth. This behavior is the only action witnessed that could have produced the marks observed on the femur.

The positioning of *V. komodoensis'* bites does not appear to be random or "mindless" (as stated by Hunt et al., 1994: p. 230). The selection of elements marked by *V. komodoensis* directly reflects its dental predisposition for defleshing. Elements that

had the most marks usually had 'substantial' amounts of meat on them. This indicates that the individuals were manipulating bones in areas where they could remove a large amount of flesh at a time with little bone obstruction, showing that *V. komodoensis* prioritizes defleshing over bone crushing or disarticulation. The few commonly modified elements that were not near large amounts of meat tended to be found on the perimeter elements of a carcass portion. These marks were produced simply because these elements were in areas that the individual could properly position in its mouth over when moving/swallowing the entire carcass portion. With the exception of edge marks, element shape does not appear to affect the frequency or type of mark production. Unlike mammals, *V. komodoensis* does not modify particular bones based on their amount of within bone nutrients (Blumenschine, 1986)

Tooth marks accurately represent the flesh specialist behavior of *V. komodoensis.* Tooth marking is simply a 'byproduct' of *V. komodoensis* using its ziphodont teeth for the purposes of flesh removal. Indeed, tooth marking during defleshing appears to be unintentional, at times causing apparent discomfort, as when a tooth is caught on bone during the production of edge marks. As a result, bone gnawing and fracturing is limited or absent, and punctures and furrows are rare and limited to bone portions with very thin cortical bone.

Fiorillo (1991a) asserted that tooth mark production by a ziphodont consumer (particularly theropods) during feeding would be limited because of the lack of bone gnawing and crushing behavior. Our data do not support this hypothesis. *V. komodoensis* does not crush bones, but a high frequency of tooth marks still results. Fiorillo also asserted that ziphodont consumers actively avoid contact with bone surfaces

because their teeth may dislodge due to a lack of firm socketing. Based on the behavior

of *V. komodoensis*, this is unlikely. Varanid dentition is pleurodont and lacks socketing

altogether, yet frequent bone-tooth contact resulted in bone modification with no tooth

loss.

The mass of flesh removed did not correlate with mark production in any way.

This may have been due to several factors; including characteristics of the feeding

individual (Table 2.2) or the carcass portion fed upon. Based on the small number of

individuals sampled, it is not possible to decouple their effects.

Applications of ziphodont controlled assemblages to fossil systems:

These results can be applied to fossil assemblages believed to be accumulated by

ziphodont taxa, most notably theropod dinosaurs, for the purposes of deducing tooth use.

Theropods are the majority of known ziphodont taxa as well as the alleged producers of

the majority of ziphodont fossil tooth marks (Table 2.1). Because of the goals of this

study, I emphasize functional/behavioral inferences. In addition, I also draw inferences

concerning taphonomic processes and research methodology. These inferences are

provisional because the tooth marks on fossil bones were not directly measured using the

same methods used for describing those in our control assemblages.

Many morphological similarities are apparent between tooth marks produced by

V. komodoensis and those reportedly produced by Mesozoic archosaurs (Table 2.1).

Jacobsen (1995) has conducted the most thorough analysis of Mesozoic tooth marks, in

which the majority are described as linear parallel scores (Figure 2.11), many of which

are striated, with punctures being less common. Other published accounts describe

similar tooth marks (assuming that 'grooves' are equivalent to scores). The dominance of

parallel scoring in Mesozoic assemblages is similar to our controlled assemblage, suggesting that *V. komodoensis* and theropods may have had similar feeding behavior and dental function in at least some respects.

Following the *V. komodoensis* model, the majority of marks in Mesozoic assemblages primarily indicate defleshing behavior, with little evidence of bone chewing or crushing. Elongate scoring indicates that theropods may also draw their apices distally across bone surfaces when defleshing. This model supports Jacobson's (1995:66) assertion that theropods drew their teeth "backwards" across a bone surface more frequently that making "vertical" contact. Other authors have proposed defleshing models for theropods involving distal tooth movement as well, whether it be the 'puncture and pull' of tyrannosaurids (Molnar and Farlow, 1990; Erickson and Olson, 1996; Rayfield, 2004), or the 'slashing' of *Allosaurus* and *Ceratosaurus* (Rayfield, 2001; Holtz, 2002; Snively, and Russell 2007).

A paucity of reported curved tooth marks on Mesozoic fossils may indicate deviation from the *V. komodoensis* feeding model, possibly related to rostrum morphology. Jacobsen (1995) states that over 90% of Mesozoic tooth marks observed are linear, contrasting the *V. komodoensis* pattern of producing noticeable curvature in over one third of all marks. Auffenberg (1981) demonstrated that the rounded rostrum is linked to the effectiveness of *V. komodoensis'* medial-caudal defleshing technique as well as the curvature of traces. He asserts this stroke would be ineffective in congenerics or juvenile *V. komodoensis* because they possess a narrow rostrum. Theropods usually possessed a relatively high, narrow rostrum (Molnar and Farlow, 1990; Busbey, 1995; Frazzetta and Kardong, 2002; Meers, 2002). This narrow rostrum may have limited

lateral movement during defleshing, resulting in mostly caudal motion with little deviation from the mid-sagittal plane. Infrequent curving of theropod tooth marks would be a likely result.

As in our controlled assemblage, parallel clusters of tooth scores are frequent in Mesozoic assemblages (Table 2.1). Researchers have proposed that the high occurrence of parallel and subparallel score clusters may indicate that several teeth score the bone surface in one bite. Based on this, the spacing between parallel marks may indicate the spacing between tooth teeth of the alleged consumer (Colbert, 1961; Jacobsen, 1995). However, based on the lack of behavioral evidence to support this, as well as our alternative hypothesis, we suggest caution be taken in correlating parallel tooth score spacing with tooth tooth spacing. The spacing would be only minimum spacing given the largely caudal movement.

Similar to our controlled assemblage, bone damage attributed to gnawing is absent in Mesozoic assemblages (Fiorillo, 1991a; Jacobsen, 1995, 1997, 1998; Chure et al., 1998). There is a limited amount of fracturing or large concentrations of pits and furrows. Like *V. komodoensis*, theropods do not appear to have crushed bone to access within-bone nutrients, supporting claims that bone-tooth contact was "incidental", and not from "routine bone chewing" (Fiorillo, 1991a:163; Jacobsen, 1995, 1997, 1998; Chure et al., 1998).

The high frequency of striated Mesozoic marks indicates that theropods moved their teeth in a lateral direction frequently. Jacobsen (1995, 2001) found striated marks on over 40 of 72 marked elements she examined, and Rogers et al. (2003) also found multiple striated marks on prey bones. Jacobsen (1995) attributes the production of

Mesozoic striations to the drawing of teeth across a bone at an oblique angle, which could

be facilitated by lateral tooth movement as in our model. Medial-caudal defleshing may

be the cause, but mark curvature argues against this. Torsion, the rotation of the head

around the midline during feeding, has been suggested as a possible feeding method for

tyrannosaurids (Molnar, 1998; Holtz, 2002). This movement could involve the lateral

tooth movement necessary for striation production. Currie et al. (1990:123) propose

another explanation for striation production, where *Saurornithoides* intentionally

positioned its carinae parallel to the bone surface for the purpose of "slicing flesh off of

bones." I cannot comment on the likelihood of either of these models because similar

behaviors have not been observed in modern ziphodont carnivores.

Controlled assemblages may be used as a gauge to determine the frequency of

tooth marks made by extinct ziphodont consumers. Several authors have commented on

the low incidence of tooth marks in Mesozoic theropod assemblages relative to those

found in recent assemblages fed on by mammalian carnivores (Fiorillo, 1991a; Erickson

and Olson, 1996). For example, Jacobsen (1995, 1998) found from 2-14% and Fiorillo

(1991a) found only 0-4% of bones marked in the respective Cretaceous assemblages they

sampled. Conversely, our *V. komodoensis* controlled assemblage yielded marks on

approximately one third of all elements, an apparently larger number than that reported

for Mesozoic assemblages. Erickson and Olson (1996) mention that diagenesis could

result in the under-representation of tyrannosaurid tooth marks. The majority of marks

found in *V. komodoensis* controlled assemblages are small and shallow pits and scores.

These mark types may be more susceptible to elimination by diagenetic processes then

marks that enter cancellous bone, resulting in a taphonomic bias against their

preservation. Second, many collections have never been systematically examined for tooth marks (Erickson and Olson, 1996). The small marks produced in our controlled assemblage are can be very inconspicuous and are only detectable using the dedicated search techniques outlined here. Marks such as these may be easily overlooked in fossil assemblages if they are not investigated specifically for bone surface modifications. Both of these mechanisms would result in a bias against the majority of *V. komodoensis*-type modifications, explaining why reports of tooth pits are virtually absent in the Mesozoic literature yet those for punctures and furrows are commonplace (Table 2.1).

Alternatively, differences in mark type may simply be the result of structural/physiological differences between *V. komodoensis* and its extinct ziphodont analogues. This may be exemplified by the higher frequency of punctures and furrows in Mesozoic assemblages mentioned above. Jacobsen (1995, 1998) reports punctures on 4% of bones sampled, which is four times the amount found in our *V. komodoensis* sample. These deep modifications are usually attributed to larger taxa (Erickson and Olson, 1996; Bakker, 1997; Chure et al., 1998; Tanke and Currie, 1998; Fowler and Sullivan, 2006), and their production may be the result of higher bite forces. Certainly, the bite force of *V. komodoensis* is much lower than the immense bite power estimated for *Tyrannosaurus rex* (Erickson et al., 1996). The occurrence of imbedded teeth in Mesozoic assemblages but their absence in those modified by *V. komodoensis'* may also be the result of the greater bite force of some theropods (Currie and Jacobsen, 1995). In addition, the labio-lingually widened teeth of tyrannosaurids possess greater bending strengths allowing for effective bone penetration (Molnar, 1998; Holtz, 2002, 2004; Meers, 2002).

A final explanation for the paucity of theropod tooth marks relative to these controlled assemblages is that the fossils that have been examined were simply just not fed upon. Although the controlled assemblages were scavenged upon, there is no evidence to suggest that all, or even a substantial portion, of bones were available to consumers. This could again be the result of research bias. Erickson and Olson (1996) state that frequently studied dinosaur fossils tend to come from bone beds, because of their high yield of bones and degree of preservation. These potentially catastrophic situations usually result in quick burial, and little scavenging would result in few feeding traces. It should be noted that these situations would not represent a 'typical' death assemblage. Examining fossil specimens 'known' to have been scavenged to determine the frequency and positioning of taphonomic traces may be directly compared to controlled assemblages in the future to shed light on this.

Limitations and Further Considerations:

Although we consider *V. komodoensis* to be the best extant taxon for understanding the frequency, position, and morphology of ziphodont tooth marks, its application to fossil assemblages for assessing behavior and dental function is limited by several factors. These factors are also explained using Theropoda as an example.

Our controlled feeding trials deviate from natural circumstances in several ways. First, our results do not account for possible effects of size, age, or sex among *V. komodoensis* on tooth mark production. Second, the goat carcass portions used in feeding trials are not representative of the possible size range and anatomical variation of wild *V. komodoensis* prey. Third, the carcass portions are also unlikely to be representative of carcasses consumed by predatory *V. komodoensis* or ones scavenging

partially consumed carcasses. Last, that carcass portions were fed to a single individual

and removed a short time after introduction is not representative of the competitive group

feeding that characterizes wild *V. komodoensis* (Auffenberg, 1972, 1978, 1981). Caution

should be used when drawing conclusions about higher-level carnivore behavior from

these controlled assemblages.

More generally, our observations of tooth marking are restricted to those produced during carcass

feeding. Fighting or killing in *V. komodoensis* may also produce tooth marks. Many

Mesozoic punctures and furrows are attributed to perimortem aggression, both intra- and

interspecifically (Sereno and Novas, 1993; Carpenter, 1998; Tanke and Currie, 1995,

1998). These conclusions are usually based on evidence of healing. We cannot attest to

the validity of these claims because we did not test tooth mark production under these

conditions in *V. komodoensis*, and cannot elaborate on how mark production may or may

not differ.

More work should be done investigating mark position. Although a qualitative

estimation of the amount of flesh adjacent to a particular element is given, quantitative

measurements of muscle masses may help form correlations between flesh position and

where on the carcass *V. komodoensis* is more inclined to feed. Also, investigations may

be made on the location on a particular element that is modified.

The controlled setting we used provides an alternative explanation for the

dissimilarity in mark frequency between our controlled assemblage and Mesozoic

assemblages. Fiorillo (1991a) proposes the paucity of modified elements in theropod

assemblages results from the ingestion of most marked elements. In nature, *V.*

komodoensis, facilitated by advanced cranial kinesis, tends to consume a large portion of

its prey including bones, cartilage, hair, feathers, and hooves (Auffenberg, 1981). This would likely result in the swallowing of many modified elements, a result prohibited during our feeding trials. Although the degree of cranial kinesis in Theropoda is uncertain, the existence of a mobile, intramandibular joint similar to that found in varanids may have facilitated similar swallowing abilities resulting in a small amount of wastage (examples in Bakker, 1986; Sereno and Novas, 1993).

Further research is necessary on theropods in order to yield more precise predictions concerning tooth mark production. The degree of ziphodonty should be considered when applying *V. komodoensis* as a modern analogue for theropods, or any extinct ziphodont taxa. Theropods possess highly variable tooth morphology, and these differences may have a functional, and consequently taphonomic, outcome. Although the dimensions of most theropod teeth scale linearly (Chandler, 1990; Farlow et al., 1991), exceptions include denticle sizes in troodontids, therizinosaurids and spinosaurids (Holtz, 1998, Holtz et al., 1998) and relative labio-lingual tooth widths within larger taxa such as tyrannosaurids (Henderson, 1998; Rayfield et al., 2001; Holtz, 2002; Meers, 2002; Smith, 2005). These exceptions are usually explained by fundamental niche difference, yet there has been little research indicating how morphological differences within ziphodonty may impact the function of a tooth, the behavior of its owner, or the type of traces produced. Although we have not identified any extant ziphodont analogues more similar to these exceptions, in-depth morphometric studies of other varanids in the future may yield candidates. Lastly, the concept that ziphodont dentition is strictly homodont is now believed to be "too simple" (Smith, 2005:867). Both Theropoda and Varanidae have significant degrees of morphometric variation along the tooth row (personal observation).

Other areas of theropod anatomy should also be studied in detail to narrow down behavioral and taphonomic predictions. As stated above, the curved structure of the rostrum is crucial in the success of medial-caudal defleshing as well as the production of curved tooth marks. Although many theropod rostra are considered narrow, there is most likely significant variation. It is reasonable to predict a higher degree of lateral motion linked with a wider rostrum, and consequently more curved marks. Unfortunately, no quantitative study has evaluated the variance of theropod rostral morphology. A comparative morphometric study would be informative in evaluating the capabilities of theropod rostra. Jaw musculature should also be considered. More inclusive studies of theropod bite forces will help determine with what ability a certain taxon could damage bone surfaces. Last, studies on neck morphology, such as Snively and Russell (2007), also will shed light on the most likely direction of head movement while defleshing.

Consistent use of descriptive terminology is essential when describing and comparing ziphodont tooth marks. Few Mesozoic researchers (Hunt et al., 1994; Currie and Jacobsen, 1995; Jacobsen, 1995, 1998) use the standard terminology outlined by Binford (1981) and adopted here, and few provide detailed definitions of their own terms (Tanke and Currie, 1998). Therefore, authors may use different terms to describe the same type of trace. For example, many authors state that furrowing is common (Table 2.1), but Jacobsen (1995, 1998), who also utilized Binford's nomenclature, states that furrowing is not found on dinosaur bones. Caution should therefore be taken when comparing published tooth mark descriptions.

More research is needed in the area of both ziphodont tooth marks and general *V. komodoensis* feeding behavior. In addition to the need for studies of *V. komodoensis*

feeding and mark production in a more natural setting, more in-depth morphometric and functional studies of both extinct and extant ziphodont dentition is necessary in order to understand the relationship between the degree of ziphodonty and the nature of bone modification. *V. komodoensis* tooth marks may also be compared to fossil traces for the purposes of consumer identification, as is often attempted in Stone Age assemblages (Blumenschine, 1986; Dominguez-Rodrigo, 1999; Munson and Garniewicz, 2003; Pobiner, 2006). Marks produced by other agents of bone modification in a controlled setting should be compared to *V. komodoensis* traces in order to determine the diagnostic characters unique to a ziphodont mark. One could then determine if a mark was produced by a ziphodont tooth, some other type of tooth, or a different agent altogether.

This type of research has great potential in the reconstruction of extinct behaviors and paleoecology. A body of actualistic studies with all types of modern dental analogues can be assembled with similar techniques, cataloging a number of dental morphotypes, behaviors, and traces. Similar experiments could also determine if prey size, predator size, group feeding, etc. have an affect on tooth mark morphology and frequency. Morphological and functional studies may be used to determine what behaviors were possible for the extinct taxa of interest, and therefore, what marks they would be capable of making. Fossil assemblages may be cross-referenced with this body of data to greatly narrow down the behavior and morphology that produced them. This would ultimately result in the identification of the consumer and environmental and ecological circumstances under which the animal died based solely upon tooth marks.

Table 2.1: A chronologically ordered account of published descriptions of marks identified as tooth marks believed to be produced by Theropoda, including the interpretation of the mark provided in the account. Quotes indicate words taken directly from the text referenced. Superscripted numbers describe the same marked specimen/assemblage. An asterisk (*) indicates a description that the authors derived from photographs published by the referenced author. Values in parentheses under "Number of Marks" are traces where the author considers their status as tooth marks "questionable".

Reference	Marked Taxon	Marked Element(s)	Number of Marks	Type of Mark	Striated Mark	Parallel clusters	Interpretation
Matthew 1908; Colbert 1961; Farlow 1976	*Apatosaurus (Brontosaurus)*	"several"	-	scores, fractures	-	-	*Allosaurus* feeding
Jensen 1968	*Camarasaurus*	-	"various"	-	-	-	Scavenged and washed downstream
Dodson 1971	-	-	-	"long, deep grooves"	-	subparallel*	*Gorgosaurus* feeding
Currie et al. 1990[1]	*Saurornitholestes*	-		"grazing tooth marks"	yes	-	*Saurornitholestes* used carniae parallel to bone surface
Rogers 1990	*Einiosaurus (Styracosaurus)*	4	-	"paired grooves"	-	-	-
Fiorillo 1991a[2]	Cretaceous Dinosauria	18	-	"U-shaped grooves", punctures	-	-	Theropoda do not crush bones for within bone nutrients
Fiorillo 1991b[2]	Cretaceous Dinosauria	3	-	scores, "scalloped surface"	-	-	Carnosaur scavenging and prey carcass utilization

Reference	Marked Taxon	Marked Element(s)	Number of Marks	Type of Mark	Striated Mark	Parallel clusters	Interpretation
Sereno and Novas 1993	*Herrerasaurus*	2	3	punctures	-	-	Perimortem *Saurosuchus*/ intraspecific aggression
Hunt et al. 1994	*Apatosaurus*	>7	-	scores	-	parallel	Early scavenging by *Torvosaurus* or *Allosaurus*
Currie and Jacobsen 1995	*Quetzalcoatlus*	1	4	scores, imbedded tooth	no	not parallel	*Saurornitholestes* scavenging
Jacobsen 1995, 1997, 1998; Ryan et al. 2001[3]	ceratopsids	17	-	unspecified marks	yes	-	Low mark frequency indicates mass death/*Troodon* feeding
Jacobsen 1995, 1997, 1998	hadrosaurids	47	-	unspecified mark	yes	-	Mark location on long bone ends indicate low prey availability
Jacobsen 1995, 1997	ornithomimid	2	2	unspecified mark	-	-	*Saurornitholestes* feeding
Jacobsen 1995, 1997, 1998	tyrannosaurids	8	-	puncture, linear scoring	yes	parallel	-
Tanke and Currie 1995, 1998	*Sinraptor*	5	28	puncture, furrow	no	subparallel	Perimortem intraspecific aggression

Reference	Marked Taxon	Marked Element(s)	Number of Marks	Type of Mark	Striated Mark	Parallel clusters	Interpretation
Tanke and Currie 1995, 1998	*Gorgosaurus (Albertosaurus)*	2	2	puncture, furrow/score, "disruptive texture"	no	-	Perimortem intraspecific aggression
Varricchio 1995	Iguanodontoids, *Troodon*	12	"few"	-	-	-	Assembalge accumulated through drought, botulism, or toxicosis
Erickson and Olson 1996	*Triceratops*	-	58 (+22)	furrows, fracture, punctures	yes	-	"Puncture and pull" *Tyrannosaurus* feeding
Erickson and Olson 1996	*Edmontosaurus*	1	5	furrows	no	subparallel*	"Puncture and pull" *Tyrannosaurus* feeding
Bakker et al. 1997	camarasaur	"a few"	-	scores, furrows	-	parallel*	*Allosaurus* disarticulation and parental behavior
Jacobsen 1997, 1999, 2001[1]	*Saurornitholestes*	1	3	"serration marks"	yes	-	Tyrannosaurid hunting or scavenging
Carpenter 1998	*Edmontosaurus*	5	3	"saddle shaped groove", pits	-	-	perimortem large Theropod bite
Chure et al. 1998	*Allosaurus*	1	"series"	"grooves", fracture	no	subparallel	theropod scavenging

Reference	Marked Taxon	Marked Element(s)	Number of Marks	Type of Mark	Striated Mark	Parallel clusters	Interpretation
Chure et al. 1998	*Camarasaurus*	1	20	"grooves"	no	parallel	theropod "nipping" meat off carcass
Tanke and Currie 1998	*Daspletosaurus*	1	1	puncture	no	-	Perimortem intraspecific aggression
Tanke and Currie 1998	*Monolophosaurus*	1	9	"raised blister-like lesions"	-	-	Perimortem intraspecific aggression
Tanke and Currie 1998	*Tarbosaurus*	-	-	"teethtrike trauma"	-	-	Perimortem intraspecific aggression
Tanke and Currie 1998	*Carcharodontosa-urus*	-	-	"facebite lesions"	-	-	Perimortem intraspecific aggression
Tanke and Currie 1998	*Tyrannosaurus*	-	-	score/furrow	-	-	Perimortem intraspecific aggression
Jacobsen and Ryan 1999	*Edmontosaurus*	-	"a variety"	punctures, "serration drags"	yes	-	*Gorgosaurus/Saurorntholestes* scavenging
Rogers et al. 2003	*Majungasaurus (Majungatholus)*	21	-	scores, "denticle drags"	yes	parallel	*Majungasaurus* cannibalism
Rogers et al. 2003	*Rapetosaurus*	1	-	scores/ furrows	no	subparallel	*Majungasaurus* predation
Carpenter et al. 2005	*Stegosaurus*	1	1	"U-shaped notch"	-	-	*Allosaurus* predation

Reference	Marked Taxon	Marked Element(s)	Number of Marks	Type of Mark	Striated Mark	Parallel clusters	Interpretation
Fowler & Sullivan 2006	ceratopsid	-	12 (+21)	punctures, scores	no	subparallel	*Daspletosaurus* scavenging
Gignac et al. 2007	*Tenontosaurus*	-	"numerous"	punctures	-	-	Determined *Deinonychus* bite force from punctures

Table 2.2: *Varanus komodoensis* individuals used in this study (DOB=date of birth, SVL=snout to vent length, TL=total length). Lengths are in centimeters and masses are in kilograms. Under "DOB", "wild" indicates an individual that was wild caught with an unknown age.

ID#	Name	Location	DOB	SVL	TL	Mass	Sex
940339	Castor	Denver Zoo	Feb-94	113.00	244.00	50.20	♂
A03015	Dipsnar	Denver Zoo	Jan-03	83.00	182.00	16.20	♂
A03009	Hudo	Denver Zoo	Jan-03	81.00	180.00	16.25	♂
A03001	Kawan	Denver Zoo	Jan-03	81.00	173.00	14.42	♂
A02440	Ramah	Denver Zoo	Nov-02	73.00	169.00	9.75	♀
A02439	Satu	Denver Zoo	Nov-02	94.00	201.00	21.10	♂
98R068	Hannibell	Miami MetroZoo	Sep-98	81.28	172.72	22.95	♀
H00957	Jack	Miami MetroZoo	wild	114.30	236.22	74.77	♂
98R069	Kaos	Miami MetroZoo	Sep-98	88.90	187.96	31.55	♂
H00958	Lubier	Miami MetroZoo	wild	99.06	185.42	47.27	♀
98R046	Nadia	Miami MetroZoo	Sep-98	86.36	177.80	23.95	♀

Table 2.3: Details of each feeding trial. 'Mass removed' refers to kilograms of flesh removed during a single trial. 'Elements marked' refers to the total number of bone elements marked during a single trial.   The 'number of marks' is the total number of tooth marks on one carcass from one trial. Trial length is in minutes. (UF=upper forequarter, TL=thoracic/lumbar, UH=upper hindquarter)

Individual	Trial	Filmed	Trial length	Section	Mass removed	Elements marked	Number of marks
940339	1st	yes	45.00	UF	0.60	6	40
940339	2nd	yes	15.00	UF	excluded	excluded	excluded
A03015	1st	yes	34.00	UH	0.30	0	0
98R068	1st	no	105.00	TL	0.77	11	330
A03009	1st	no	73.00	TL	0.57	1	1
H00957	1st	yes	85.00	UF	?	13	258
98R069	1st	yes	70.00	UF	0.56	8	91
A03001	1st	yes	63.00	TL	0.75	3	16
H00958	1st	no	105.00	TL	?	16	123
98R046	1st	yes	100.00	UH	0.77	3	55
A02440	1st	no	63.00	UH	0.21	2	77
A02440	2nd	no	32.00	TL	0.05	1	1
A02439	1st	yes	38.00	TL	0.45	7	32
A02439	2nd	yes	102.00	UF	0.20	0	0
Sum			930.00		5.22	71	1024
Median			66.50		0.56	3	40
Mean			66.43		0.48	5.46	78.77
St. Dev			30.31		0.25	5.25	104.1

Table 2.4: Morphometrics of all tooth marks. Values are for all marks where length and/or width was measurable. All values are in millimeters. In a small amount of cases, scores were too faint to obtain one or both of these values. Therefore, "N" is not consistent within 'score'.

	score		pit		puncture		furrow		edge	
	length	width	length	width	length	width	length	width	length	width
N	837	830	86	86	14	14	7	7	70	70
average	4.51	0.42	0.88	0.42	2.29	0.94	8.74	1.41	2.61	0.67
st. dev.	3.56	0.38	0.74	0.22	1.22	0.42	4.00	0.93	2.22	0.48
median	3.45	0.31	0.66	0.38	2.11	1.00	7.13	1.00	1.67	0.50
maximum	25.08	4.29	4.98	1.25	5.55	1.90	16.17	2.58	9.47	2.19
minimum	0.38	0.06	0.19	0.06	0.50	0.25	5.01	0.31	0.50	0.13

Table 2.5: The average occurrence of tooth marks on element types of all carcasses portions fed. The mean frequency of tooth marks is calculated by dividing the total number of marks found on an element by the number of that type of elements fed to all *Varanus komodoensis* specimens. All introduced elements are included. 'Thoracic', 'Cervical', 'Lumbar', 'Caudal', and 'Sacral' all represent vertebral elements. 'Sternum', 'Sacral', and 'Caudal' values represent all elements from all positions of that element type. A '+' under 'proximal flesh' indicates a substantial amount of flesh adjacent to the element.

Cervical-thoracic				Sacral-caudal				Thoracic-lumbar			
Element	**Total marks**	**Marks per element**	**Proximal flesh**	**Element**	**Total marks**	**Marks per element**	**proximal flesh**	**Element**	**Total marks**	**Marks per element**	**Proximal flesh**
Scapula	96	24	+	Femur	73	24.33	+	Rib 13	108	18	+
Rib 1	65	16.25	+	Tibia	32	16	+	Lumbar 5	103	17.17	+
Thoracic 1	46	11.5	+	Innominate	27	9	+	Thoracic 5	63	10.5	-
Humerus	34	8.5	+	Caudal	0	0	-	Lumbar 4	62	10.33	+
Cervical 7	23	5.75	+	Patella	0	0	-	Lumbar 3	36	6	+
Cervical 5	19	4.75	+	Sacral	0	0	-	Thoracic 6	36	6	-
Rib 2	16	4	+					Lumbar 2	27	4.5	+
Axis	14	3.5	-					Rib 12	11	1.83	+
Cervical 4	14	3.5	+					Rib 6	11	1.83	-
Cervical 3	13	3.25	+					Thoracic 8	9	1.5	-
Sternum	30	2.14	-					Rib 11	7	1.17	-
Cervical 6	8	2	+					Thoracic 13	7	1.17	-
Rib 6	2	2	-					Rib 10	5	0.83	-
Rib 5	5	1.25	-					Thoracic 12	5	0.83	-
Rib 3	4	1	-					Thoracic 7	4	0.67	-
Atlas	0	0	-					Thoracic 9	3	0.5	-
Rib 4	0	0	-					Thoracic 10	3	0.5	-
Thoracic 2	0	0	+					Rib 8	1	0.17	-
Thoracic 3	0	0	+					Rib 9	1	0.17	-
Thoracic 4	0	0	-					Thoracic 11	1	0.17	-
Thoracic 5	0	0	-					Lumbar 6	0	0	+
								Rib 7	6	0	-

Figure 2.1: View of *Varanus komodoensis* cranium displaying both premaxillary (pm) and maxillary (mx) dentition (FMNH 22200, Field Museum of Natural History, Chicago, IL). The distal carina is facing left in all teeth. Notice the convex profile formed by the teeth along tooth row from this perspective. This specimen is missing its right quadrate element. (Scale= 50 mm)

Figure 2.2: A) The curvature of an elongate mark is determined by comparing the angle of one end of a mark in relationship to the other end. From left to right; 'straight', <45°, 45-90°, and >90°. Note that all marks represented have different curvatures, but the same 'length' by our methodology (as indicated by the dotted line connect the ends). B) On the left is a diagrammatical cluster of parallel marks with different lengths and curvatures. The dotted lines indicate areas where one mark is parallel to another. On the right are several diagrammatical marks that are not parallel, but have the same lengths and curvatures.
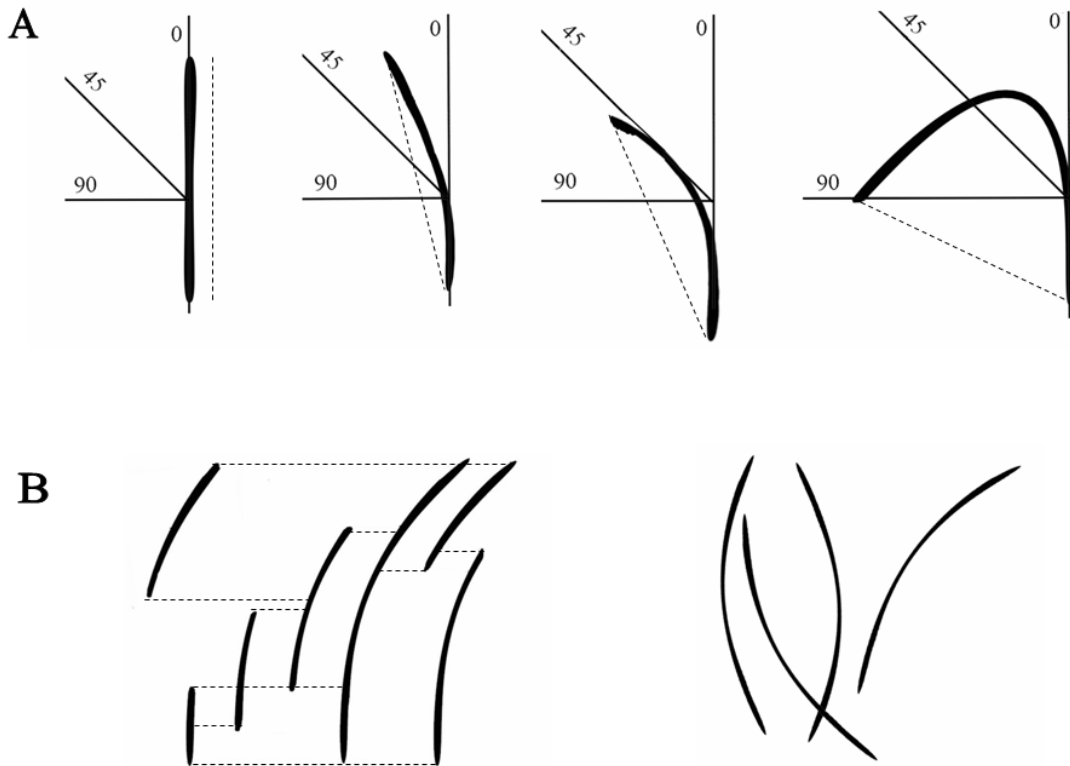
Figure 2.3: *Varanus komodoensis* demonstrating a single, medial-caudal defleshing stroke. The arrows represent the direction of head movement. A) The rostrum is positioned by being drawn laterally and cranially as the jaw is opened over a portion of the carcass. The rostrum is then drawn back in a medial-caudal arc while the jaw is adducted; cutting the substrate with the teeth and possibly marking underlying bone. B) This is a diagrammatical representation taken from stills from actual feeding footage. Each "decapitated" rostrum is layered in chronological order, with the final rostrum at the surface. The dotted line represents a hypothetical food source, with the caudal direction towards the top of the figure. Notice that motion starts mostly medial and ends mostly caudal, resulting in an arcing motion. Teeth of the right side of the rostrum are cutting in this particular stroke.
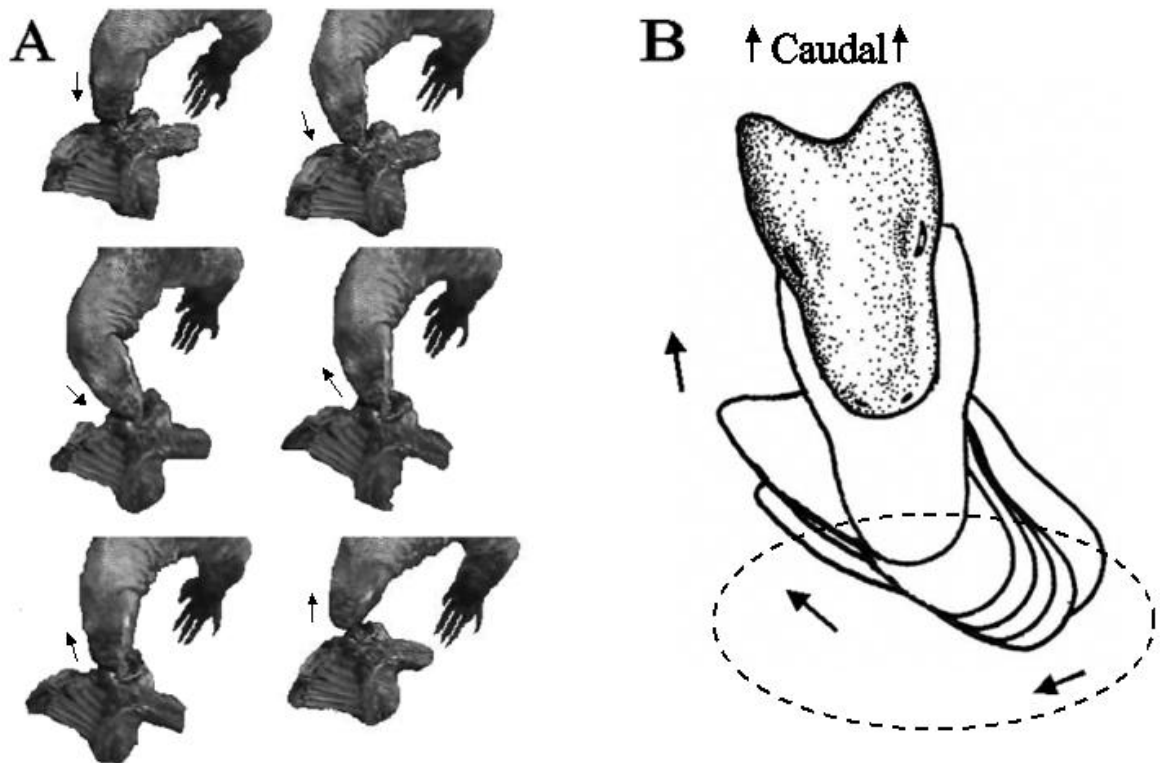
Figure 2.4: Number of tooth marks (N) in each class defined here that were produced on all introduced carcass portions. Gray areas indicate portions of each mark that possess denticle drags.
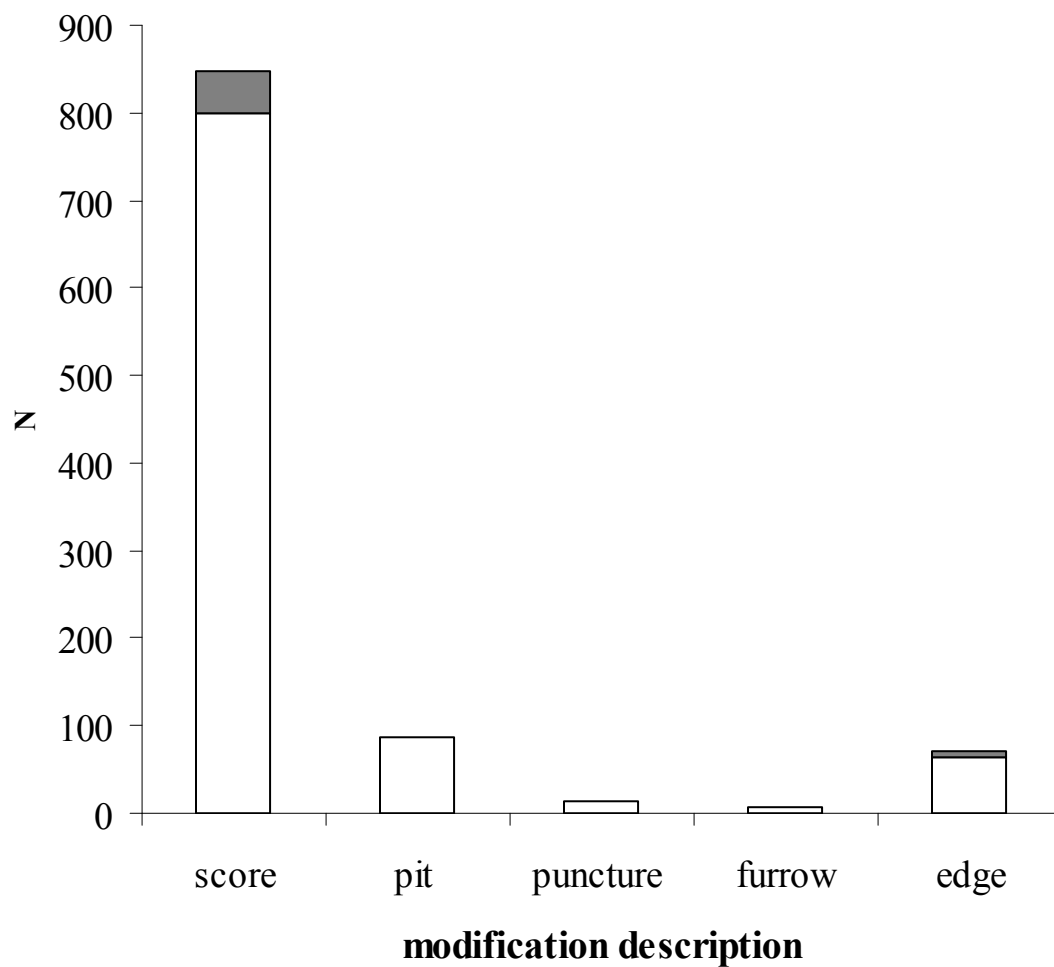
Figure 2.5: Parallel clusters of scores. A, C, and D consist of marks that are either straight or curved less <45°, and B depicts several marks curved 45-90°. (Scale = 10mm.)
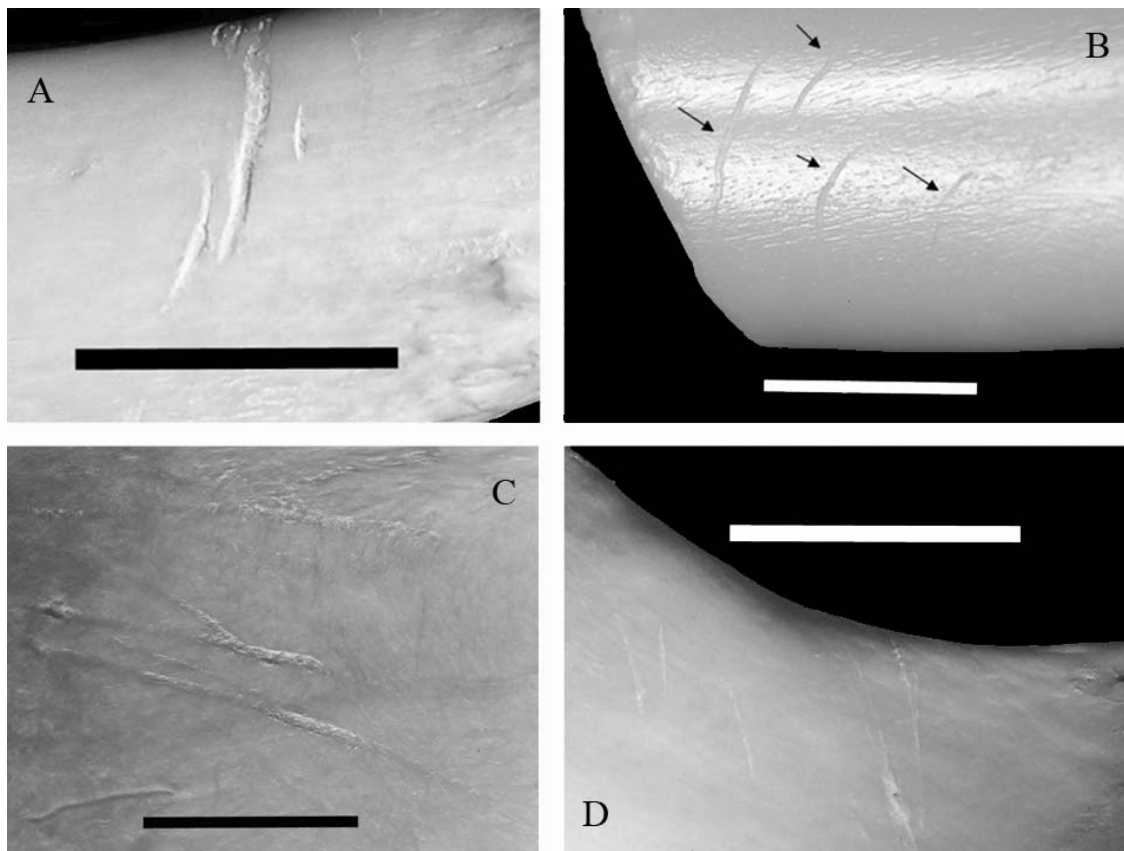
Figure 2.6: Pitting and puncturing (arrows) and scoring (not indicated) on a cranial rib (left) and lumbar vertebral process. All marks indicated by arrows are pits with the exception of the furthest right on B, which is a small puncture. Note the similar width between scores and pits. (Scale = 10mm.)
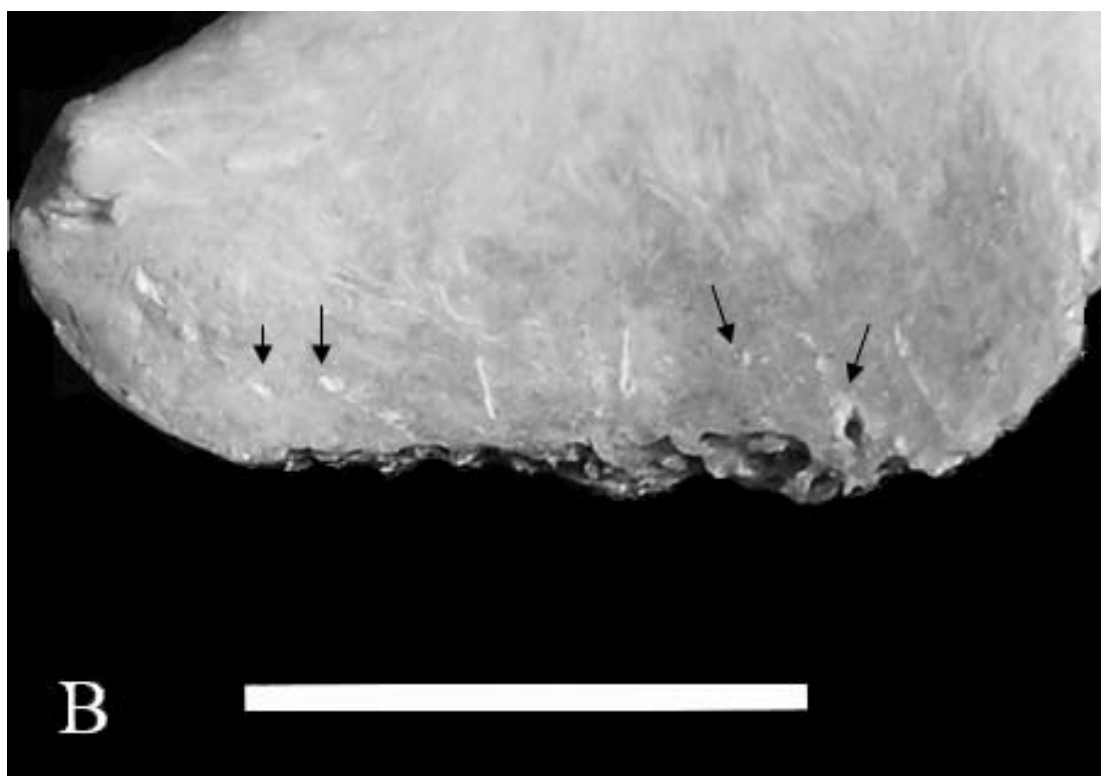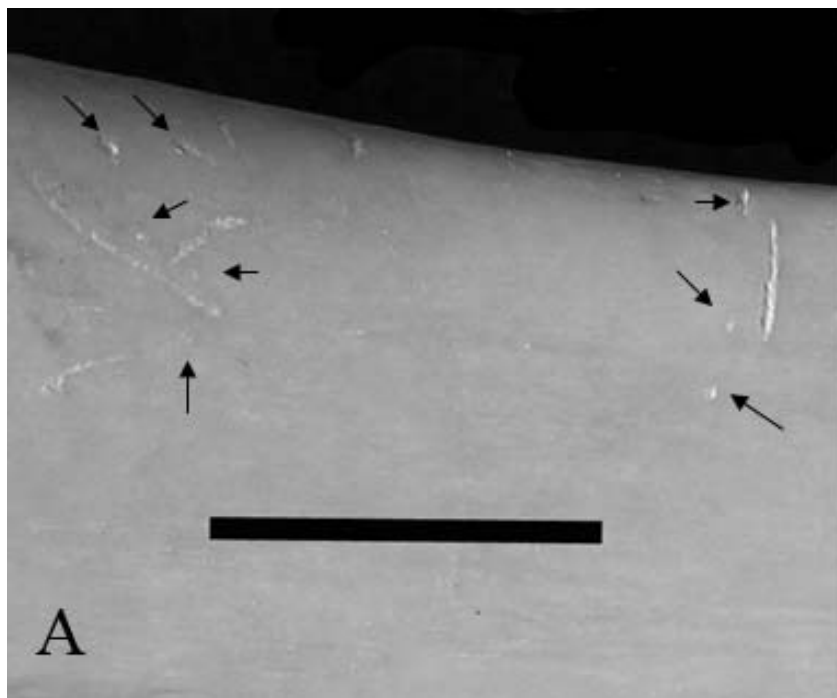
Figure 2.7: A) Parallel clusters of edge marks on the caudal edge of a proximal rib. Note the large width to length ratio. B) Curved striated marks on a caudal rib. The left two are scores and the far right one is a furrow because it entered cancellous bone. (Scale = 10mm.)
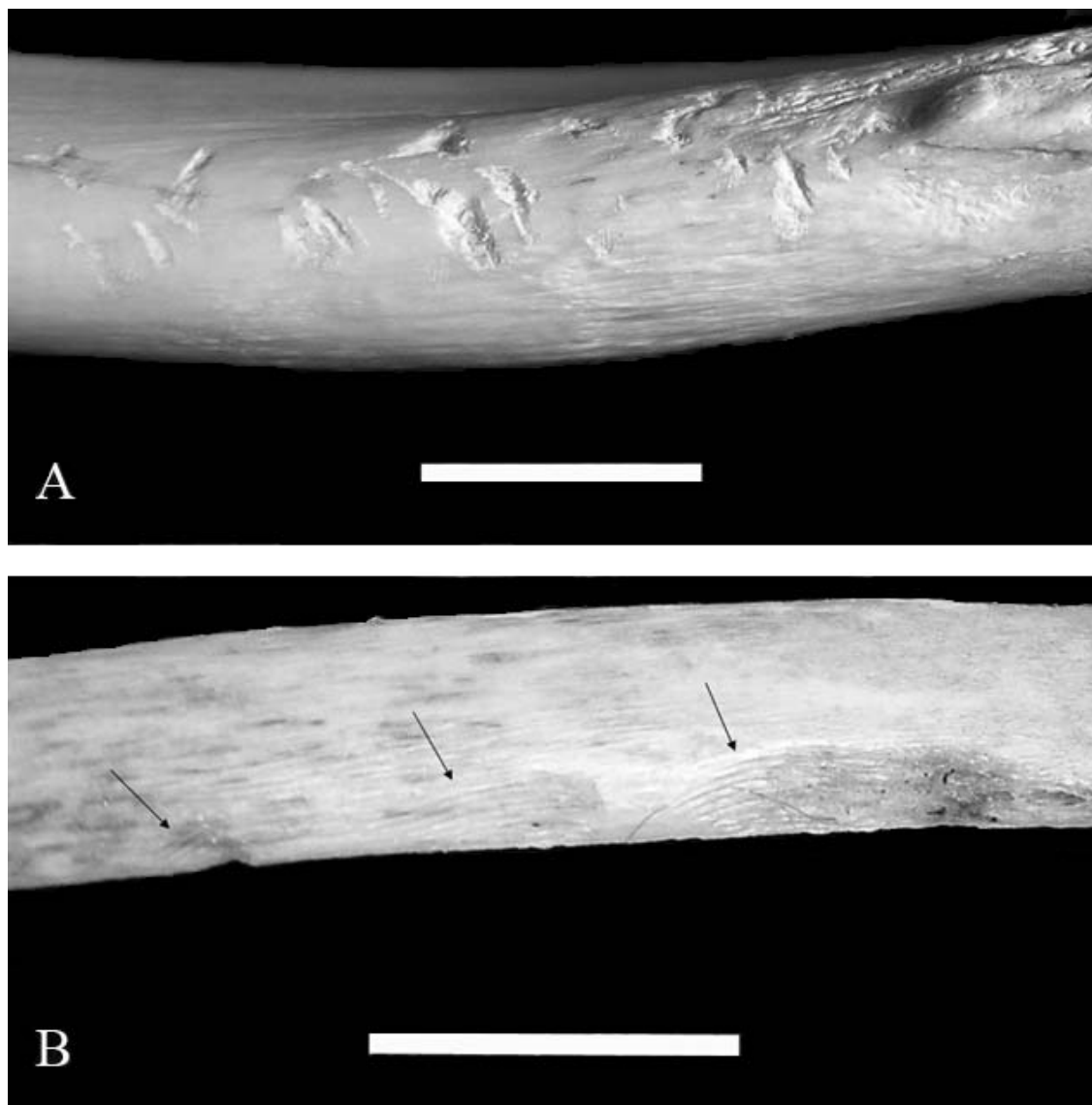
Figure 2.8: Medians and inter-quartile ranges for the lengths and widths of the five mark types produced by *Varanus komodoensis*. For total ranges, see table 4.
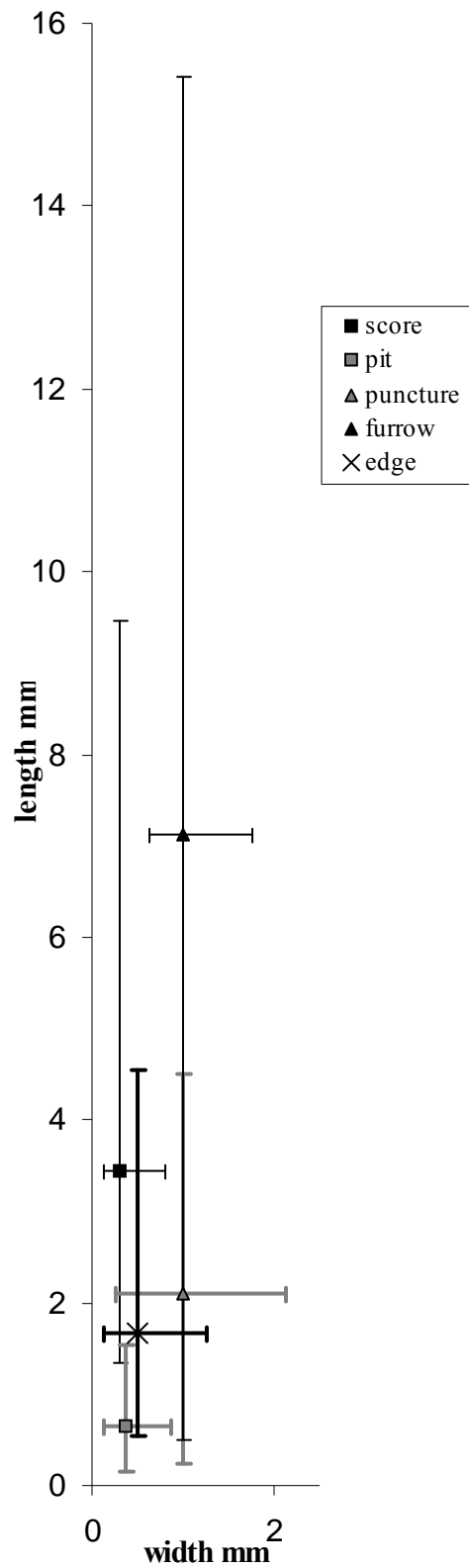
Figure 2.9: Characteristics of parallel clusters of marks. The top graph indicates the frequency of clusters of parallel marks on each marked element. Unmarked elements were not included.The bottom graph indicates the number of parallel tooth marks within each cluster independent of element.
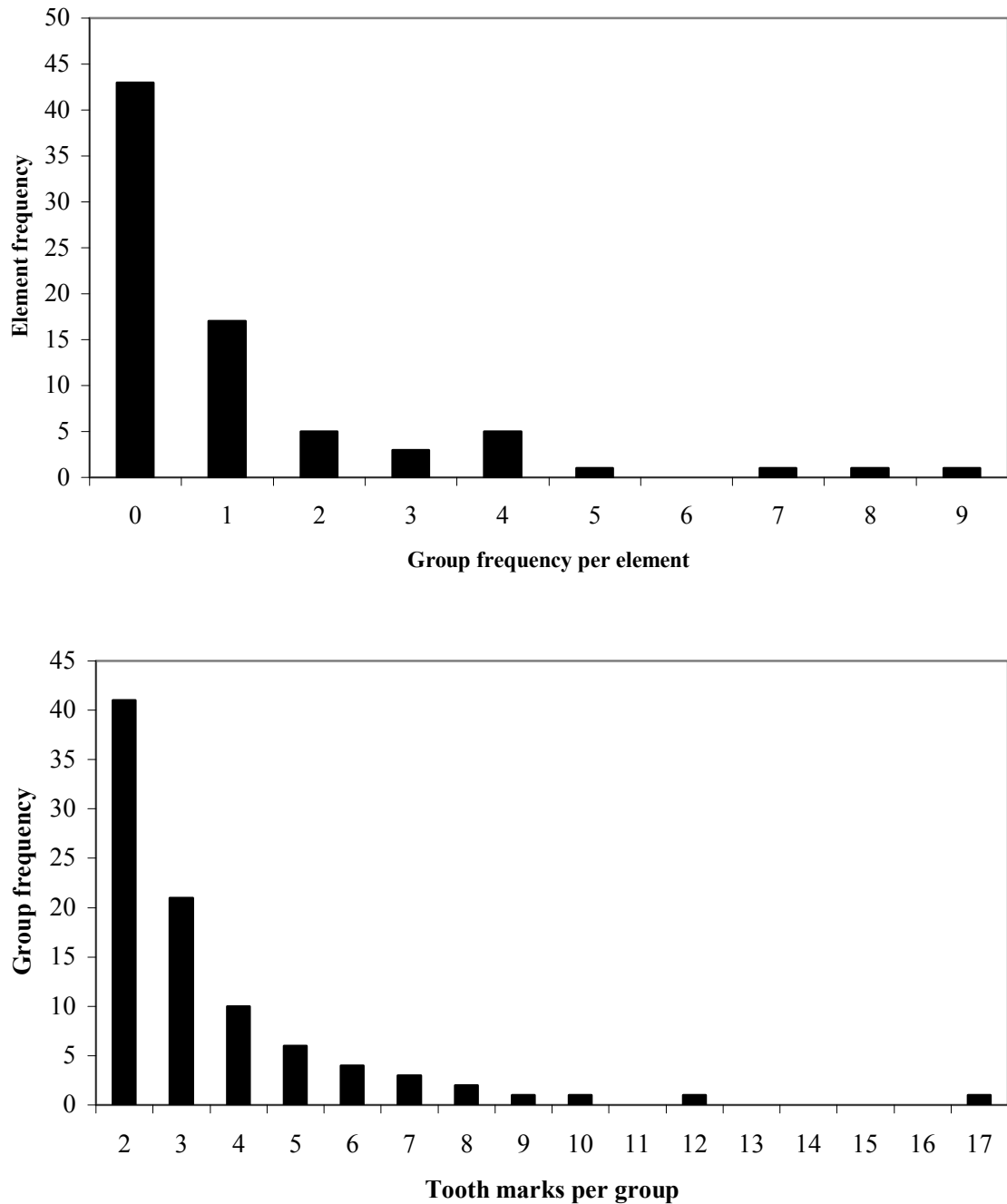
Figure 2.10: A diagrammatical representation of tooth mark production in *Varanus komodoensis*. The tooth depicted is the seventh maxillary tooth, thick lines represent the surface of cortical bone, and the arrows indicate the direction of tooth movement. For A and C the distal carina is facing right, with the labial surface visible. For B, the only visible carina is distal, with the labial surface facing right. A) A typical score is produced by the distal dragging of the tooth apex across the bone surface. This surface may be flat or rounded. B) Striations are produced by dragging the mesial carina across the bone surface in the labial/lingual direction. C) An edge mark is produced by contact between the distal carina and an elongate, flat section of bone.
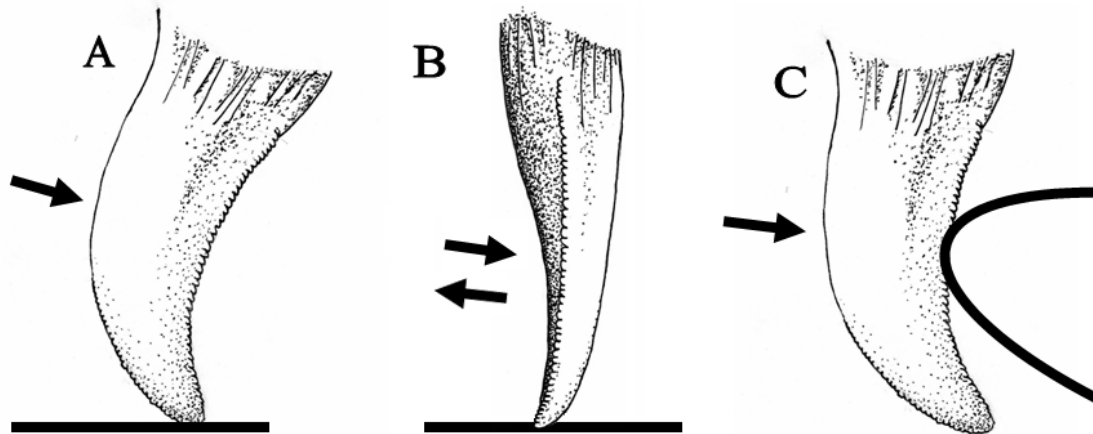
Figure 2.11: Traces on a hadrosaur ischium (RTMP 79.14.733: Royal Tyrrell Museum, Alberta, Canada) believed to be linear, parallel, theropod tooth scores. Note the similarities between these and the scores in Fig. 4. Photographs were taken by A. R. Jacobsen. (Scale = 10mm.)
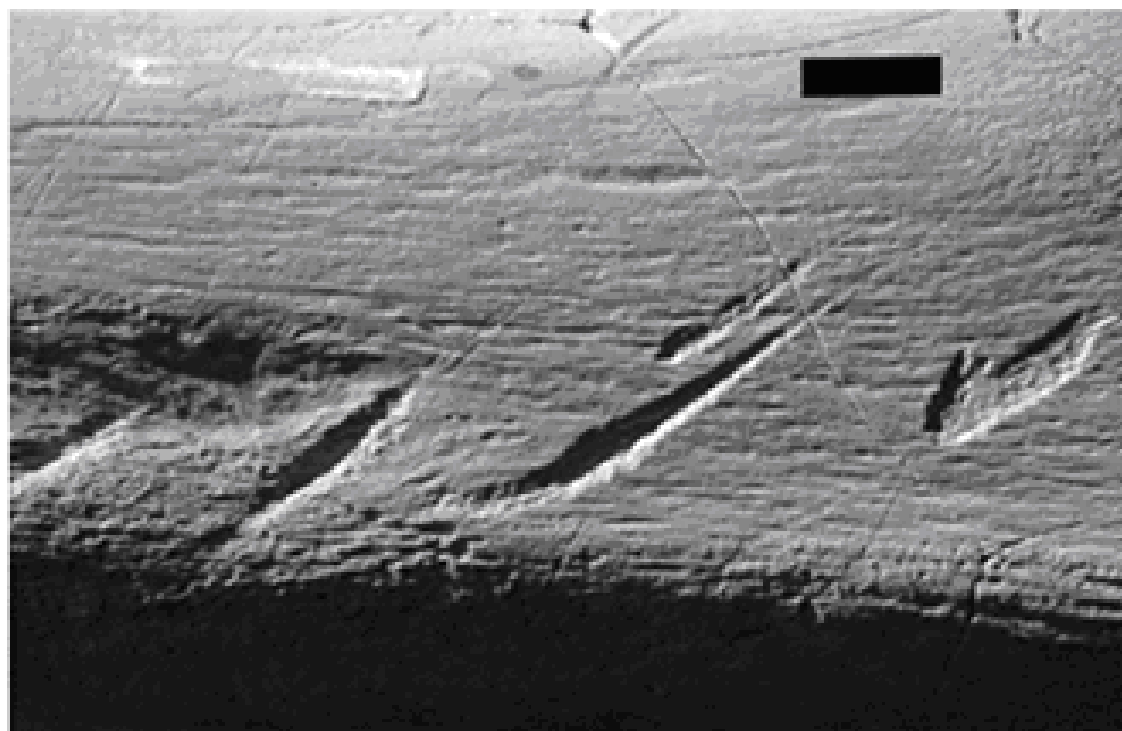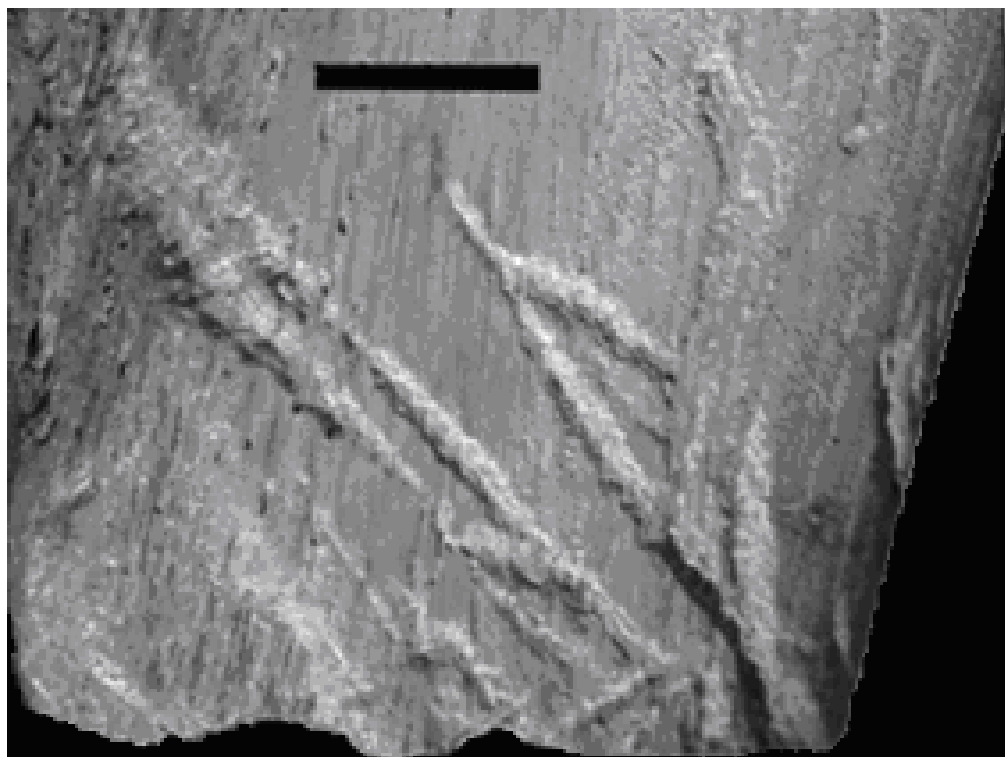
CHAPTER 3: **Predicting body size in theropod dinosaurs using striated tooth marks on bone: a model based on feeding observations of the Komodo monitor, *Varanus komodoensis*.**

ABSTRACT

Striated tooth marks are believed to be due to contact between bone surfaces and the denticles of ziphodont teeth. Ziphodont theropods are often linked to Mesozoic striated marks on fossil bones by comparing the striation widths (SW) with denticle widths (DW) of contemporaneous taxa. Captive Komodo monitors (*Varanus komodoensis*) produced marks during controlled feedings. *V. komodoensis* and selected theropod dental, cranial, and body morphometrics were taken from museum specimens and published accounts. This study determines 1) behavior linked with striated mark formation, 2) DW and its relationship to body size, and 3) body size determination by SW. Striation production is usually due to mesial denticle contact during rostral movement early during defleshing. DW correlates to tooth size independent of position in the jaw. DW predicts body size based on negative allometry in both theropods and *V. komodoensis*. A highly similar slope between these groups implies this relationship persists independent of taxonomic distance. SW cannot overestimate DW, therefore maximum SW usually reliably indicates DW. Under ideal circumstances body size can be determined by the evaluation of a striated mark. This predictive power decreases with increasing body size. Certain theropods deviate from these trends, perhaps due to fundamental niche differences.

INTRODUCTION

Tooth marks on bone surfaces are especially useful taphonomic traces because they directly link consumers to fossil assemblage formation. The ability to accurately identify a consumer's taxon, size, and/or feeding behavior based on tooth marks is an integral component in the reconstruction of paleoecological interactions in extinct systems (Brain, 1981; Gifford, 1981; Blumenschine et al., 1996;). Tooth marks have been identified in many Mesozoic assemblages, and most have been attributed to theropod dinosaurs. Behavioral and paleoecological inferences have been made from these feeding traces, including consumer identification (Matthew, 1908; Currie and Jacobsen, 1995), feeding and defleshing techniques (Fiorillo, 1991; Erickson and Olson, 1996; Jacobsen, 1995, 1998), scavenging (Chure et al., 2000; Fowler and Sullivan, 2006), intra-specific social interactions (Sereno and Novas, 1994; Tanke and Currie, 2000; Bakker, 1997), bite force (Erickson et al., 1996), and even cannibalism (Rogers et al., 2003). None of these inferences, however, have been substantiated through the comparison of fossil tooth marks to those produced by the feeding activity of an extant dental analogue to Theropoda.

Striated tooth marks in particular hold exceptional promise for identifying prehistoric consumer traits. Although these traces are rare, reports of striated tooth marks have been made for several Mesozoic assemblages (Currie et al., 1990; Jacobsen, 1995; Erickson and Olsen, 1996; Rogers et al., 2003). The majority of Mesozoic terrestrial carnivores were archosaurs possessing ziphodont dentition, most notably theropod dinosaurs. Ziphodont teeth are characterized by labio-lingually compressed, distally curved, serrated tooth teeth (Langston, 1975). These serrations are referred to as

denticles. Striated marks are believed to form by contact between bone surfaces and denticulated carinae, and have often been referred to as 'denticle drags'. Several researchers have attempted to identify consumers by comparing the width of the striations with denticle sizes of contemporaneous ziphodont carnivores (Currie et al., 1991; Jacobsen, 1995, 2001; Rogers et al., 2003). On occasion, consumers have been identified to genus, and behaviors such as carcass processing techniques and cannibalism have been speculated upon.

Several conditions must be met to accurately determine denticle sizes from denticle drags for the purpose of consumer identification. One is that the denticle morphometrics of all potential ziphodont consumers in a prehistoric community must be known. Several studies have catalogued the dimensions of theropod denticles for the purposes of identifying isolated teeth (Currie et al., 1991; Sankey et al., 2002; Smith et al., 2005). Chandler (1990) and Farlow et al. (1991) compared denticle and tooth morphometrics and found that the number of denticles per unit of tooth length decreases allometrically as tooth size increases. Several non-theropod species, including large varanids, phytosaurs, and sharks display a similar relationship (see also Holtz et al., 2000).

In addition to dental morphometrics, a thorough understanding of modern analogues is essential for the rigorous interpretation of dental function and mark production. *Varanus komodoensis*, the Komodo monitor (family Varanidae), is one of the few living ziphodont reptiles. Because of this dental similarity, researchers have proposed that Mesozoic archosaurs had feeding habits most similar to *V. komodoensis*

(Burden, 1928; Molnar and Farlow 1990; Farlow et al., 1991; Abler, 1992; Busbey, 1995; Rayfield et al., 2001; Senter, 2003).

In fact, tooth marks believed to be produced by theropods indicate behavior that is reminiscent of *V. komodoensis* feeding behavior (Fiorillo, 1991; Erickson and Olson, 1996; Jacobsen, 1998). Feeding studies with *V. komodoensis* demonstrate great similarity in general tooth mark morphology to those from Mesozoic assemblages allegedly accumulated by theropods (Chapter 2). Both assemblages have a predominance of parallel scores of variable lengths and limited widths. Few marks entered cancellous bone, and little evidence of gnawing was seen. Mark production reflects the dragging of tooth tips, or apices, across bone surfaces during defleshing. Although fewer than 5% of *V. komodoensis* tooth marks are striated, our earlier study demonstrates that a ziphodont carnivore is capable of producing striated tooth marks.

The purpose of this study is to determine if body size may be determined from the striation widths of marks produced by *V. komodoensis*, and if this relationship applies to Theropoda. The study develops three concepts. First, I discuss in detail the behavioral circumstances under which striated tooth marks are produced based on *V. komodoensis* feeding observations. Second, *V. komodoensis* and theropod dental morphometrics taken from both museum specimens and published accounts are compared to known or estimated body size characters. Although fine taxonomic determination is an ultimate goal, establishing a relationship between denticle width and body size is more attainable at present. Also, characteristics such as carina and tooth position in the jaw are evaluated to determine if they influence denticle widths within either ziphodont group. Third, actualistically derived *V. komodoensis* striated marks are evaluated to determine if

striated tooth marks accurately predict body size. This is the first study to

neotaphonomically test if striated marks accurately reflect known denticle widths, and

whether denticle widths predict known consumer size.

METHODS

Institutional Abbreviations:

AMNH, American Museum of Natural History, New York, NY; CM, Carnegie Museum of Natural History, Pittsburgh, PA; FMNH, Field Museum of Natural History, Chicago, IL; NCSM, North Carolina State Museum, Raleigh, NC; SGM, Ministére de l'Energie et des Mines, Rabat, Morocco; UCMP, Museum of Paleontology, University of California at Berkeley, Berkeley, CA; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, CT.

Tooth description nomenclature:

Because there is no standardized nomenclature for the description of ziphodont teeth (Smith and Dodson, 2003, Sweetman, 2004), I use the nomenclature proposed by Smith and Dodson (2003); mesial, towards the premaxillary and mandibular symphyses; distal, away from the premaxillary and mandibular symphyses; lingual, towards the tongue; labial, towards the lips; apical, towards the tip of the tooth/the apex; basal, towards the base of the tooth/where the tooth meets the host bone; carina, the denticulated mesial/distal region; substrate, the material that the tooth modifies. The direction of tooth movement through substrate is defined by the leading carina. For example, a tooth that is 'drawn distally' is describing the host bone moving the tooth so that it is leading with the distal carina. This is movement relative to the substrate, and *not* the movement of the tooth relative to any other skeletal elements.

Tooth Mark Analysis:

Controlled feeding studies were conducted with a total of 14 *Varanus komodoensis* individuals at two locations; the Miami Metrozoo in Miami, Florida, and the Denver Zoo in Denver, Colorado. Skinless Australia goat (*Capra hircus*) carcass portions attached to a tether for retrieval purposes were introduced to isolated *V. komodoensis* individuals. Individuals were left to feed with minimal disturbance, and carcasses were removed only after individuals became disinterested with the carcass or at the request of the zoo staff. After retrieval, remains were stripped of flesh and examined using low-power microscopy. Tooth marks were described using the system of nomenclature outlined by Binford (1981). Feeding bouts were recorded via handheld camera, and mark production was correlated to feeding behaviors witnessed. A complete description of overall experimental methodology, feeding behaviors, and mark descriptions is in Chapter 2.

Tooth marks are defined here as bone surface modifications produced by the teeth of animal (Binford, 1981), in this case *V. komodoensis*. Striated marks are tooth marks that exhibit parallel or sub-parallel striations that may be seen with equal or less magnification than a 40x dissecting microscope. Striations may run along all or part of the length of a tooth mark. All striations that appear to be formed from one tooth in one action are included as one mark. Striations that cannot be seen without a dissecting microscope are not considered.

Tooth marks were identified by systematically scanning all surfaces of each bone with the naked eye or a 10x hand lens under strong, 100W light (following Blumenschine et al., 1996) and further analyzed using a dissecting microscope set at 40x magnifications.

The tooth marks, being impressions in the bone surface, are easily identified and observed under this lighting and magnification. Because the carcass portions were butchered into sections before acquisition, there were a small number of knife and saw marks. These artificially produced marks were easily distinguished from tooth marks using criteria outlined by Blumenschine et al. (1996). Once a striated mark was determined, molds were made of each mark using vinyl polysiloxane dental putty (3M EXPRESS) making it easier to examine and photograph the mark's striation characteristics under the microscope. Nine marks required data to be taken directly from the bone because faintness prevented adequate mold production. The average striation width (**SW**) per mark is the distance between the outermost striations at their widest point of divergence divided by the number of striations within the mark. These measurements are accurate to the nearest .03mm, based on the micrometer disc used.

The spacing between the striations is categorized as either 'regular' or 'irregular'. Marks with regular spacing have the majority of striations at similar distances from one another throughout the length of striated region. This was judged qualitatively. Although striations may diverge, displaying increasing separation along the length of the mark, these changes are gradual. I suggest that regularly spaced striated marks are most likely the result of the dragging of denticles over bone surfaces. True ziphodont dentition has isolated, regular denticles (Langston, 1975; Prasad & Lapparent de Broin, 2002). This type of denticulation would result in striated marks of similar regularity. Irregularly spaced striations show variable striation widths and spacing, and if these variables change along the length of the mark they do so in a sporadic manner. Irregular marks could have

formed from any number of sources including damaged or worn apices or carinae, or sand or another granular substance at the point of contact between the tooth and bone.

Striated marks may display variable degrees of striation divergence along their length. 'Branched' marks possess striations that converge along the mark into a score. 'Sub-parallel' marks have striations that would coalesce if extended further, but do not actually converge along the length of the mark. 'Parallel' marks possess striations that are parallel to one another.

Morphometric Analysis:

V. komodoensis dental morphometrics were taken from the tooth teeth of nine dry skull museum specimens (Table 3.1). Only *in situ* teeth were considered. The dissecting microscope under which the teeth were photographed was not large enough to fit the skull on the stage when it was oriented in certain ways. Therefore, premaxillary and the mesial-most maxillary teeth could not be measured because the cranium needed to be positioned perpendicular to the stage.

The spacing between adjacent denticles is known as the "cella", and the point where they converge is the "diaphysis" (Figure 3.1). The width of a single denticle is defined here as the straight-line distance between its flanking diaphyses. Connected to each denticle and past the diaphyses on the tooth itself is a raised elongation, or "cauda" (described in tyrannosaurids by Abler, 1992:173). In between each cauda is a linear valley, or "interdenticular sulcus" (Smith, 2007:110), that connects to the diaphysis. Because these sulci are apparent beyond the actual denticles on the tooth itself, even the most stout/worn denticles can be identified.

Our standard measurement for tooth size is the Crown Base Length (**CBL**) (Smith et al., 2005). This is the distance between the mesial and distal-most points where the tooth meets the host bone. This is also known as 'fore-aft basal length' (Farlow et al., 1991; Sankey et al., 2002; Smith & Dodson, 2003), 'mesial-distal width' (Chandler, 1990), and 'maximum tooth width' (Holtz et al., 2000). I selected CBL out of the several measurements of tooth size available because it correlates well with most other tooth morphometrics. Consequently, as CBL increases, general tooth size increases linearly. It is also easily derived from photographs and has been most commonly used in the past to evaluate denticle measurements for Theropoda (Farlow et al., 1991; Holtz et al., 2000; Smith et al., 2005).

Digital photographs of teeth of all museum specimens were taken from the labial perspective, perpendicular to the long axis of the tooth. All denticles were visible from this perspective. Two photographic sets were taken of each tooth: a high-magnification view from a mounted camera on a dissecting microscope with no scale, and a wide-angle photograph with a scale bar. Landmarks were plotted on photographs with TpsDIG 2.10 (Rohlf, 2006) and morphometric values were derived from the Euclidian distances between those landmarks. Denticles were only visible in high-magnification photographs, and landmarks were placed at the diaphysis between all denticles along the mesial and distal carinae. The width of a single denticle is the distance taken from adjacent landmarks (in pixels). Gaps and breaks in the sequence of denticles were not included. This is an improvement over previous methods because only one denticle is measured by a straight line distance, as opposed to a single line representing the total width of all denticles within an arbitrarily selected section of the carina (as used by

Chandler [1990] and Smith et al. [2005]). Landmarks were also placed at the mesial and distal-most points where the tooth meets the host bone in both sets of photographs, consequently measuring the CBL. The CBL could be calculated in millimeters from the wide-angle photographs, and was used as a standard and compared to the CBL (in pixels) from the high magnification photographs. All distances including the width of the individual denticles were then converted from pixels to millimeters. The average width in millimeters of all denticles for a single carina on a tooth is defined as 'denticle width' (**DW**) for all regression analyses. Percent error was calculated through one repeat measurement on each of 20 teeth from one individual (AMNH 37911). The average percent error was low for all measurements; CBL= 4.01%, mesial DW= 2.15%, and distal DW= 3.12%.

Two measures of body size are used. Skull lengths (**SL**) were obtained for all specimens using landmarks plotted on digital photographs taken from the dorsal perspective. For the nine dry skull *V. komodoensis* specimens, SL is the distance from the rostral-most point on the premaxilla to the rostral-most point where the squamosal meets the quadrate along the mid-sagittal plane. SL was also approximated from the *V. komodoensis* live specimens involved in the controlled feeding trials that yielded the tooth marks. This was determined as the distance from the rostral-most point to the quadrate-area mid-sagittally, usually indicated by a change in scale size and topography. I feel that the SL values for the live specimens and the dry skull specimens are consistent, and both versions are plotted together. Body length (**BL**) is considered the total length of the animal from snout to tail. The zoo staff recorded BL routinely for live specimens, but this measure is not available for the dry skulls. Because head and body length correlate

isometrically in Varanidae (Thompson & Withers, 1997), BL was extrapolated for the dry skull specimens by inputting the measured SL into a best-fit linear function derived from SL versus BL for the live specimens (see Table 3.2 for regression information).

Similar data were acquired for theropod dinosaurs from published accounts. CBL and distal DW from 354 *in situ* teeth of known theropod taxa were taken from Farlow et al. (1991) and Smith et al. (2005). Mesial DW was found for over 80% of these teeth. Tooth orientations in Smith et al.'s photographs are very similar to ours. Farlow et al. used calipers to record all measurements, and our tests show that calipers record a similar CBL in *V. komodoensis* to those derived from photography. Both previous studies measure denticles via "serration density", or the number of denticles per unit distance. This was converted into the DW by dividing serration density by the unit distance used. I collected dental morphology data directly from only one specimen (*Ceratosaurus* USNM 4735), using methods identical to those used above for *V. komodoensis*. SL and BL data were taken from several sources (Table 3.1). Body size estimates are only available for 116 of these teeth among 12 individuals. Although SL is measured uniformly in all sources, BL values are frequently estimations resulting with varied values depending on the investigator. In these cases, I arbitrarily elected to use the maximum estimate for all taxa. Mass was not used in either group because there are no mass values for *V. komodoensis* skeletons, and there is a large amount of variability in estimated theropod masses in the literature.

Certain theropod families deviate from the general trend in denticle widths seen for all other theropod families (Farlow et al., 1991). Troodontidae and Therizinosauroidea possess exceptionally large denticles for their tooth size (Holtz et al.,

1998). Conversely, Spinosauridae has relatively small denticle widths (Charig and Milner, 1997). Although they figure prominently in paleobiological discussion, I exclude these groups from our regressions for the purposes of consistency. The remaining taxa are hereafter referred to as 'typical theropods'.

Four major regression groups are analyzed (Table 3.3). First, DW is plotted against CBL for all teeth available (similar to Farlow et al., 1991). Functions for each carina are compared *within* each taxonomic group to see if there are significant differences between carinae. Second, DW is plotted against SL for each tooth position for all *V. komodoensis*. These positional series are plotted together for each housing bone and carina and then are compared. This procedure is similar to the tooth size/body size regressions from Shimada (2004) and Shimada and Seigel (2005). This exercise determines if relative DW increases with body size regularly, independent of position. This regression analysis is not possible for typical theropods due to the limited number of teeth available as well as ambiguity in tooth position. Third, DW is plotted against SL and BL. Functions for each carina are compared *between* taxonomic groups. Last, the SW of the actualistically derived tooth marks is plotted versus the body size of the captive specimen that produced them. Regressions are produced for all marks, as well as the maximum SW for all marks produced during a single feeding trial. These regressions are compared to DW versus body size functions for all dry skeletal *V. komodoensis*.

Two different statistical paradigms, null hypothesis testing and information criteria, are applied to all groups of regressions using PROC MIXED in SAS 9.1. DW and SW are always response variables. Dependent variables are tooth or body sizes (CBL, SL, or BL). The natural log of these dependent variables is used in order to

display the functions linearly. Classes consist of carinae, tooth positions, taxonomic

groups, or SW versus DW (Table 3.3). An analysis of covariance (**ANCOVA**) compares

the slopes of the regressions. I predict that the null hypothesis, in which the slopes of the

trends are not significantly different as indicated by a high significance value ($>.05$), will

be supported. I also conduct a second order information criterion (**AIC_c**) to compare

models of a particular response variable against size, or against both size and class.

AIC_c is not a 'test', but selects the 'best' model to explain the information generated by

the data without overfitting.   It is a variant of Akaike's information criterion that

incorporates a bias correction term to account for smaller sample sizes when necessary.

A lower AIC_c score indicates a higher goodness of fit (Burnham and Anderson, 2002). I

compare AIC_c scores between two models; the response versus the dependent variable

alone, and the response versus the dependent variable *and* class. I predict that the best

model to explain the response variable will *not* include class. This is indicated by ΔAIC_c,

which is the lowest AIC_c score subtracted from score for this predicted best model. A

ΔAIC_c of zero would indicate that this is the best model, whereas the model is not

supported if this value is >2 (Table 3.3).

RESULTS

<u>Striated mark characters:</u>

Of the 1,024 tooth marks produced by *V. komodoensis* specimens sampled here, 54 have visible striations (Table 3.4; also see Appendix 1A). 52 of these marks have striations that could be measured. Striations are only found on certain types of marks. The majority of marks produced by *V. komodoensis* are scores (Chapter 2), and the vast majority of striated marks were scores as well (Table 3.4). Scores are linearly extended marks caused by dragging of the tooth apex along the surface of the bone after initial contact (Binford, 1981). Striated scores have a higher average width than unstriated scores (.83 mm versus .42 mm) but similar lengths (4.13 mm versus 3.45 mm). One furrow, a score-like mark that enters cancellous bone, also displayed striations. These striations are found on an area of the furrow that had not penetrated into the cancellous region. Seven examples of edge marks were striated. Edge marks, unique to ziphodont teeth, are created by distal carina contact with the edges of processes or elongate elements (Chapter 2). Pits and punctures occur, but these are not striated.

Most of the striated marks are regularly striated (Table 3.4). Out of these, there are over 3 times as many parallel striations as there are either sub-parallel or branched striations. Branched and sub-parallel marks are usually curved along their length giving them a tassel-like appearance (Figure 3.2). Irregular marks have a higher number of striations over a smaller distance on average.

<u>Tooth morphometrics:</u>

Distal DW was available for all 179 *V. komodoensis* teeth examined and mesial denticles were present and measured for 152 of these teeth (Appendix 1B). The distal carina was almost entirely denticulated, with only the basal- and apical-most areas being

bare (Figure 3.1). This carina is usually smooth and evenly curved, although a small protrusion may occur at the basal-most portion of the denticulated area. Mesial denticles occur along about half the carina length, usually basal to the point of maximum curvature and continuing up to the apex.

In *V. komodoensis*, the distal carina has an average of over 34 denticles per tooth, whereas the mesial carina has an average of about 16. The mesial denticles typically appear more stout and flattened than the distal (Figure 3.1). In several instances only the interdenticular sulci are visible mesially; where as distal denticles are almost always prominent. Although I rarely sampled premaxillary teeth, I never observed mesial denticles on the first to third premaxillary teeth. Because these were universally absent and lacking remnants of denticular character, I assume that denticles were never present as opposed to being eliminated by wear.

Most *V. komodoensis* DW fall into a limited range between .15 and .25 mm (Figure 3.3). The average mesial denticle width is .20 mm (SD= .05) and distal denticles are .22 mm (SD= .04). Individual denticle widths increase in the apical direction for both mesial and distal carinae, with the range usually within .1 mm. For typical theropods, the average mesial denticle width (.41 mm, SD= .15) is virtually identical to the distal (.40 mm, SD= .14). Tyrannosaurids have the largest denticles at around .6 mm. Small coelurosaurids and dromaeosaurids have the smallest at .11 mm or more.

In *V. komodoensis* CBL variance indicates oscillating "size heterodonty" (Shimada, 2002:53), or a change in scale. In *V. komodoensis*, tooth size increases as one moves distally in position along the tooth row with the largest teeth being found approximately midway along both the upper (ninth maxillary) and lower tooth row

(seventh dentary). Past this point there is a gradual decrease in size distally (Figure 3.1).

For the upper tooth row, this results in a convex appearance from the labial view

(Auffenberg, 1981). Conversely, the dentary is concave, and the largest teeth are at the

bottom of the arc resulting in all apices of the lower tooth row achieving a similar height

relative to one another. In reality, *V. komodoensis* dentition shows "shape-size

heterodonty", because the degree of curvature increases along the tooth row (see also

Mertens, 1942; Rieppel, 1979). A measurement of shape or its influence on function is

beyond the scope of this study. It should be noted that this arrangement of the dental

arcade is evident in many theropods (Molnar & Farlow, 1990).

Regression Analysis:

DW correlates well with CBL and is best represented by logarithmic trends in

both *V. komodoensis* and typical theropods (Table 3.2 and Figure 3.3). The correlation is

stronger for the distal than the mesial carinae. ANCOVA indicates that DW does not

differ significantly in slope between mesial and distal carinae in *V. komodoensis*, but it

does in typical theropods (Table 3.3). AIC_c indicates that carinae should be considered

when modeling DW in both groups. Dissimilar to *V. komodoensis,* typical theropods

have slopes that cross one another with DW values that generally overlap.

Denticle width increases regularly with body size regardless of tooth position in

V. komodoensis. All positions produce linear regressions with slopes that are not

significantly different from one another for either the maxillary and dentary tooth rows

for either carina (Table 3.3 and Figure 3.4). Although slopes are similar, tooth positions

that tend to possess larger teeth have larger y-intercepts. These positional size

differences did not impact the variance enough to be acknowledged by AIC_c. It should

be noted that sample size decreases as one moves rostrally along the tooth row, and r^2

values tend to decrease as the sample size is reduced (see METHODS).

DW correlates well with both body size characters for both taxonomic groups

(Table 3.2). *V. komodoensis* cluster along the curves established by typical theropods,

and both taxonomic groups display highly similar trends for each body size character

(Table 3.3 and Figure 3.5). Taxon is an unnecessary model component. These trends

are strikingly similar concerning SL. BL is somewhat similar between the two taxonomic

classes but not as similar as SL, as best exemplified by the mesial carina displaying a

significance value right at .05. *Acrocanthosaurus* denticle widths are noticeably smaller

than expected from both tooth and body sizes for both carinae (noted previously by

Currie and Carpenter, 2000). *Deinonychus* has noticeably smaller mesial DW (as

reported in Chandler [1990] and Farlow et al. [1991]), but its distal DW falls along the

typical theropod trend.

The majority of SW values fall within the range of DW for individuals of similar

body sizes. A noticeable portion of SW values fall below the lower limit of DW values

for similar sized individuals, but rarely do any values exceed the maximum DW values

recorded. Maximum SW reflects increasing slopes that are not significantly different

from DW slopes from either carina (Table 3.3 and Figure 3.6). Conversely, SW slopes

are significantly different from DW when all marks are considered. Carina did not

influence this. AIC_c did not consider class an important component in any of these

comparisons. All SW regressions have relatively low r^2 values (Table 3.2). It should be

noted that the average SL of the live individuals is smaller than the average SL of dry

skulls. Regardless, maximum SW values not only correlate well with the smaller dry

skull SL values, but also correlate with the *function* produced by all dry skull SL values.

This function therefore predicts that the SW values would directly correlate with DW if

the both sets of SL were the equal.

DISCUSSION

Production of denticle drags in *Varanus komodoensis:*

The dragging of *V. komodoensis* denticles across bone surfaces most commonly produces striated marks, because the vast majority of striated marks are regularly spaced. These striations represent the regular spacing of denticles. Although striated tooth marks could be formed by several sources, the abundance of regularly spaced marks indicates that denticles are the dominant mechanism for striated mark production in ziphodont carnivores.

We argue that striated marks result most frequently from contact between the bone surface and the mesial carina. In order for striation production to occur this way, two conditions must be met simultaneously (Figure 3.7). First, the tooth must be positioned so the curved mesial carina is in a plane parallel to the bone surface. Second, the direction of tooth movement must be perpendicular to the tooth's lateral surfaces, as opposed to in the direction of the distal carina. This positions the denticles so traces left by each denticle are next to one another, instead of overlapping and forming a score. If these two conditions are met, the denticles may be dragged across the surface producing striations. The dragging of this broad surface as opposed to the relatively narrow apex accounts for the relatively large width of striated scores.

V. komodoensis defleshing facilitates this perpendicular reorientation of the carina. When feeding, *V. komodoensis* orients the rostrum relatively perpendicular to the mid-sagittal plane of its own body (Figure 3.8.). In order to modify flesh, the rostrum is then drawn medial in reference to this plane, as well as caudal to its original position. This results in an arcing motion termed the 'medial-caudal arc', which reorients the

rostrum back into a position parallel to the midline of the remainder of the body (Chapter 2). This rostral reorientation specifically produces the striations. At the beginning of a defleshing stroke, rostral movement is mostly medial and gradually transitions to almost strictly caudal as the stroke continues. A given tooth will therefore move perpendicular to its lateral surface at the start of a stroke (Figure 3.8). Any teeth with mesial carinae contacting bone at that point would produce striations. As the stroke continues the motion of the rostrum becomes mostly caudal, and tooth movement is transitioned distally. This brings the carina parallel to the direction of movement. If contact with bone surfaces is made throughout, the striations will converge into a score.

The degree of striation divergence is directly influenced by the timing of bone-tooth contact in relation to the angle of the mesial carina (Figure 3.8). As rostral rotation transitions the direction of movement of the rostrum from medial to caudal, contact between the carina and bone may commence at any point. If contact is consistent during this transition, the tooth mark will originate in striations and converge into a score, appearing branched. Sub-parallel striations result from contact beginning while the carina is being rotated parallel to the direction of movement, but ceasing before it reaches that point. In both situations, the carina is gradually repositioned less perpendicular to the direction of movement throughout mark production. Parallel striations result from contact when the carina's orientation is static relative to the direction of tooth movement, early on in the defleshing stroke.

Due to the concave shape and positioning of the distal carina, it is less likely that the distal denticles regularly drag across bone surfaces. *V. komodoensis* teeth curve distally, so the entire length of the distal carina is parallel and adjacent to the tooth

distally positioned to it (Figure 3.1). That tooth would consequently obstruct the distal

carina from making contact with bone surfaces. Only if a bone element were to make

contact with the distal-most tooth, or if a smaller element gets caught in the space

between adjacent teeth or where a tooth has been shed, would the distal carina of any

given tooth make contact. Striated edge marks are almost definitely produced by these

methods. Striated edge marks would result from the distal carina sliding as it contacts the

bone surface during defleshing, or resulting from subsequent behaviors intended to

dislodge teeth from elements (Chapter 2). Striated edge marks are very rare, however,

and I suggest that denticle drag production by distal carinae in uncommon in ziphodont

reptiles. Conversely, the positioning of the mesial carina allows the denticles

unobstructed access to bone surface because curvature reorients the mesial denticles so

they are not "shadowed" by an adjacent tooth. The assertion that the mesial carina more

frequently contacted bone surfaces is further supported by the fact that mesial denticles

are stout, which could potentially be a consequence of heavy wear. Further evidence may

be derived by a comparison of micro-wear on the carinae in future studies.

Denticles as a predictor of body size across ziphodont taxa:

In all groups of regressions with the exception of those comparing distal and

mesial carinae, our predictions are supported. ANCOVA indicates no significant

difference between the slopes projected based on position, taxon, or maximum SW versus

DW, and AIC_c signifies that none of these classes are necessary to properly model DW.

Denticle size appears to be primarily influenced by tooth size in both taxonomic

groups, as indicated by the strong correlation between CBL and DW per tooth regardless

of individual or species. The significant r^2 and p values support this correlation in *V.*

komodoensis, which has previously been attributed to typical theropods (sensu Farlow et al., 1991 and Smith et al., 2005). Farlow et al. stated two linear trends represent the data best: a trend for 'large' and 'small' theropod taxa. I feel that a single logarithmic model represents the data best based on high r^2 values, while still maintaining the negative allometry that Farlow et al. witnessed.

V. komodoensis possesses mesial and distal carinae with DW functions noticeably different from one another, as indicated by different y-intercepts, means, and resultant high ΔAIC_c values (Figure 3.3). Nevertheless, the slopes of these two functions are not significantly different. Conversely, a slope disparity does occur between typical theropod carinae, regardless of the similarity in mean value. This most likely results from smaller theropod teeth (particularly *Richardoestesis, Liliensternus*, *Masiakasaurus*, *Velociraptor*, and *Deinonychus*) having smaller mesial denticles than distal, whereas many large theropods display the opposite condition. Smaller ziphodont carnivores may be predisposed to having larger distal DW. Chandler (1990) explains this as a developmental consequence of high distal curvature, which is apparent among smaller theropods. That *V. komodoensis* possesses a larger relative distal DW and highly curved teeth lends support to this as well. The transition from smaller to larger relative mesial DW is an example of a character that may only be evident across a vast range of body sizes. Because the *V. komodoensis* trend is mono-specific and only represents a limited body size (and a small body size in relation to theropods), changes that are only visible on a large scale may be obscured. Allometric changes not evident on a smaller scale, such as this change in relative denticle size, would therefore only be observed in typical theropods.

Tooth position does not significantly influence DW relative to SL. The similar slopes for all positions indicate that relative DW increases in a predictable and uniform manner throughout ontogeny. This occurs on both carinae at all tooth positions. Because DW and CBL scale allometrically, smaller DW values in certain tooth positions are merely the result of the relatively smaller teeth that happen to be in those positions due to the size-heterodonty.

DW is an accurate predictor of body size based on a negative allometry/logarithmic model in both taxonomic groups. Although tooth size variability exists within individuals, size heterodonty is such that the resultant range of DW is limited and correlates well with body size. This results in the rate of growth for denticle characters relative to body size being consistent and predictable for *V. komodoensis* and typical theropods independently.

In addition to these separate relationships, there is striking similarity in slope *between* these two groups. Therefore, the allometric relationship of DW to body size persists independent of the large taxonomic distance between these two ziphodont groups. Although the *V. komodoensis* trends are only represented by a cluster of points at the lower extreme, the trend predicts that a specimen with the same body size as a large theropod would possess a very similar DW. The higher degree of similarity in SL as opposed to BL may be because many of the BL values are extrapolations as opposed to direct measurements, therefore reducing the accuracy of the trends.

For most ziphodont taxa DW must increase at a similar rate as each shed tooth is replaced (sensu Molnar, 1978). As stated above, DW has a negative allometric relationship to tooth size. Since reptiles increase tooth size with each shed as body size

increases, DW increases with body size. But DW must also become smaller relative to

tooth size with each subsequent shedding. Consequently the rate of DW increase slows

as an individual increases in body size, displaying the negatively allometric relationship

seen here. Replacement rates in both modern and extinct archosaurs slow with tooth size

and presumably age (Erickson, 1996a, 1996b), whereas several species of lizards show

no slowing of replacement rates (Edmund, 1969). I suggest that replacement rate should

not affect denticle sizes relative to either tooth or body size.

Striations as indicators of denticle width:

The majority of SW values fall well within the range of DW for similar sized *V.

komodoensis* individuals. This shows that DW is transcribed well enough in the majority

of instances to produce SW values within the consumer's DW variance.

Not all marks are loyal reproductions of consumer DW. Several SW values are

noticeably lower than the range of DW for similar sized *V. komodoensis* individuals.

These low values may be explained by tooth orientation during bone-tooth contact. SW

is directly correlated to how perpendicular the carina is to the direction of tooth

movement (Figure 3.9). In *V. komodoensis*, the accurate transcription of DW to SW

would occur in cases where bone-tooth contact is initiated with the carina fully

perpendicular to the direction of the defleshing stroke. If the carina made contact with

the bone surface and moved across its surface perpendicular to the direction of movement

every time, all SW values would accurately represent the actor's DW. Jacobsen (1995,

2001) stated that in theropods this would be rare, and that theropod teeth would more

often approach bone at an oblique angle. This would cause SW to be smaller than the

denticles that produced them. If the carina is positioned less than perpendicular to the

bone surface during a defleshing stroke in *V. komodoensis*, the resultant SW will under-represent the consumer's DW.

The fact that striations increase in divergence along the length of the tooth mark in both branching and sub-parallel striated marks indicates that the denticles do leave regular striations when the carina is not perpendicular to the direction of movement (Figure 3.9). This also indicates that circumstances may occur where mark production may begin and/or end when the carina is less than perpendicular. Therefore, many of the marks produced do have SW values underestimating the DW of the tooth that produced them. I assert that the marks with SW values significantly lower than the DW range of similar sized individuals were produced this way.

Based on this logic SW may underestimate, but cannot overestimate, the DW of the tooth that made the mark. Maximum SW is therefore the most reliable method for determining DW. This is supported by a general increase in SW with body size increase; signified by the similar slope to DW. This slope similarity does not occur when all marks are considered. Therefore, total or average SW values are less reliable indicators of DW. These values would most likely be influenced by a number of marks that underestimate the actor's DW, such as many of the marks collected here.

Maximum SW also exhibits "scatter" indicated by low r^2 values. This may be explained by the relative size of the denticles making contact. Maximum SW values coming very close to the maximum DW for similar sized individuals in some cases may be the result of relatively larger denticles contacting the bone surface. The distal carina has larger denticles, and although I argue that distal carina contact was relatively rare, it would only need to occur once per feeding to be acknowledged as the maximum SW

value. Another mechanism for higher values is a bias towards contact with larger teeth. The largest teeth on the upper tooth row extend furthest away from the maxilla, perhaps giving them the highest likelihood of contacting bone. These large teeth would have large denticles, resulting in high SW. Maximum SW values that are noticeably low relative to DW for individuals of similar size may simply be the result of carinae that never were positioned perpendicular to tooth movement during the feeding bout. Another possibility is that in these instances only smaller teeth (possessing smaller denticles) happen to have made contact.

Conclusion: predicting body size from striated tooth marks:

Under ideal circumstances the body size of a ziphodont consumer can be estimated solely by the evaluation of a striated tooth mark. This is facilitated by the predictable negative allometry in DW across the majority of ziphodont taxa and the reliable transcription of DW to SW on bone surfaces.

Regardless of the high r^2, most SW values, and all maximum SW values fall within DW ranges for similar sized individuals. Because the SW of denticle drags can underestimate, but never overestimate, the DW of the tooth that produced it, the maximum SW of the regularly spaced marks on a particular carcass is the most reliable indicator of DW of ziphodont consumers. The more striated marks found on a particular carcass, the more likely that the mark with the maximum SW accurately represents a DW within the range possessed by the consumer. Irregularly spaced striations must not be used because they most likely do not result from denticle contact alone.

The DW values determined from denticle drags can be cross referenced with the body size functions similar to the ones established here to determine a range of possible

SL or BL. DW correlates to body size allometrically in ziphodont reptiles regardless of

taxonomic distance with few exceptions. Because of the strikingly high degree of

consistency in these relationships, reliable inferences can be made regarding body size

traits independently of heterodonty or taxonomy. This method is especially useful for

discriminating among smaller theropods. However, the predictive power of DW

decreases with increasing body size. If one takes into account that the range of DW for

all teeth possessed by a single individual increases in variability with larger taxa, our

method becomes somewhat ineffective if the BL of the consumer is higher than 10 m,

corresponding to a DW of about .4-.6 mm. Chandler (1990) supported this through the

observation that *Allosaurus* and *Tyrannosaurus* denticle widths are not significantly

different even though their tooth and body size characters differ dramatically. Therefore,

knowledge of the ziphodont taxa living during the time of accumulation will help to

narrow down the possible consumers.

Although the statistical approaches used here indicate pronounced differences

between the functions produced by mesial and distal carinae, there is still a large amount

of overlap between the ranges of their actual DW values. Because of this overlap, Farlow

et al. (1991) stated that carinae do not need to be considered separately in most instances.

I assert that this overlap is significant enough that body size can be derived accurately by

considering either carina in the majority of cases.

Farlow et al. (1991:192) noted "remarkable evolutionary convergence" between

ziphodont representatives that were taxonomically distant, and the fact that varanids and

typical theropods fall along very similar trends further supports this. With the exception

of tooth attachment (pleurodont versus thecodont), there are striking similarities in both

denticle properties and size-shape heterodonty exhibited between these groups (examples in Madsen, 1976; Russell, 1970; Molnar and Farlow, 1990). In fact, past excavators have confused the isolated tooth teeth of ziphodont crocodilians for varanid teeth (Molnar 2004). Although not tested, this similarity between *V. komodoensis* and typical theropods may be best explained by similarities in dental function, feeding behavior, and fundamental niche structure. This may also explain the deviation seen in troodontids and spinosaurids, in that these taxa are believed to have maintained at least partially herbivorous and piscivorous niches respectively (Holtz, 1998; Holtz et al., 2000; Rayfield et al., 2007). These 'atypical' theropods deviate from the typical theropod trends observed here, and this dissimilarity could bring about potential confusion when identifying consumers based on SW. Fortunately, it is likely that these specialized theropod clades modified the bone surfaces of typical theropod prey items less frequently due to their other avenues of nutrient acquisition.

I have only evaluated controlled assemblages accumulated by a single consumer species. Carcass consumption by a single species was most likely unusual in the Mesozoic as it is for mammals in natural setting today (e.g., Pobiner and Blumenschine, 2003). Sorting out differences between tooth marks produced by two or more ziphodont actors on the same carcass may be uniquely challenging. Because the majority of terrestrial vertebrate predators for most of the Mesozoic were ziphodont archosaurs, the presence of denticle drags alone does not significantly narrow the list of potential consumers. A large range of SW also does not necessarily indicate multiple actors because small SW can result from larger DW when the angle of carina movement is acute. The maximum SW may enable researchers to determine the body size of the

largest consumer, but the range of SW alone will not allow for the identification of or discrimination between multiple ziphodont consumers. More work must be done to determine what evidence other than SW is diagnostic of the specific carnivores. Other lines of taphonomic evidence, such as breakage patterns, skeletal part profiles, and electron microscopy have been applied to other extinct systems to distinguish multiple actors (e.g., Pobiner and Blumenschine, 2003; Drumheller, 2007). Similar investigations should be conducted in the future to better distinguish potential Mesozoic assemblage accumulators.

Table 3.1: General measurements for ziphodont specimens used here in ascending order by skull length (SL). N represents the number of teeth analyzed per specimen. Tooth base length (CBL) and denticle width (mesial=m. DW and distal=d. DW) are averages for all teeth from a particular specimen regardless of location, and are measured in millimeters. Body size measurements are in meters. Data taken directly from published sources is represented by a superscripted symbol (Smith et al., 2005*; Therrien and Henderson, 2007[1]; Paul, 1988[2]; Seebacher, 2003[3]; Brochu, 2003[4]; Currie and Carpenter, 2000[5]).

Genus	Museum	#	SL	BL	N	CBL	m. DW	d. DW
Varanus	AMNH	37908	0.15	1.76	28	3.15	0.16	0.18
Varanus	FMNH	22200	0.18	2.16	22	4.20	0.16	0.21
Varanus	AMNH	37910	0.18	2.25	14	4.30	0.18	0.21
Veloceraptor	AMNH	6515	0.19[1]	2.14[1]	7	3.55	0.15*	0.17*
Varanus	AMNH	37912	0.21	2.63	21	5.58	0.22	0.24
Varanus	AMNH	74606	0.21	2.67	25	5.03	0.21	0.22
Varanus	AMNH	37913	0.21	2.68	12	5.34	0.19	0.22
Varanus	AMNH	109498	0.21	2.70	20	4.93	0.21	0.23
Varanus	AMNH	37911	0.22	2.77	21	5.76	0.23	0.24
Dromaeosaurus	AMNH	5356	0.23[2]	2.61[1]	11	6.41	0.30*	0.26*
Varanus	AMNH	37909	0.24	3.09	16	6.19	0.22	0.24
Deinonychus	YPM	5232	0.33[1]	3.43[1]	11	6.47	0.18*	0.27*
Dilophosaurus	UCMP	37302	0.52[2]	6.03[2]	4	17.28	-	0.35*
Ceratosaurus	USNM	4735	0.63[2]	5.90[1]	4	22.35	0.40	0.43

Genus	Museum	#	SL	BL	N	CBL	m. DW	d. DW
Allosaurus	YPM	1930	0.68[1]	7.40[2]	3	12.50	0.43*	0.42*
Acrocanthosaurus	NCSM	14345	1.23[1]	11.50	26	28.02	0.34*	0.34*
Tyrannosaurus	CM	9380	1.36[2]	12.00[3]	12	36.95	0.51*	0.47*
Tyrannosaurus	AMNH	5027	1.36[1]	11.49[1]	10	39.42	0.55*	0.54*
Tyrannosaurus	FMNH	PR2081	1.39[1]	12.00	17	35.32	0.59*	0.51*
Carcharodontosaurus	SGM	Din 1	1.60[1]	13.28[1]	6	41.96	0.54*	0.49*
Tyrannosaurus	UCMP	118742	1.75[2]	13.60[2]	5	38.75	0.56*	0.54*

Table 3.2: Selected values of all regression evaluated. Data was taken from museum specimens (an asterisk indicates values were taken from live *Varanus komodoensis*). (Skull length=SL; body length=BL; tooth base length=CBL; mesial denticle width=m. DW; distal denticle width=d. DW; striation width= SW; maximum striation width=max SW)

Taxon	Response	Dependent	N	M	B	r2	p
*Varanus**	SL*	BL*	12	7.09	2.20	0.68	<0.01
Varanus	m. DW	CBL	152	0.11	0.15	0.43	<0.01
Varanus	d. DW	CBL	179	0.10	0.18	0.60	<0.01
Theropoda	m. DW	CBL	284	0.16	-0.06	0.77	<0.01
Theropoda	d. DW	CBL	354	0.13	0.03	0.73	<0.01
Varanus	m. DW	SL	152	0.16	0.45	0.56	<0.01
Varanus	d. DW	SL	179	0.12	0.42	0.47	<0.01
Theropoda	m. DW	SL	90	0.17	0.46	0.70	<0.01
Theropoda	d. DW	SL	116	0.13	0.42	0.60	<0.01
Varanus	m. DW	BL	152	0.14	0.08	0.56	<0.01
Varanus	d. DW	BL	179	0.11	0.12	0.47	<0.01
Theropoda	m. DW	BL	90	0.20	0.03	0.69	<0.01
Theropoda	d. DW	BL	116	0.15	0.10	0.58	<0.01
Varanus	max SW	SL	8	0.11	0.40	0.11	0.41
Varanus	max SW	BL	8	0.15	0.10	0.32	0.14
Varanus	SW	SL	45	0.07	0.28	0.03	0.28
Varanus	SW	BL	45	0.07	0.11	0.05	0.15

Table 3.3: Analysis of covariance (ANCOVA) and second order information criterion (AIC$_c$) values for all groups of regressions. ΔAIC$_c$ values are AIC$_c$ values for the model considering the response and dependant variables minus the lowest AIC$_c$ value determined. (Akaike weights were not necessary because AIC$_c$ values were never within 2 units between models. Skull length=SL; body length=BL; tooth base length=CBL; mesial=m.; distal=d.; striation width= SW; maximum striation width=max SW)

Response	Dep.	Class	Levels	AIC$_c$	ΔAIC$_c$	ANCOVA: F	ANCOVA: P
Theropoda DW	CBL	m. vs. d. carinae	2	-1517.20	2.70	19.33	<0.01
Varanus DW	CBL	m. vs. d. carinae	2	-1556.90	61.60	2.34	0.13
Varanus d. DW	SL	Dentary tooth position 1-13	13	-334.40	0.00	1.45	0.19
Varanus m. DW	SL	Dentary tooth position 1-13	13	-389.90	0.00	1.07	0.40
Varanus d. DW	SL	Maxillary tooth position 4-13	10	-416.90	0.00	1.06	0.40
Varanus m. DW	SL	Maxillary tooth position 4-13	10	-490.00	0.00	0.47	0.88
d. DW	SL	Theropoda vs. *Varanus*	2	-894.20	0.00	0.04	0.84
m. DW	SL	Theropoda vs. *Varanus*	2	-699.10	0.00	0.17	0.68
d. DW	BL	Theropoda vs. *Varanus*	2	-874.40	0.00	2.45	0.12
m. DW	BL	Theropoda vs. *Varanus*	2	-688.30	0.00	4.02	0.05
d. DW/SW	SL	DW vs. max SW	2	-792.50	0.00	0.04	0.85
m. DW/SW	SL	DW vs. max SW	2	-648.10	0.00	0.43	0.51
d. DW/SW	BL	DW vs. max SW	2	-792.50	0.00	0.65	0.42
m. DW/SW	BL	DW vs. max SW	2	-648.10	0.00	0.10	0.75
d. DW/SW	SL	DW vs. all SW	2	-898.80	0.00	2.11	0.15
m. DW/SW	SL	DW vs. all SW	2	-760.90	0.00	4.27	0.03
d. DW/SW	BL	DW vs. all SW	2	-898.80	0.00	1.39	0.24
m. DW/SW	BL	DW vs. all SW	2	-760.90	0.00	3.87	0.05

Table 3.4: Data on *Varanus komodoensis* striated tooth marks. 'A.' represents the number of tooth marks for all categories. The left margin indicates what type of mark is represented. The top margin indicates the details about the striations. 'B.' represents simple statistics of striation characteristics. 'SW' represents the width of striations in millimeters. 'S#' represents the number of striations per mark. 'Irregular' and 'regular' indicate the regularity in spacing between striations.

A.

	striated	unstriated	regular	irregular	parallel	sub-parallel	branched
score	46	801	39	6	27	9	9
edge	7	63	5	1	5	1	0
furrow	1	6	1	0	1	0	0
all	54	1024	45	7	33	10	9

B.

		mean	median	standard deviation	range
SW	**irregular**	0.10	0.08	0.07	0.21
	regular	0.16	0.17	0.04	0.19
	all	0.15	0.16	0.05	0.21
S#	**irregular**	5.71	6.00	3.30	8.00
	regular	3.24	3.00	1.49	6.00
	all	3.58	3.00	2.02	8.00

Figure 3.1. A) View of *Varanus komodoensis* (FMNH 22200) premaxillary and maxillary dentition. Notice the convex appearance of the tooth row margin. Note that the quadrate is missing in this specimen (Scale= 5cm). B) Left tenth dentary tooth (AMNH 37912) from the lateral perspective, with enlargements of both the mesial (bottom/right) and distal (left) carinae. Notice the difference in the height of the denticles. Morphological characters listed are: 1) CBL, 2) diaphysis, 3) cella, and 4) interdenticular sulcus. The CBL is 6.17 mm.
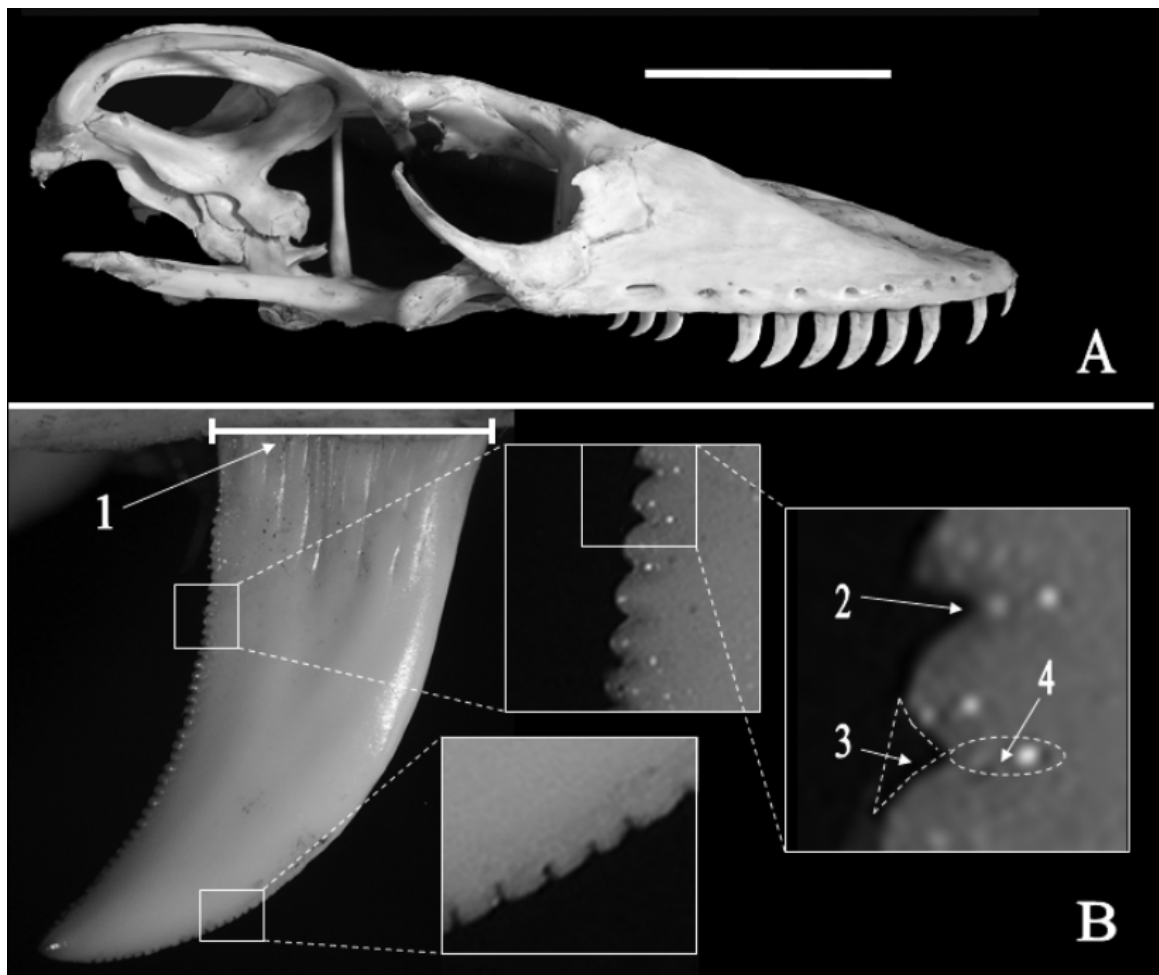
Figure 3.2: Examples of striated tooth marks. A-C represent marks with parallel striations. Marks D-E have sub-parallel striations. Marks F-H are branching. D is a striated edge mark, but all others are scores. F was taken from the bone surface, where as all other photographs are of molds. The contrast was increased in these photographs for the purposes of visibility. (Scale = .5 mm)
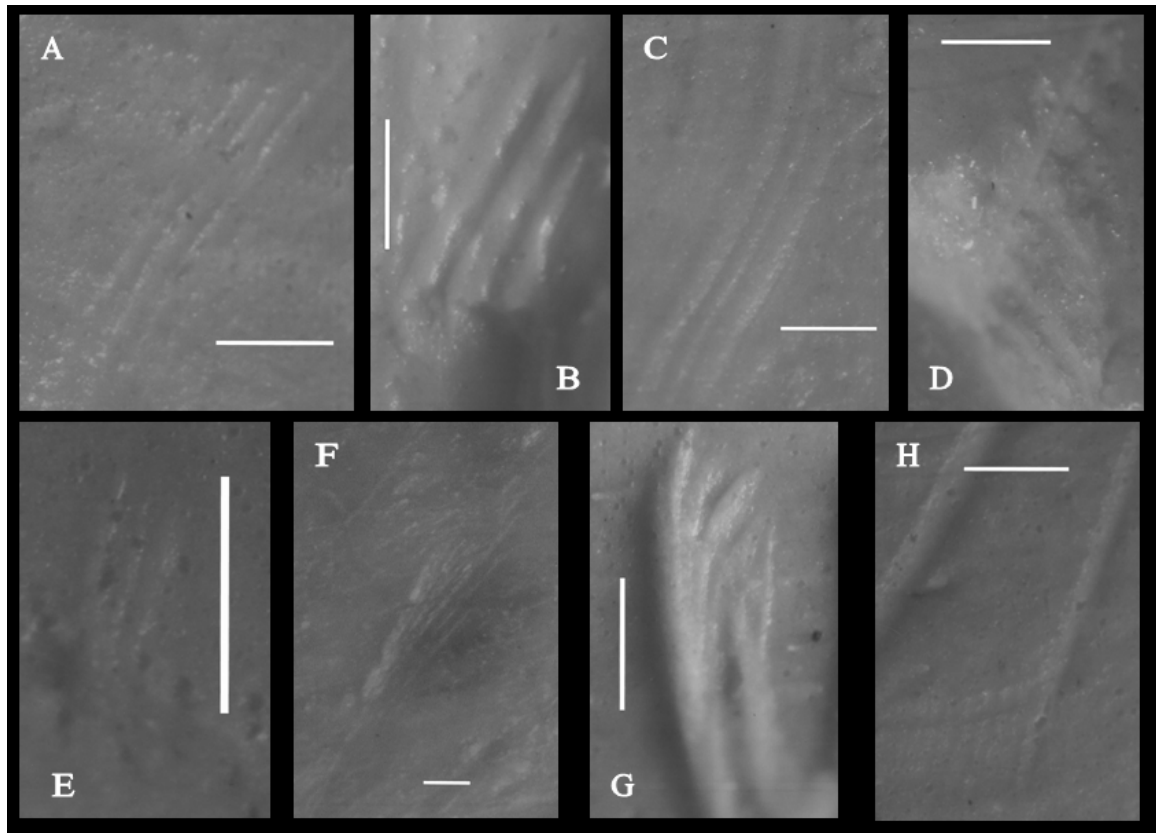
Figure 3.3: Denticle width (DW) versus tooth size in *Varanus komodoensis* (A.) and typical Theropoda (B.). Troodontidae and Spinosauridae (circled) are plotted but not included in the theropod trend. See table 1 for regression information.
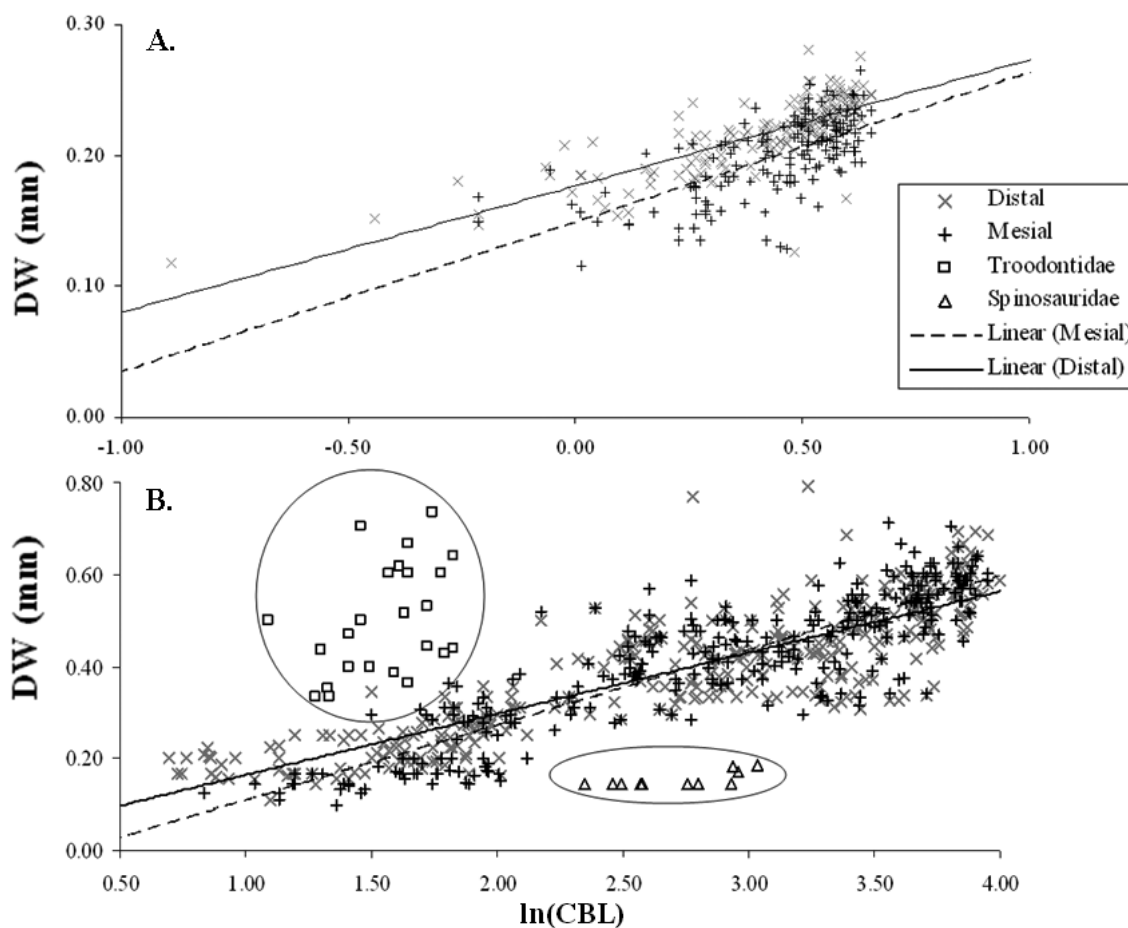
Figure 3.4: Denticle width (DW) for both the mesial and distal carinae versus skull length (SL) for both maxillary and dentary teeth in *V. komodoensis*. Numbers represent each tooth position along the dental arcade, with a larger number symbolizing a more distal position.
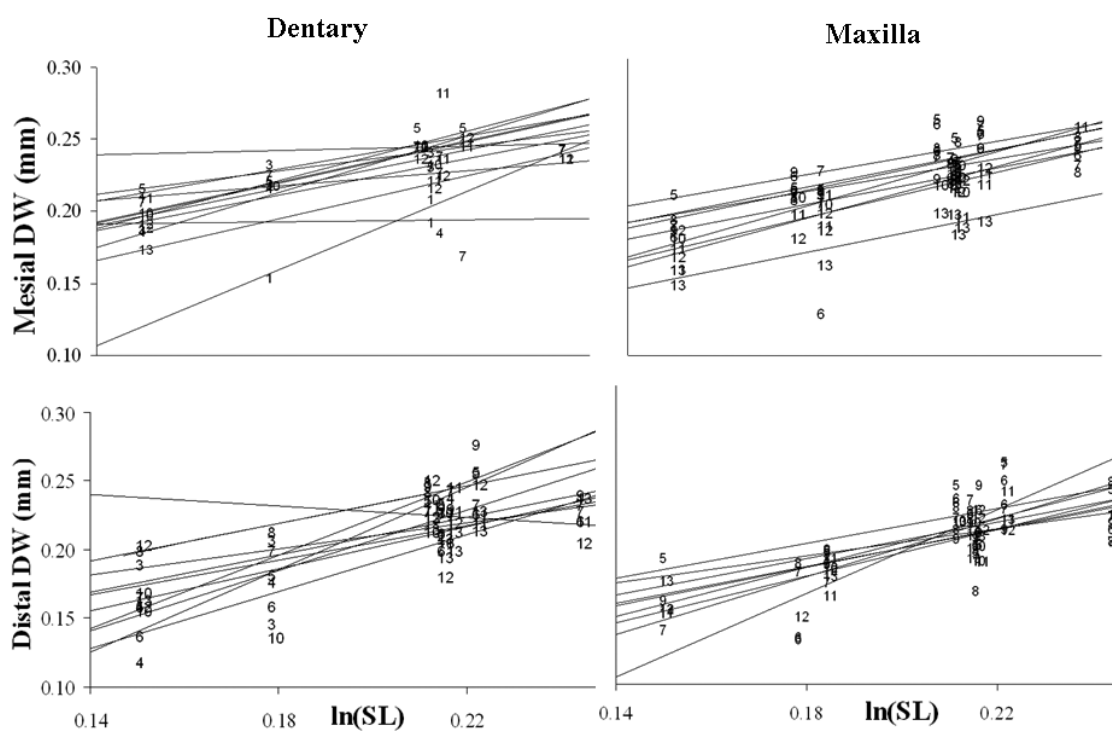
Figure 3.5: DW versus body size (skull length=SL, and body length=BL) comparing typical theropods to *Varanus komodoensis*. See table 1 for regression information.
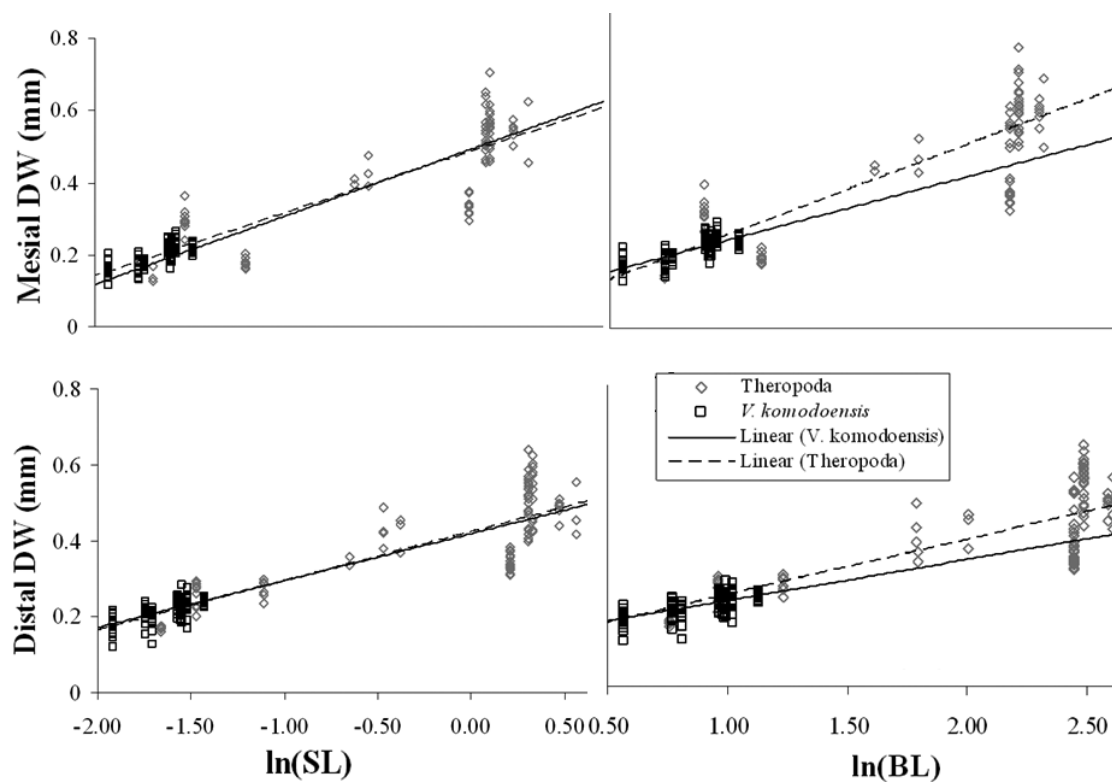
Figure 3.6: Striation width (SW) per specimen versus body size (skull length=SL, and body length=BL) for live *Varanus komodoensis* specimens plotted with denticle width (DW) versus body size for each carina. See table 1 for regression information.
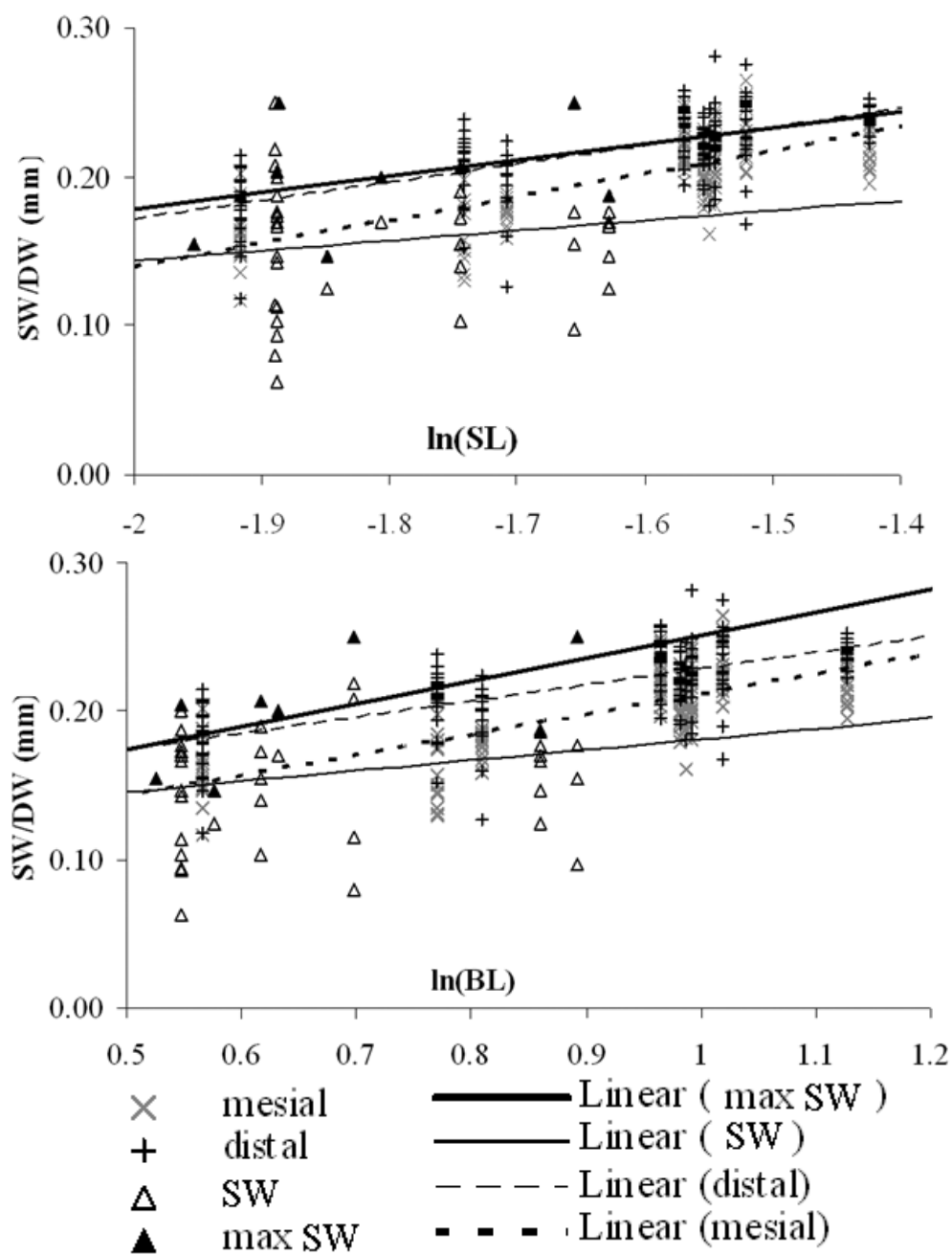
Figure 3.7: Diagrammatical representation of striated score production. The thick line represents the cortical bone surface. A.) Typical score production results from apical contact. B.) The tooth apex is reoriented, transitioning contact to the mesial carina. C.) Medial motion of the rostrum towards the midline of the body changes the direction of movement perpendicular to the mesial carina.
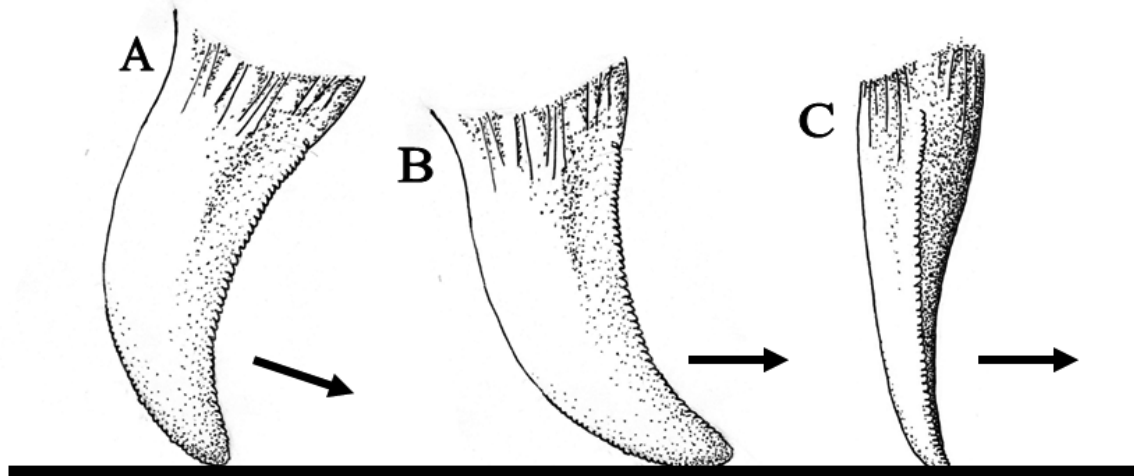
Figure 3.8: A.) Diagrammatical representation of a single 'medial-caudal arc' defleshing stroke, reproduced from frames from feeding footage. Each rostrum layers in chronological order, with the final rostrum at the surface. Notice the rostrum is progressively reoriented towards the midline of the body as well as caudal. B.) Diagrammatical representation of denticles dragging along a bone surface. As rostral motion becomes mostly caudal, the striations produced by each denticle converge to form a score.
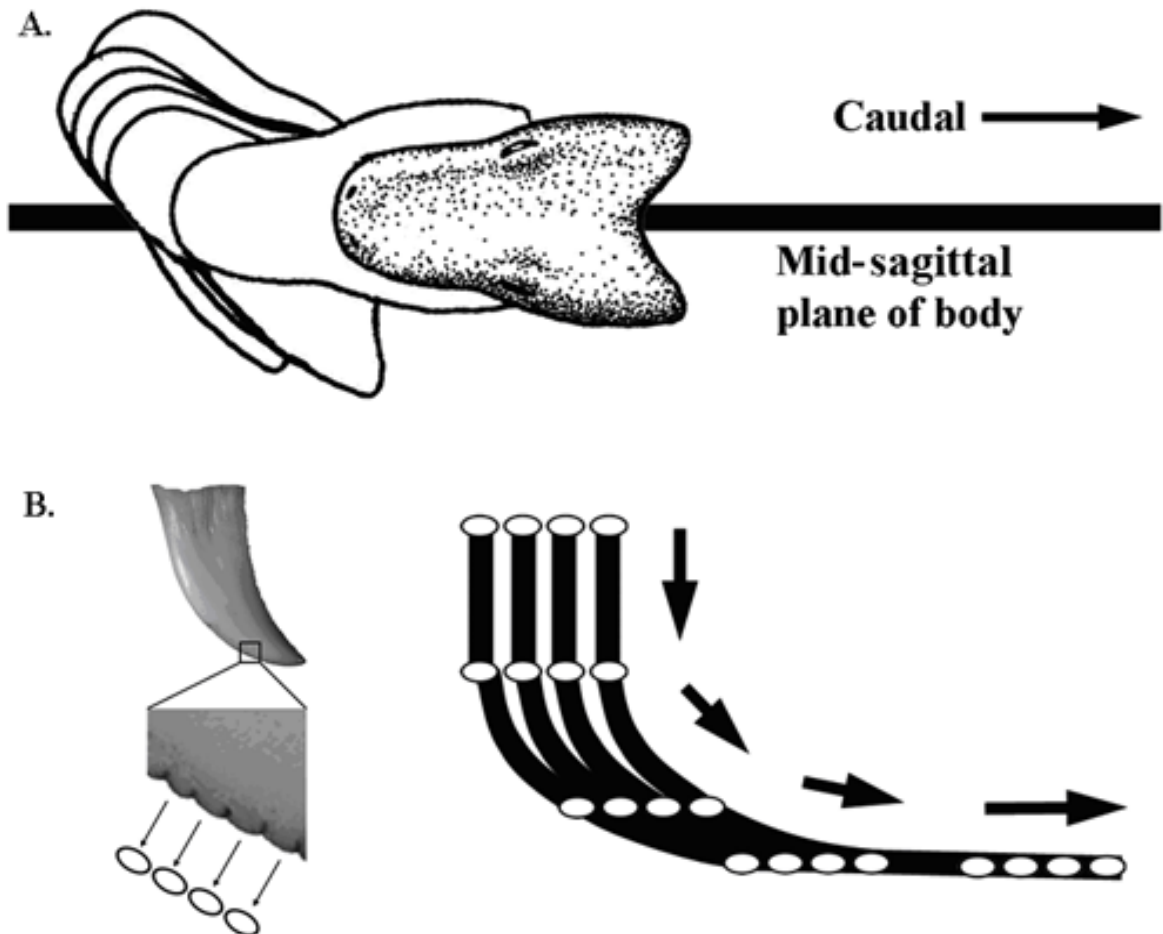
Figure 3.9: Part A. displays a diagrammatical representation of mesial denticles. If this denticulated carina moves perpendicular to itself along a bone surface (B.), the width of the denticles (DW) is accurately transcribed in the tooth mark. If the carina is less than perpendicular to the direction of movement (C.), striation width (SW) will under-represent DW.
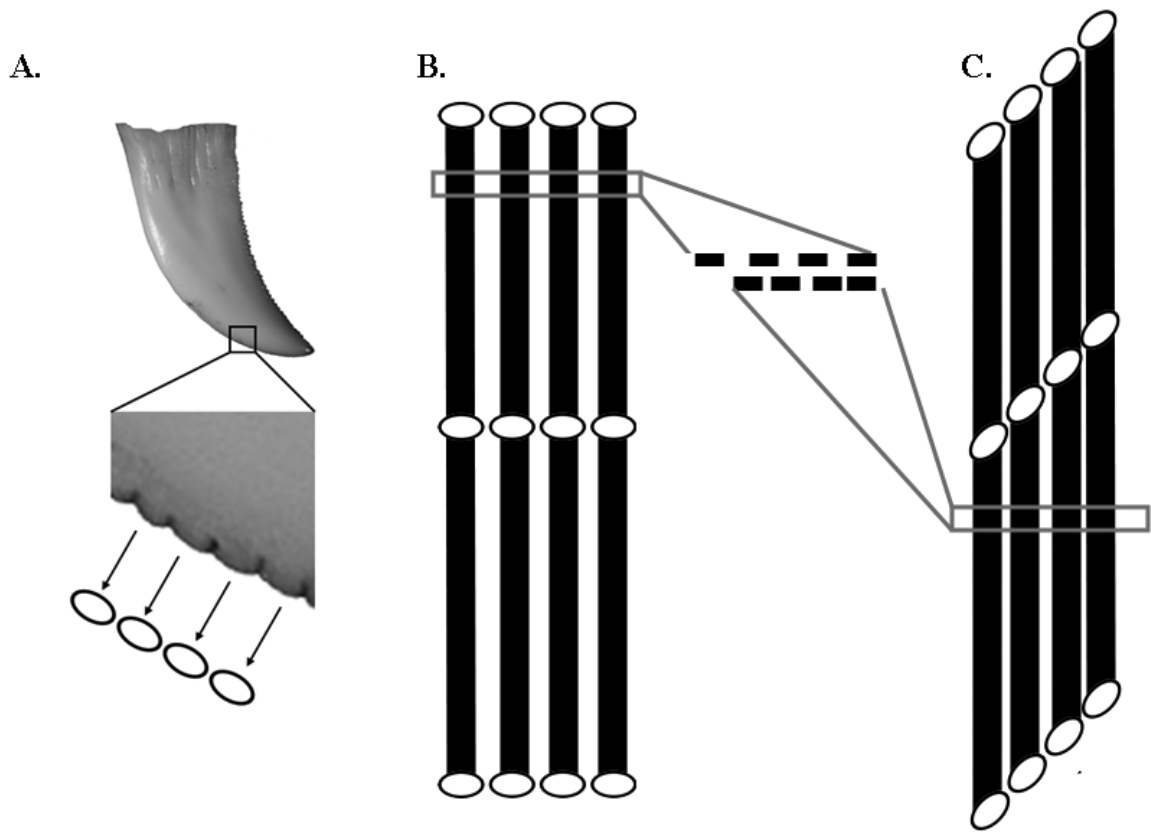
CHAPTER 4: A functional explanation for denticulation in theropod dinosaur teeth

ABSTRACT

The serrated, or denticulated, ziphodont teeth of theropod dinosaurs display variability in their extent of denticulation. A functional model is proposed to test the hypothesis that denticles will not exist in areas that do not frequently contact the substrate. This area, defined as the 'dead-space,' is determined by the direction the tooth moves through the fleshy substrate. The extent of denticulation, as well as the dead-space dimensions, is measured from photographs of 235 isolated and *in situ* theropod teeth, to determine a meaningful relationship between the two variables. Both Euclidean and geometric morphometric methods are employed, and the data are expressed in both bivariate and ordination plots. The model predicts the direction of tooth movement through the curvature of the tooth tip/apex. Tooth position and taxon are considered. The results show that the mesial margin is usually partially denticulated, while the distal margin is usually totally denticulated. Curved teeth have large dead-spaces, and tend to be less denticulated mesially. Straighter teeth are more extensively denticulated, to the point where they became symmetrical. The extent of mesial denticulation is determined by the dead-space, showing it is dictated by the substrate contact. The dead-space almost always predicted less extensive denticulation though, which was a consequence of the limitations of the model. Tooth curvature increases as one moves distal in position, and this variability is due to rotation based on the proximity to the hinge. Denticulation indicates that theropods used a distally oriented puncture to modify the substrate, similar to modern analogues. Although there is little taxonomic variation, Troodontidae show unique and extreme degrees of mesial denticulation.

INTRODUCTION

Theropod dinosaurs were the major terrestrial predators for most of the Mesozoic. Due to their large size and structural features, there is immense interest in the feeding dynamics of these animals. Therefore, theropod functional morphology in the context of feeding behavior has been investigated from many perspectives. Modeling cranial structuring, musculature, and kinesis has given insight into the skull's resistance to stress, potential bite force, and niche partitioning among species (Busbey, 1995; Henderson, 1998, 2002; Mazzetta et al., 1998; Molnar, 1998; Rayfield et al, 2001, 2007; Rayfield, 2004). Forelimb structure indicates a range of ability for securing prey with the manus (Ostrom, 1969; Sereno, 1993; Holtz, 2002; Tykoski and Rowe, 2004). Hind limb structure, as well as general size and body dimensions, is correlated with the theropod running speed (Farlow et al., 1995; Larson, 1997; Fastovsky and Smith, 2004; Seller and Manning, 2007), leading to several conclusions about the hunting and/or scavenging abilities (Horner and Lessem, 1993; Horner 1994). Although dentition is most definitely involved in food processing, and most likely acquisition, significantly less research has been done concerning the morphology of theropod teeth from a functional perspective.

This may be due to the unique dental morphotype of theropods. The majority of theropod dinosaurs possess ziphodont dentition, which is characterized by laterally compressed, curved, serrated teeth (Langston, 1975; Prasad and Lapparent de Broin, 2002). The degree of curvature and flattening can vary greatly (i.e. tyrannosaurids have lost much of their lateral compression), but all appear to possess serrations. These serrations, referred to as denticles, rest on carinae located along the margins of the tooth. The majority of carnivorous archosaurs throughout the Mesozoic era possessed

ziphodonty (Benton 2004). These include theropods, crurotarsians, and basal archosaurs (Farlow et al. 1991; Senter 2003; Benton 2004; Holtz 2004; Smith et al. 2005). Within modern archosaurs though (i.e. crocodylians) it has been replaced by undenticulated, conical teeth. Ziphodonty has also convergently appeared in other tetrapod clades, including Permian pelycosaurs such as *Dimetrodon* (Farlow et al., 1991). Ziphodonty only occurs at present in certain members of the squamate family Varanidae (Auffenberg, 1981; Molnar, 2004).

Several comparative morphometric studies have been conducted on the diversity of theropod teeth, but most of these have focused primarily on the description and/or taxonomic identification of isolated teeth (Currie et al., 1990; Molnar, 1998; Sadlier and Chapman, 1999; Sankey et al. 2002; Carr and Williamson, 2004; Smith 2005; 2007; Smith et al. 2005). Consequently, there has been little analysis of dental function. Chandler (1990) suggested that theropod teeth are designed to cut by a combination of puncturing and drawing through flesh; the primary substrate modified by theropods. Farlow et al., (1991) depict these teeth as multipurpose implements, used for killing, cutting, and crushing bone. Because of increased tooth width and bending resistance, bone crushing may have been possible in larger taxa such as tyrannosaurids (Meers, 2002). Henderson (1998, 2002) used tooth lengths, heights, and orientations in addition to theropod skull measures to determine relative skull strengths and potential niche partitioning among theropods. Sadlier and Chapman (2002) used geometric morphometrics to determine that tooth shape reflects the variability in force applied to different tooth positions within individuals.

In order to gain better insight into the function of theropod teeth, researchers have also investigated the morphology and behavior of living ziphodont varanids analogues, especially the Komodo monitor, *Varanus komodoensis.* Studies of *V. komodoensis* indicate a unique feeding methodology associated with ziphodonty (Auffenberg, 1979, 1981; se also Chapter 2), and cranio-dental similarities between theropods and *V. komodoensis* suggest similar food processing methods (Paul, 1988; Molnar and Farlow, 1990; Busbey, 1995; Carpenter, 1998; Rayfield et al., 2001).

Denticles are assumed to be a crucial component in theropod tooth function, yet few studies have described their functional value. In a study of the teeth of elasmobranch sharks, Frazzetta (1988) proposed that the serrated edges allow a blade to move through a substrate with less force than a smooth blade would require. As the serrations are drawn across this substrate they bind to a small portion of it and tear it, a mechanism described as "grip and rip" (Abler, 1992:178). Less force is needed to draw the serrated surface across the substrate because friction is reduced. Serrations are functionally analogous to denticles, so that a denticulated shark tooth would theoretically move into and through flesh more efficiently than one with smooth edges.

Abler (1992) simulated denticulated tooth performance in tyrannosaurids by using tooth casts and actual metal blades to determine the force needed to modify flesh. His results suggest that tyrannosaurids did not use their denticles to cut through meat by widening the size of a wound, as do sharks. Instead, tyrannosaurids used their teeth to "puncture and grip", and denticles facilitated this (Abler, 1992:179).

Based on these results, it would seem to be advantageous to have denticulated carinae along the portions of the tooth margins that contact the substrate. Several authors

have noted that the entire margin may not be denticulated. This is especially true for the

mesial, or leading edge, of a tooth tooth (Figure 4.1). Chandler (1990:38) stated that

mesial denticles near the base "become so small that they often appear to merge to form

an unserrated keel". Currie et al. (1990) report that mesial denticles in dromaeosaurids

occur on less than half the length of the margin. Molnar and Carpenter (1989) note a

similar condition in tyrannosaurids (see also Carr and Williamson, 2004). Abler (1992)

states that in tyrannosaurids the mesial denticulation "tends to end where the tooth meets

it maximum width." Smith (2007) reported that the denticulated mesial carina terminates

above the tooth base, but distal denticulation extends to the base. Smith also noted a

trend of decreasing mesial denticulation as each tooth moves closer to the hinge.

This study proposes a model that explains the variability in denticulation in

functional terms. The model predicts that denticulated carinae will only exist in areas

that make frequent contact with the substrate during typical feeding behaviors. These

denticles will modify the substrate they contact, assisting the tooth in processing food.

Conversely, areas with little contact with the substrate will lack denticles.

The amount of contact any portion of a tooth has with the substrate is based on the

direction the tooth moves relative to the substrate. Rieppel (1979:812) describes this

tooth movement or "line of action" for *Varanus salvator*. The orientation and curvature

of the line of action of any tooth depends on its position relative to the hinge or hinges

that the host bone rotates around, and the necessity that the apex of the tooth makes

contact with the substrate. The apex has the smallest volume, focusing the force onto a

smaller area and increasing the likelihood of puncturing the substrate (see also Frazzetta,

1988; Chandler, 1990; Lucifora et al., 2002). This results in axial loading of the tooth, which increases efficiency and reduces the chance of breakage.

As a tooth moves along its defined line of action, the degree of contact with the substrate will vary across the tooth's area. Opposite to the line of action is an area of the tooth that may not contact the substrate; this area is defined here as the tooth's 'dead-space' (Figure 4.2). This model predicts that because the dead-space does not make contact with unmodified substrate, it should have no denticles. The purpose of this study is to test this model of theropod tooth function by comparing the extent on denticulation with the dead-space. Theropod teeth are photographed and analyzed using both Euclidean and geometric morphometrics, focusing mainly on apex characters and denticulation. The line of action is determined based on the apex morphology, and a dead-space is proposed for each tooth. This dead-space is then compared to the degree of denticulation. If denticulation does reflect the extent of contact between a given tooth and the substrate, I hypothesize that the height of the dead space will correlate with the degree of denticulation. Conversely, the null hypothesis states that there is no meaningful relationship between the dead-space and the extent of denticulation. This is also examined in relationship to tooth position in the dental arcade, as well as the clade of the theropod it came from.

MATERIALS AND METHODS

Sampling and photography:

Data were collected on a total of 235 teeth of theropod dinosaurs (Appendix 1). Sixty-eight of these were *in situ* and the rest were isolated. Teeth with extensive damage and those obscured by matrix were not included. Partial data were collected on

specimens with limited damage and/or incomplete carinae. The best represented clade

was Dromaeosauridae (n=81), followed by Tyrannosauridae (n=64), Abelisauridae

(n=26), *Dryptosaurus* (n=17), Troodontidae (n=12), and Allosauridae (n=6). Previous

researchers have identified the phylogenetic affinity of 209 teeth, and this was used to

assign each tooth to a specific clade. The only deviation from this was that 10 isolated

teeth considered 'dromaeosaurid' were instead included in the troodontid clade. These

were reclassified based on their distinctively large denticles, which are characteristic of

Troodontidae (Holtz et al., 1998; Makovicky and Norell, 2004). Twenty-nine isolated

teeth were placed in an 'unknown' group. All abelisaurid teeth were taken from a cast of

one individual in which no denticles could be observed, and most allosaurid teeth had

damaged mesial carinae. Consequently, the majority of teeth with denticulation values

available are members of Coelurosauria from the Cretaceous of North America. Tooth

position is also considered for all *in situ* teeth available. The *in situ* sample is represented

only by Abeliesauridae, Allosauridae, Dromaeosauridae, and Tyrannosauridae. Certain

teeth were eliminated because the host bone was so damaged that the absolute position

was impossible to determine. Teeth were sampled from the collections of the American

Museum of Natural History (AMNH) in New York, NY and the Smithsonian Institution

National Museum of Natural History (USNM) in Washington, D.C. In addition, casts of

in situ teeth of two specimens from the Field Museum of Natural History (FMNH) in

Chicago, IL are also used.

Because there is no standardized nomenclature for the description of ziphodont

teeth (Sweetman, 2004), the nomenclature used here is proposed by Smith and Dodson

(2003) (Figure 4.1); mesial, towards the premaxillary and mandibular symphyses; distal,

away from the premaxillary and mandibular symphyses; lingual, towards the tongue; labial, towards the lips; apical, towards the tip of the tooth/the apex; basal, towards the base of the tooth/where the tooth meets the host bone; carina, the denticulated region of the mesial/distal margin; substrate, the material that the tooth modifies. The direction of tooth movement through the substrate is defined by the leading margin. For example, a tooth that is 'drawn distally' is describing the host bone moving the tooth so that it is leading with the distal margin. This is movement relative to the substrate, and *not* the movement of the tooth relative to any other skeletal elements.

When measuring unworn, *in situ* teeth, the position of the denticles was first quantified. The extent of the denticulated carinae was noted for both the mesial and distal margins of all teeth. The basal-most denticle on each carina, referred to here as the terminal denticle (**TD;** mesial [**MTD**] and distal [**DTD**]), was located and marked using a 16x hand lens. Marks were made on the tooth's labial surface directly under the TD using a grease pencil. Although wear is apparent on many specimens, the diaphysis (Abler, 1992) of a worn denticle is usually still visible. Theropod denticles run from the TD all the way to the apex, shrinking in size at close proximity to the apex. This was found to be the case in the majority of the sample (for exceptions see Smith, 2007). Therefore, marking the apical-most denticle was not necessary. Teeth possessing no denticles are described as having a 'non-denticulate' carina. Fifteen specimens had non-denticulated mesial carinae, while all teeth were distally denticulated.

Digital photographs of all teeth were taken from the labial perspective (Figure 4.3). For the majority of tooth length, the opposing carinae run parallel to one another along their respective sides. The camera was positioned perpendicular to a plane

connecting the two carinae. In many teeth, the mesial carina curves lingually before terminating. In such cases, the camera was positioned in reference to only the portion of the carina occurring apical to this lingual curving. For teeth with no carinae at all, the camera was simply positioned perpendicular to the long axis of the tooth.

Coordinate digitization:

Coordinates were digitized from tooth photographs using TpsDig 2.10 (Rohlf, 2006). Each tooth had a total of 62 assigned coordinates from which all data were extrapolated (Figure 4.3). Ziphodont teeth have very few distinct morphological features making it difficult to produce 'true' landmarks, or coordinates that denote discrete homologous anatomical loci (Zelditch et al., 2004). Coordinates were placed at the pencil mark at the MTD and DTD, indicating the extent of denticulation. These may be considered optimal, or Type 1, landmarks because they are denoted by distinct morphological structures that are locally defined (Bookstein, 1991, 1997; Zelditch et al., 2004).

Another coordinate is placed at the tooth tooth apex (**CA**). Finding a repeatable method for identifying the apex has proven difficult in the past, because the apex is often rounded and may occupy a large area (Smith et al., 2005). Many studies do not detail how the apex is identified (Rieppel, 1979; Molnar, 1998; Henderson, 2002; Sankey et al., 2002) and others derive tooth heights instead of apex positions (Farlow et al., 1991; Smith, 2005, 2007; Smith et al., 2005).   I defined the apex as the point along the tooth where the most acute angle is formed and the two carinae meet. This angle was approximated qualitatively. Because this was defined by a maximum of curvature and

not a morphological structure, it is a Type 2 landmark. Regardless, this landmark is

essential in defining to the tooth's puncturing ability and line of action.

The establishment of a tooth base is necessary to measure the relative position of

the apex and denticles. Therefore, two more coordinates were placed at the base of the

tooth (Figure 4.3). This is the basal most point where the tooth's mesial and distal

margins meet the host bone, and may be defined as Type 1 landmarks because they

define a "discrete juxtaposition of tissues" (Zelditch et al., 2004:31). This method can

result in a portion of the tooth's dimensions represented by exposed roots, especially in

tyrannosaurids. This is functionally significant because although the root probably was

covered by tissue and did not make direct contact with the substrate, its height in

relationship to the host bone will dictate aspects of its interaction with the substrate.

Therefore, the exclusion of the root would artificially 'shorten' the tooth relative to those

with more embedded roots.

Fifty-six semilandmarks function to outline the mesial and distal margins of the

tooth (Figure 4.3).   These do not demarcate morphological characters (Zelditch et al.,

2004). The margin is defined here as the 'outline' of the tooth from the base landmark to

the apex on a given side. Chainman3D (Sheets, 2005a) converted random points plotted

along each margin into 30 equidistant semilandmarks, dividing up each margin into 29

equal increments. The first and last semilandmarks are equivalent to the CA and basal

landmark, and are not considered further. Previous researchers have also used 30

coordinates to represent the mesial margin (Smith et al., 2005). The general shape of the

margin is conserved in most teeth, but the resolution is also low enough that slight

inconsistencies are not represented. Because an analysis of general tooth shape

morphometrics is beyond the scope of this study, no direct data are taken from semilandmarks.

Chainman3D also converts all the landmarks and semilandmarks into a two point registration (Zelditch et al., 2004). This process converts the distance between two arbitrary coordinates to 1 unit (Bookstein coordinate), thus scaling the remainder of the points. For the two points the basal-most landmarks were chosen, positioning them along the x-axis. Transferring the Bookstein coordinates to an Excel spreadsheet allows for easy calculations for all teeth simultaneously. Using a two point registration eliminates size as a factor, and using the base of the tooth is the most appropriate region to standardize because it is often considered the standard metric for tooth size (Farlow et al., 1991; Holtz et al., 1998; Sankey et al., 2002; Smith et al., 2005).

The line of action and the dead space:

The line of action is crucial in the determination of a tooth's dead-space. Based on axial loading (see INTRODUCTION), I hypothesize that the apex indicates the direction in which the tooth must move when initially contacting the substrate. Although this aspect of the line of action can be accounted for, the rotation of the host bone cannot. Factors that contribute to this, such as cranial kinesis, tooth position, and distance from the hinge(s) (Rieppel, 1979) are unavailable for most teeth. Due to the exclusion of rotation, the line of action is based solely on the orientation of the apex resulting in a straight line.

The line of action is determined similarly to Rieppel (1979) by deriving a "tangential line". This is a straight line drawn through the apex, and is determined by tooth morphology (Figure 4.3). First, two points on each of the margins are selected. On

the distal margin, this point is the tenth semilandmark from the apex. On the mesial margin, the landmark closest to the length between the apex and the distal margin's tenth landmark was used. This results in both margins having points that are a similar length from the apex. A tangential line is then formed connecting CA with the midpoint of these two points. This is the line of action. Arbitrarily choosing these particular semilandmarks results in less than the apical third of the tooth influencing the line. This eliminates compounding factors, such as how elongate the body of the tooth is, that can reduce the line of action if more of the tooth is included.

A coordinate is then placed along the mesial margin in accordance to the line of action. This coordinate denotes the hypothetical terminal denticle (**HTD**), and is significant because it dictates the height of the dead-space as determined by the line of action. If the proposed model is correct, all of the tooth margin basal to this coordinate should have no denticles. The coordinates of all semilandmarks along the mesial margin are compared to points on the line of action function of equal x value, and the semilandmark that is farthest from that function becomes the HTD (Figure 4.3). Although not a 'true' landmark by definition, this will be referred to as a landmark for the purposes of the model.

Last, the line of action as converted to an angular measure was derived. This is similar to curvature, recurvature, or pitch in previous studies because it dictates the angular orientation of the apex relative to the base. This has been described for theropods (Molnar, 1998; Henderson, 2002; Smith, 2005, 2007, Smith et al., 2005), varanids (Rieppel, 1979), and elasmobranch sharks (Lucifora et al., 2002). The angle of the line of action (**LOA°**) is the difference in degrees between the function derived above, and the

two basal landmarks on the x-axis. Mathematically, this is the tangent of the CA y-value

divided by the difference between CA x-value and the function's x-intercept. Because

the LOA° is independent of denticle characters, it was calculated for all teeth sampled.

Euclidean distances:

The percentage of mesial and distal denticulation was calculated for all teeth with

denticulated carinae. The length of the denticulated carina is distance from the TD to the

CA along the margin. This was then divided by the total length of the margin; the

summation of the distance between the thirty adjacent coordinates along the margin. A

hypothetical percentage of mesial denticulation was also calculated based on the position

of the HTD in a similar manner.

The relative height of three landmarks is determined. The position of the MTD,

DTD, and HTD is determined perpendicular to the base. Because the two point

registration positions the base on the x-axis, these data are simply the y-value for each

landmark. MTD, DTD, and HTD are converted into percentages of the tooth height by

dividing them by CA. In addition, DTD was subtracted from MTD to yield a value

quantifying symmetry in TD height.

Basic statistics are performed on all angular and Euclidean variables. The

number, average, median, and range are calculated for each value. Bivariate plots were

constructed to compare height variables and the LOA°. Regressions lines are plotted, and

r^2 and p-values are calculated where appropriate. All plots have the different clades of

theropod indicated. *In situ* teeth were plotted by position against the LOA° and certain

linear variables. Percent denticulation was not used in any regression analyses because

these data appear to be strongly influenced by tooth tooth keeling.

<u>Geometric morphometric analysis:</u>

Teeth complete enough to produce all six landmarks were entered into a landmark based morphometric analysis using a multivariate ordination technique (n=175). The six landmarks were input into a principal component analysis using PCAGen6p (Sheets, 2005b). This program performs a generalized least squares Procrustes superimposition on the data, and calculates the partial warp scores for each landmark. From these partial warps, the factor loadings for both x and y values for each landmark are listed. These consist of Pearson's correlation coefficients and p-values, and are considered significant if they are above .4 and below .05 respectively. From this, a series of principal components was generated representing shape variances between the landmarks. Each tooth is assigned a component score along each principal component axis, and principal components were plotted against one another.

<u>Methodological modifications for worn and/or isolated teeth:</u>

A naturally occurring TD tends to be smaller than the majority of the denticles, making it easily distinguishable. Many teeth had 'abbreviated' carina where the basal-most denticle is the result of damage to the tooth, and under 'natural' circumstances denticulation would extend basal to that denticle. Isolated teeth may have broken apical to the TD or the carina itself may be chipped or damaged. Teeth with abbreviated MTD were not sampled, but most teeth have abbreviated DTD. Because this abbreviation usually occurred at the base of the tooth, the basal-most distal denticle was always considered the DTD.

In a tooth with an apex that shows little damage or modification, the CA landmark is easily placed. However, many teeth sampled had either worn or broken apices (Figure

4.4). A worn apex tends to be smooth and rounded, with no sharp or jagged edges. The worn area is also easily distinguished because it is polished and may be a different color than the rest of the tooth. A broken apex displays sharp edges where it was broken, with no polishing. Concerning worn apices, CA is placed approximately equidistant to the edges of the worn area. Teeth with broken apices were not sampled. I assume that there is only a slight deviation in overall shape between worn apices, whereas broken teeth can deviate greatly from the unmodified condition.

Because isolated teeth did not have the host bone available for reference, the basal landmarks are positioned at the mesial and distal most point where the tooth breaks. One cannot rule out the possibility that the base landmarks in isolated teeth may not always represent similar positions to *in situ* teeth, but instead represent artifacts of preservation. Although I found no way of safeguarding against this possibility, the methodology used here allows for the most repeatability and consistency in sampling due to a lack of discrete anatomical features. Past authors have used the extent of enamel to indicate these points (Chandler, 1990; Farlow et al., 1991; Sankey et al., 2002; Smith et al., 2005). In this sample, the enamel was indistinct or damaged in many specimens.

RESULTS

Simple statistics and regression analysis:

There is a large difference in the extent of denticulation between the mesial and distal carinae of a theropod tooth (Table 4.1). Median and average mesial denticulation is about 66%. Therefore, the basal one-third of the mesial margin possesses no denticles on average. Conversely, most teeth are denticulated along nearly the entire distal margin. Only 45 of the 174 teeth sampled had less than 90% distal denticulation. The majority of these teeth was tyrannosaurid or 'unknown', and appeared to have a noticeable amount of exposed root. Distal denticulation is also less variable than mesial. The relative heights of the MTD and DTD further support this. The MTD is found at average 44% of height from the base, but is still highly variable based range and standard deviation (Table 4.1). Again, the DTD has a noticeably smaller range than the MTD and is usually positioned close to the base.

The height of the dead-space (HTD) is usually apical to the MTD. Its average relative height is 26% greater than the MTD. If the HTD dictated the extent of mesial denticulation instead of the MTD, the mesial margin would be around 22% less denticulated. Figure 4.5 displays the relative heights of these values plotted against one another. The vast majority of the teeth have a greater HTD than MTD, as indicated by their position above the threshold in a one to one ratio.

Tooth curvature is highly variable in theropods as indicated by LOA°. LOA° ranges from about 20 to over 112 degrees. Teeth with LOA° values between 20 and 70 degrees persist within most families (Figure 4.6). It should be noted that taxa with ample sample size (Dromaeosauridae, Tyrannosauridae, *Dryptosaurus*) occupy the majority of

the range of LOA˚ values. Larger taxa, such as tyrannosaurids, allosaurids, and abeilisaurids, are the only groups that show a noticeable number of teeth that exceed 70 degrees.

Theropod teeth range in height from approximately one to four times their base size (Table 1). Heights are variable for all clades sampled, but tyrannosaurids are the only clade to have teeth greater than 2.5 times the base. Taller, thinner teeth relative to the base appear to exhibit less curvature. The height of the apex (CA) increases as LOA˚ decreases (Figure 4.6). The larger teeth, especially those of tyrannosaurids, reflect this condition, but variability increases with increased LOA°.

LOA° shows a significant negative correlation with the relative heights of both the MTD and HTD, with r^2 values above .33 (Fig. 6). As LOA° becomes less acute, these landmarks drift closer to the base. LOA° shows a very weak positive correlation with DTD as indicated by a very low r^2. There is also an increase in tooth symmetry as the LOA° becomes less acute. The height of the mesial and distal terminal denticles converge as LOA° increases towards 90 degrees (Figure 4.7). All regressions have p-values less than .0001.

Tooth position correlates significantly with mesial denticulation and apex orientation (Figure 4.8). All trends have r^2 values of 0.3 or greater. These trends persisted for both the upper and lower tooth rows. Most teeth sampled have similar data for a given tooth position, as opposed to different specimens or families following different trajectories. LOA° negatively correlates with an increase in distal tooth position. MTD and HTD relative heights correlate positively with increasing distal tooth position, although few *in situ* teeth had an MTD available. There does not appear to be a

meaningful correlation between tooth position and the DTD or CA (not shown). There appears to be a slight plateau effect as one moves distal in position along the upper tooth row that is not as evident in the lower tooth row.

Troodontidae displays a unique 'bimodal' mesial denticulation. Five of the twelve troodontid teeth have mesial margins that are almost fully denticulated, with the height of the MTD under 1% (Figure 4.5 and Figure 4.6). Conversely, the remainder of troodontid specimens have 'non-denticulated' mesial margins, representing over half of all teeth with that condition in our sample. All others with this condition were 'unknown'. Aside from these disparities, troodontids have almost fully denticulated distal margin, and HTD positioning and LOA° values do not appear to be dissimilar to other theropods (Figure 4.6).

Principal component analysis:

Four principal components were generated, accounting for over 94% of the overall variance for the six landmarks (Table 2). PC1 accounts for over 39% of the variance, and primarily defines the height of the tooth relative to the base (Figure 4.9). Teeth with high scores on this component are differentiated from those with low ones by being tall and elongate. This is symbolized by a negative correlation between the x-value coefficients for landmarks on the mesial margins. Although size was factored out, it appears that larger teeth display higher scores. The sample above 0.1 units is mostly large tyrannosaurid teeth, and the stout dromaeosaurid and troodontid teeth are the most negatively positioned. PC1 may therefore be considered an indirect size component. PC2, representing 28.5% of the variance, primarily depicts an increase in mesial denticulation along the component (Figure 4.9). MTD has large coefficients that only

correlate with HTD significantly. This component shows that distance between the dead-space and mesial denticulation is not always uniform. Troodontids have the highest values with their uniquely well denticulated mesial carinae. All other clades appear evenly dispersed throughout. Tooth position does not correlate with either of these components. The line of action, as indicated by mesio-distal movement of the CA, does not appear to play a significant role in any of these components.

Representing over 17% of the variance, PC3 is the most biologically significant component for the purposes of this study (Table 4.2). It is highly correlated with the mesio-distal movement of the apex (Figure 4.10). The coefficients of the apex and mesial basal landmark negatively correlate with the distal basal landmark, indicating that the apex rotates along the component. Teeth high on this axis are elongate with their apices in the center of the base, giving them a tall, straight appearance. Tooth shape, as well as the extent of denticulation, is symmetrical. As the component decreases the apex drifts distally, indicating a higher degree of curvature and consequently a more acute line of action. With this, MTD moves apically and the DTD moves basally, as indicated by negatively correlated coefficients for the y-values of these landmarks. There appears to be no distinction between clades based on this axis, which the exception of tyrannosaurids occurring solely above .15. The principal component value of these teeth also decreases and the position becomes more distal.

PC4 represents only about 9% of the variance, and displays a similar rotation of the apex along the component. In addition, this component accounts for variance in the distance between the DTD and the apex (Figure 4.10). The DTD has the largest coefficients, and they are negatively correlated with the CA y-value. This value

correlates with tooth curvature, and correlates well with *in situ* teeth similar to PC3. As the tooth becomes more curved, the overall size of the distal margin, as well as distal denticulation, decreases.

DISCUSSION

Denticulation and substrate modification:

The mesial margin of a tooth is usually partially denticulated, whereas the distal margin is usually almost entirely denticulated. The height of the position where mesial denticulation terminates correlates with the distal curving of the tooth. Teeth with a high degree of curvature have the least denticulate mesial margins. As the tooth curvature decreases, mesial denticulation increases resulting in a straight, tall tooth with more symmetry between the two faces. Both Euclidean distances and a significant amount of principal component variance, especially PC3, support this.

The dimensions of the dead-space, as determined by the hypothesized line of action, do show a correlation with the extent of mesial denticulation. This indicates a degree of dependency between the two factors. Therefore, the null hypothesis that there is no relationship between these two variables is rejected. The height of the dead-space and the extent of mesial denticulation *do not* have similar dimensions though. They differ from one another in a consistent and predictable manner, with the height of the dead-space (HTD) almost always apical to the MTD. If function is still considered the major force driving the extent of tooth denticulation, then the mesial margin is 'excessively' denticulated according to the model. The fact that the MTD is basal to where it is predicted to be indicates that more of the mesial margin is contacting and modifying the substrate than the dead-space predicts.

One explanation for the disparity between the dead-space and mesial denticulation is that the apex may not accurately determine the line of action. This would result in an inflated dead-space. LOA° correlated negatively with the height of the dead space, as

symbolized by the HTD. One could argue that the line of action should be less acute, which would move the HTD basal and closer to the position of the MTD. I find this hypothesis unlikely for several reasons. If the line of action were less acute, the tooth would contact and puncture the substrate with the mesial carina first. Axial loading would not occur (Rieppel, 1979), decreasing the efficiency of the tooth and promoting tooth damage. This would be especially likely for large, potentially bone modifying theropods (Farlow et al., 1991; Meers, 2002). Also, teeth with very distally oriented apices would form another dead-space along the upper portion of distal carina: an area that is always denticulated.

A more likely explanation is based on the limitations of using fossils. Because there is little data on the tooth position in relation to any hinge(s), rotation was not factored in. During jaw adduction, rotation would result in a curved line of action (Rieppel, 1979) as opposed to the straight line proposed in this model (Figure 4.11). By factoring in rotation, the tooth can still enter the substrate apex first, and then rotate along the hinge(s) so that more of the mesial carina comes in contact with the substrate. As inferred by this logic, the extent of mesial denticulation *does* predict the height of the dead-space. The disparity seen is because the model artificially inflates the dead-space height by having a straight line of action.

Regardless of the limitations of this model, the extent of denticulation in a theropod tooth is still determined by contact made with the substrate during movement in the direction of the line of action. Even with rotation factored in, a large portion of the mesial margin will avoid contact with the substrate in teeth with an acute line of action (Figure 4.11). This produces a large dead-space, resulting in the mesial margin

maintaining a relatively small degree of denticulation. As the apex becomes less curved, the line of action becomes less acute and the dead-space is reduced. This results in more of the mesial margin contacting the substrate, and consequently more denticulation. Eventually a tooth's apex becomes such that the line of action is perpendicular to the base. This results in similar degrees of contact with the substrate for both carinae, as reflected by symmetry in the amount of denticulation.

Because the angle at which the tooth moves through the substrate is very rarely over 90 degrees, the majority of the distal carina always makes contact with the substrate under most circumstances. This results in the extensive denticulation seen, and its apparent independence from curvature. The exceptions within Tyrannosauridae are the result of these teeth having a noticeable amount of exposed roots, which would most likely not contact the substrate.

Serial homology in theropod dentition:

As reported by several previous researchers (Ostrom, 1969b, 1978; Colbert, 1989; Chandler, 1990; Smith, 2005), a trend of gradually changing apex and denticulation characteristics is apparent in the *in situ* sample. Shimada (2002) describes this serial homology as shape heterodonty. For both the upper and lower tooth rows, apices become more curved at more distal positions. This correlates with decreased mesial denticulation and increased dead-space height. Clade membership does not play a significant factor in this, suggesting that the factors influencing heterodonty are consistent among most theropods. Dromaeosaurids appear to exhibit the greatest curvature for a given tooth position. This may be functional or allometric in nature, and the author is in the process of increasing the sample size so further conclusions can be made.

This serial homology may be interpreted functionally. Rieppel (1979) proposes a mechanism for why tooth curvature is directly influenced by tooth position, and bases it on the distance from the cranial hinge(s) (see also Sadlier and Chapman, 2002). Teeth positioned at different points along the jaw will vary in their distance from the hinge. In ziphodont carnivores the teeth tend to be somewhat similar in size, and the point at which the tooth strikes the substrate during rotation differs along the tooth row. A distal tooth will contact the substrate very early on during jaw adduction, whereas a mesial tooth will contact the substrate when the jaw is closer to being closed (Figure 4.12). Unless it is dramatically shorter than its mesial counterparts, a distal tooth must be curved in order to avoid striking the substrate with the distal margin first. A mesial tooth's apex will strike when the jaw is further adducted. If the tooth is too curved, the mesial margin will contact instead.

As jaw adduction occurs, all teeth located along the tooth row will be rotated around the hinge(s). Because of the elongate nature of the theropod rostrum, this rotation will occur along the plane parallel to the mesial and distal carinae for the majority of teeth (Figure 4.12). The mesial-most teeth in the dental arcade are subjected to unique influences due to the morphology of the jaw. Because medial curvature occurs along the rostrum, the mesial-most dentary and premaxillary teeth instead rotate perpendicular to their mesial and distal margins. Hence from the labial perspective (from which all teeth were analyzed here), it would appear that these teeth move perpendicular to the base with no rotation at all. As expected, these teeth have apices oriented perpendicular to their base to allow for axial loading and very similar degrees of denticulation along both margins. The carinae can also be repositioned lingually in coelurosaurids, giving them a

'D-shaped' cross-sectional appearance that has been noted by several authors (Molnar, 1978; Smith, 2005). It should be noted that our isolated sample lacks teeth with this distinct morphotype for dromaeosaurids, *Dryptosaurus*, and troodontids. This is most likely due to taphonomic or collecting bias against these teeth, and not that they do not occur.

As stated above, teeth have varied curvature because they are positioned along a hinge and are similar in size. Although size was not quantified here, theropod teeth do exhibit some variability in size (giving them shape size heterodonty according to Shimada [2002]). The profile of the maxillary dentition has been compared to that of a 'scalpel blade', with teeth possessing the greatest heights located mid-way down the tooth row (Molnar and Farlow, 1990). This may be facilitated by an increase in exposed root (personal observation). If teeth become larger in more mesial positions, curvature does not need to be reduced because the point of contact between the apex and the substrate would be earlier during adduction. This is reflected in the plateauing in dental characters distally along the upper tooth row (Figure 4.8), and may represent a trend towards increasing tooth size while maintaining curvature. The condition ceases mid-way along the dental arcade because large mesial teeth would not allow the jaws to close fully. Additional size data are needed to fully test this hypothesis.

Theropod feeding methodology:

The orientation of theropod tooth apices can elaborate upon their feeding behavior. Many of the theropod teeth observed are strongly curved, some with less than a 30˚ LOA˚. A bite with little additional movement would most likely not result in apical contact, so there must be an additional mechanism that allows for the curved teeth to

achieve axial loading. Bakker (1998) and Rayfield et al. (2001) suggested that

Allosaurus had a wide gape, and retractile forces during jaw adduction would allow for

axial loading. Rieppel (1979) proposed a different mechanism for ziphodont varanids:

cranial kinesis increases the number of hinges in the jaw mechanism, which allows for

the tooth row to be abducted dramatically without an excessive gape. Both these

mechanisms allow for the teeth to be drawn in the distally through the substrate.

An alternative mechanism to allow for the distal repositioning of the tooth is

proposed here based on a modern ziphodont carnivore. *Varanus komodoensis* has highly

curved teeth (Auffenberg, 1981). Although the skull is kinetic, this kinesis is not

dramatic enough to reorient tooth apices to the extent Rieppel (1979) suggests

Auffenberg (1981; see also Burden, 1928; Chapter 2). It also does not display a wide

gape when defleshing. Instead, *V. komodoensis* rotates its rostrum both laterally (more

specifically in the medial direction towards the mid-line of the rest of body) and caudally

during adduction. This 'medial-caudal arc' not only forces the teeth into the substrate

due to adduction, but also draws them a significant distance distally in relationship to

where they started (Chapter 2). This distal repositioning of the teeth during defleshing

gives these teeth a very acute line of action when modifying the substrate.

Theropods may have used a method similar to that of *V. komodoensis* for

defleshing based on both morphological and taphonomic similarities. There are striking

similarities in both denticle properties and tooth shape between these two groups (Molnar

& Farlow, 1990, Farlow et al., 1991). In addition, tooth mark similarities may also be

used to support this model in Theropoda. Elongate, curved scores are typical feeding

traces left by *V. komodoensis* (Chapter 2). Theropods have been reported to produce

elongate linear scores (Jacobsen, 1995; Erickson and Olson, 1996). This may indicate the distal drawing of teeth as well, although the technique may have differed due to rostral differences between these taxa.

This model also supports Abler's (1992) model of tooth use as well. Abler stated that in tyrannosaurids the denticles allow for the tooth to fully puncture the substrate, and the same basic principle apply here. Frazzetta (1988:95) describes modifying the substrate by puncturing as "puncture cutting". These data suggest that teeth were drawn distally during feeding. Theropods therefore processed the substrate with what is essentially a distally oriented puncture cut. The extent of denticulation is directly related to the efficiency of this. Denticles still fundamentally function to assist in a puncture (Abler, 1992), but they assist in the distal repositioning of the tooth relative to its starting position during this puncture. The dead-space that is produced during this puncturing is what allows for the removal for flesh.

This behavioral model has been witnessed in *V. komodoensis* (Chapter 2). This animal sections off portions of flesh by simultaneously puncturing and drawing teeth distally through the substrate. This process is repeated until a portion of the prey is removed. In addition, many authors have proposed defleshing models for Theropoda. These include the 'puncture and pull' method of tyrannosaurids (Molnar and Farlow, 1990; Erickson and Olson, 1996; Rayfield, 2004), or the 'slashing' method of *Allosaurus* and *Ceratosaurus* (Rayfield, 2001; Holtz, 2002; Snively and Russell, 2007). Jacobsen (1995:66) also asserted that theropods drew their teeth backwards through the substrate.

Although heterodonty is apparent in theropods, the morphometric variation observed does not suggest specialized functions of specific teeth. Tooth position relative

to the hinge seems to be the only major factor influencing variability in denticulation and apex orientation. This suggests that most teeth modified the substrate through puncture cutting. This supports Farlow et al. (1991) in that theropod teeth were multipurpose general instruments. Several studies have suggested that theropod heterodonty indicates that certain teeth were specialized for certain aspects of hunting, killing, and defleshing (Molnar, 1998). Although this may have been the case, theropod teeth most likely achieved these variable tasks by universally modifying the substrate through puncture cutting.

Denticulation conforms to the model proposed here for all theropod clades sampled except Troodontidae. Other studies have noted the unique tooth morphology of troodontids, mostly focusing on the their significantly large denticles relative to their tooth size (Farlow et al., 1991; Holtz et al., 1998). These data show that this is coupled with a unique, bimodal extent of mesial denticulation. Theropods are believed to be primarily carnivorous (Van Valkenburgh and Molnar, 1998), and the morphological consistency seen across the majority of the clades sampled here suggests that they all used their teeth to puncture compliant, fleshy substrate. The exception of Troodontidae is most likely the consequence of differences in tooth use. Troodontid dentition is reminiscent of herbivorous lizards and ornithischians, indicating the incorporation of plant material into their diet (Holtz et al., 1998). The mechanical demands of tough, fibrous plant material are quite different from those from those imposed on the teeth of a flesh specialist. This would result in different selection pressures on the sizes of both denticles and carinae.

More work is needed to further test the validity of the model proposed here. It should be noted that tooth denticulation was analyzed solely from a labial, two-dimensional perspective. The mesial carina bends lingually in many theropod taxa (Farlow and Pianka, 2002), which may reflect a 'screw-like' effect during puncture (J. O. Farlow, personal communication). Similar morphometric analyses should be conducted on teeth from other perspectives. Farlow et al. (1991:192) notes a "remarkable evolutionary convergence" in ziphodont teeth within and outside of Theropoda. A larger sample would help determine if this trend is consistent across most theropods, and across most ziphodont taxa. Tooth wear and wear facets should be further investigated to shed light on tooth movement through the substrate. Chandler (1990) found there was more wear apparent on the tooth apex than on the carinae, further supporting that the apex is receiving the initial resistance from the substrate. There are also wear facets common on tyrannosaurid teeth, which may be due to wear from food items and occlusion with the opposing tooth row (Farlow and Brinkman, 1994; Schubert and Ungar, 1995). Although cranial kinesis is postulated for several theropods based on skull morphology (Versluys, 1910; Bakker, 1986; Mazzetta et al., 1998), it has never been rigorously tested. More information concerning this would help determine if cranial kinesis also contributed to the line of action as proposed by Rieppel (1979).

Modifying actual substrate with ziphodont teeth may also test this model. Following Abler (1992), experimental systems may be set up with artificial teeth to test whether apex orientation and denticle position affects the efficiency of a tooth puncture. The feeding behavior of modern ziphodont carnivores may also be quantitatively analyzed. Studies of *V. komodoensis* indicate a feeding method analogous to the model

proposed here. Tracking the tooth and head movements of feeding individuals may allow

researchers to quantify the direction of tooth movement through the substrate, rather than

relying on speculation based on tooth morphology.

Table 4.1: Table 1: Simple statistics for Euclidean and angular variables. The angle of the line of action (LOA) is in degrees and the height of the tooth apex (CA) is in Bookstein coordinates. The mesial (MTD), distal (DTD), and hypothetical terminal denticle (HTD) heights are all percentages of the CA. The extent of denticulation is a percentage of the total margin length.

	LOA	CA	MTD	DTD	HTD	MTD-DTD	Percentage distal denticulation	Percentage mesial denticulation	Percentage hypothetical denticulation
Mean	53.69	1.78	0.45	0.08	0.70	0.37	0.92	0.66	0.48
Standard Deviation	16.69	0.54	0.19	0.12	0.18	0.21	0.11	0.13	0.14
Range	95.32	3.77	0.98	0.57	0.99	1.07	0.51	0.68	0.76
Median	52.57	1.65	0.44	0.01	0.73	0.38	0.99	0.66	0.45
N	235	235	175	175	175	175	174	175	175

Table 4.2: Variances and eigenvalues (A) and factor loadings (B) for Principal components (PC). Factor loadings consist of Pearson's correlation coefficients (above) and p-values (below) for both x and y coordinates for all landmarks.

A.

Component	Variance	Eigenvalues
PC1	0.392	0.019
PC2	0.285	0.014
PC3	0.175	0.009
PC4	0.089	0.004
Sum	0.941	0.046

B.

Landmark		PC1	PC2	PC3	PC4
Mesial	x	0.38	0.11	-0.63	0.58
basal		<0.01	0.14	<0.01	<0.01
	y	-0.86	0.25	-0.28	0.20
		<0.01	<0.01	<0.01	<0.01
Distal	x	-0.55	0.18	0.78	-0.01
basal		<0.01	0.02	<0.01	0.89
	y	-0.56	0.31	0.54	-0.15
		<0.01	<0.01	<0.01	0.05
Apex	x	-0.88	0.04	-0.08	-0.32
(CA)		<0.01	0.60	0.30	<0.01
	y	-0.16	0.09	-0.75	0.52
		0.04	0.23	<0.01	<0.01
Mesial	x	0.54	-0.71	-0.34	0.18
terminal		<0.01	<0.01	<0.01	0.02
denticle	y	0.25	-0.86	0.41	0.16
(MTD)		<0.01	<0.01	<0.01	0.03
distal	x	-0.67	-0.21	0.34	-0.36
terminal		<0.01	<0.01	<0.01	<0.01
denticle	y	0.30	-0.34	-0.53	-0.71
(DTD)		<0.01	<0.01	<0.01	<0.01
hypothetical	x	0.83	0.51	-0.11	-0.02
terminal		<0.01	<0.01	0.13	0.80
denticle	y	0.72	0.63	0.26	0.01
(HTD)		<0.01	<0.01	<0.01	0.87

Figure 4.1: Visual depiction of directional terms used for theropod teeth. Terms are taken from Smith and Dodson (2003).
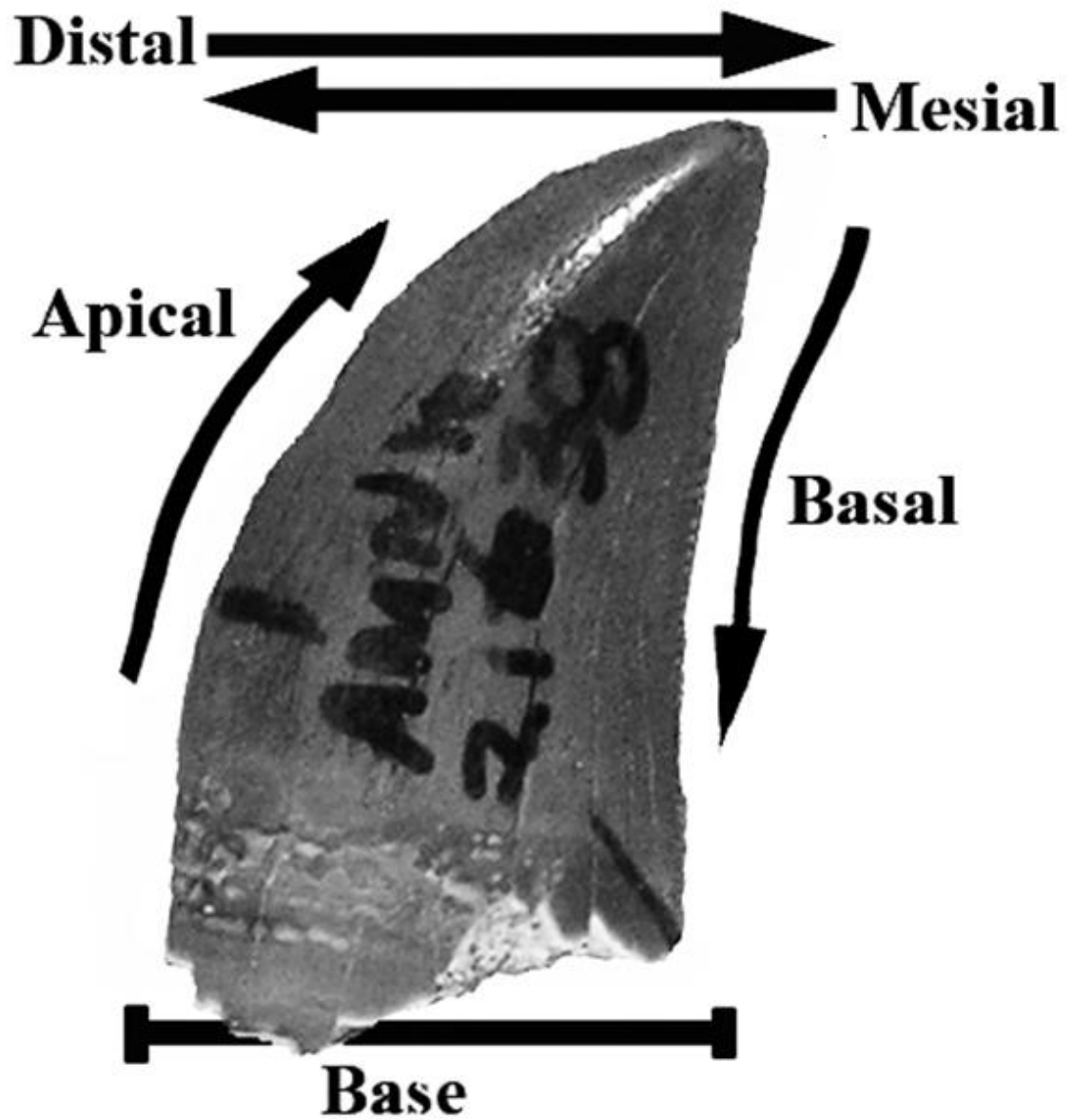
Figure 4.2: A diagrammatical representation of a theropod tooth and its interaction with the substrate. 1.) The tooth moves toward the substrate in the direction of line of action. 2.) The tooth punctures the substrate apex first to allow for axial loading. 3.) The tooth continues to move through the substrate along the line of action. Opposite this motion a dead-space forms (black). The arrow indicates the height of the dead space, which is the point where denticulation would terminate if it is dictated by frequent contact with the substrate.
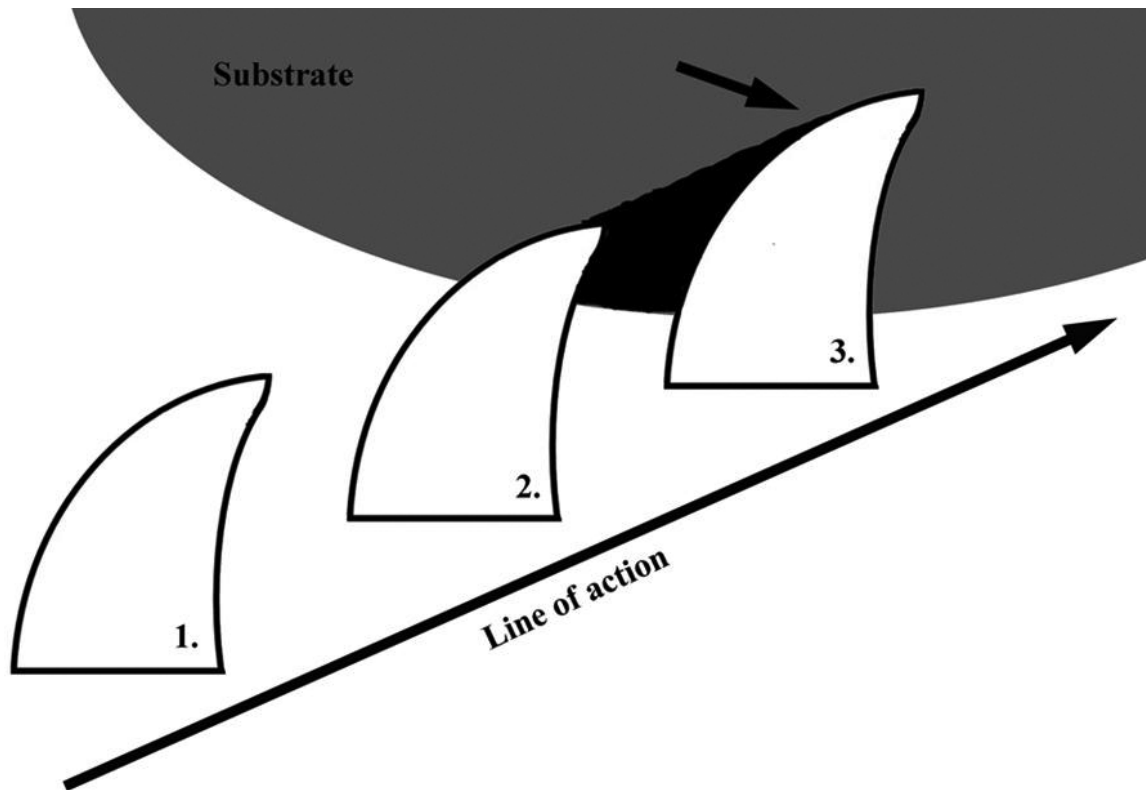
Figure 4.3: The digitization of theropod tooth coordinates. All axes are in Bookstein coordinates (Bookstein, 1997). A) All teeth were photographed and landmarks and semilandmarks (m.=mesial, d.=distal) were digitized from these photographs. B) A two point registration moves the base to the x-axis. C) A function is produced from the straight line between the midpoint of two semilandmarks along either margin, and the apex. This function is the line of action. D) The mesial semilandmark farthest from the line of action becomes the hypothetical terminal denticle (HTD) (1=mesial basal landmark, 2=distal basal landmark, 3=CA, 4=MDT, 5=DTD).
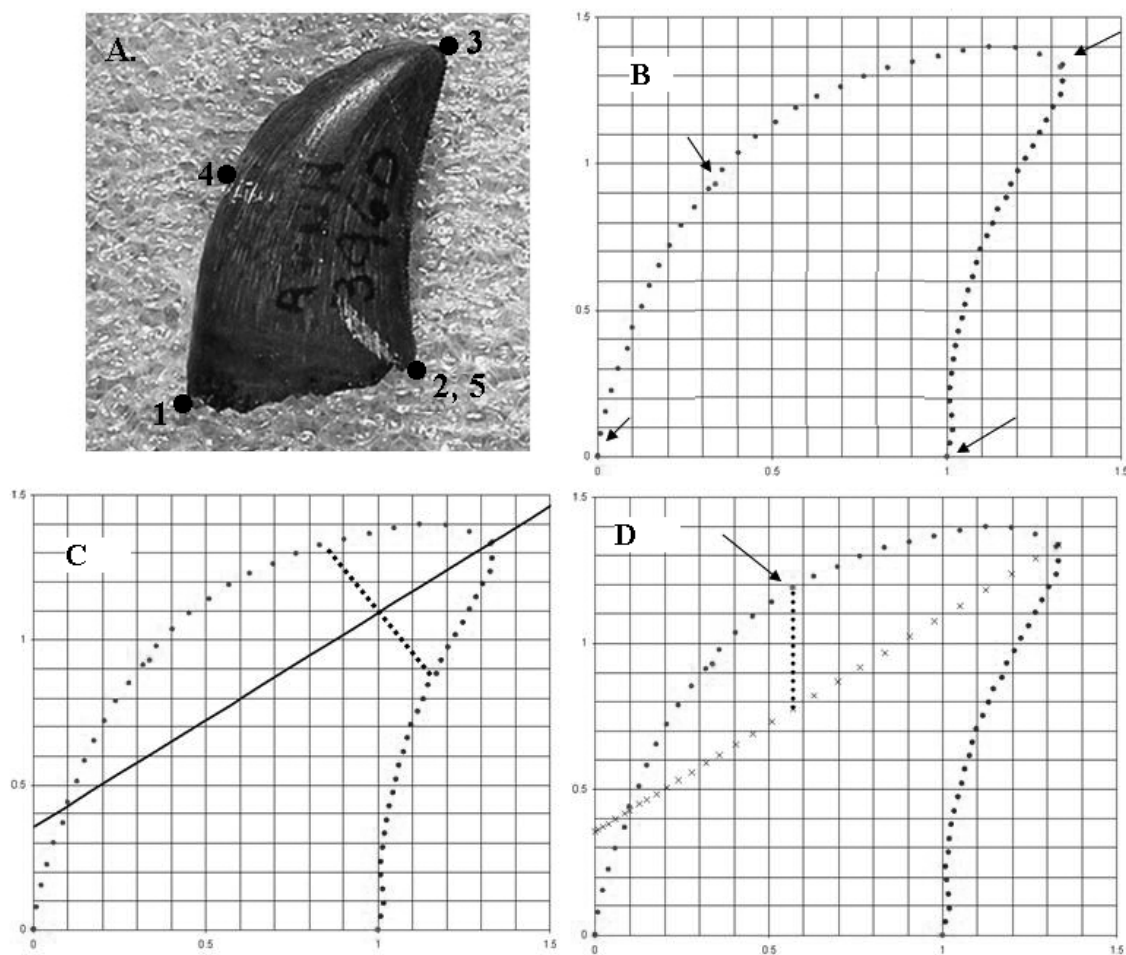
Figure 4.4: Three types of apex conditions in theropod teeth An unworn apex is easily distinguished (*left*). An apex that has been worn (*middle*) is indicated by a change in color and a rounded, polished appearance. A broken apex has jagged edges with little polishing (*right*). A black spot signifies the apical landmark. (Scale = 5mm)
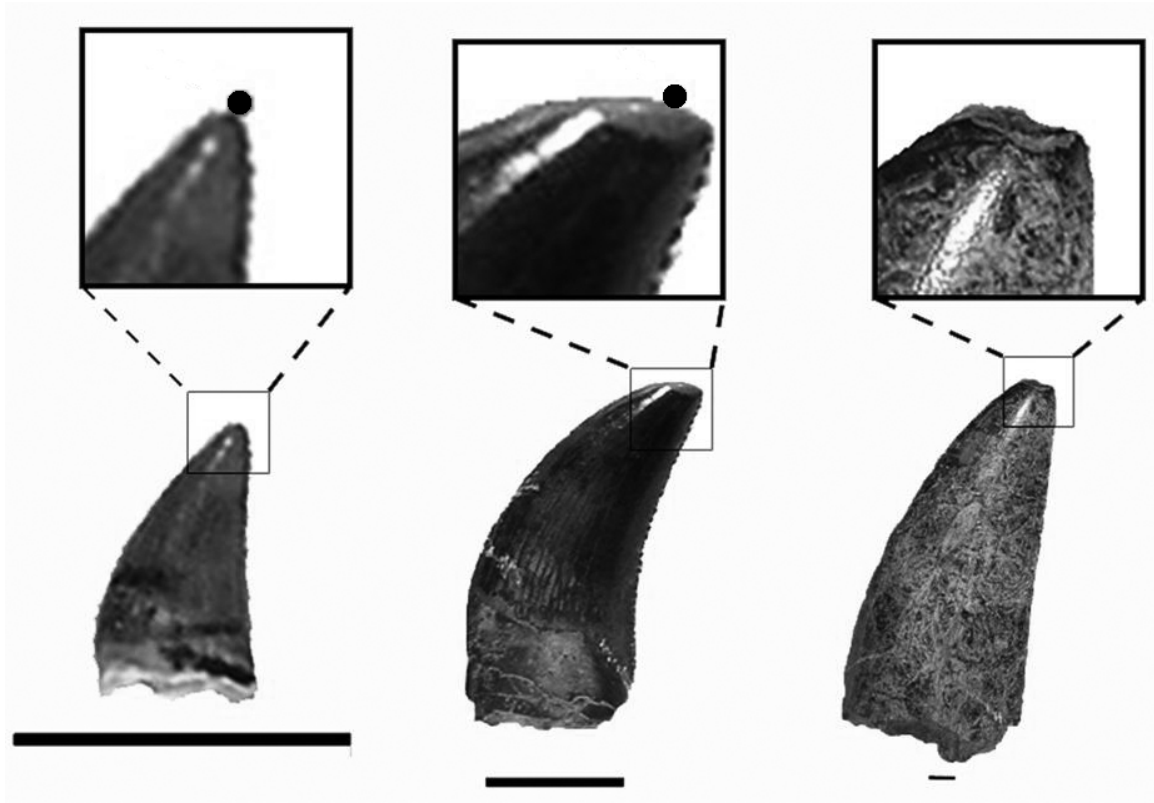
Figure 4.5: The hypothetical terminal denticle (HTD) plotted against the mesial terminal denticle (MTD). The solid line is the regression function for these data. The segmented line indicates a hypothetical regression that would exist if HTD were made equal to MDT.
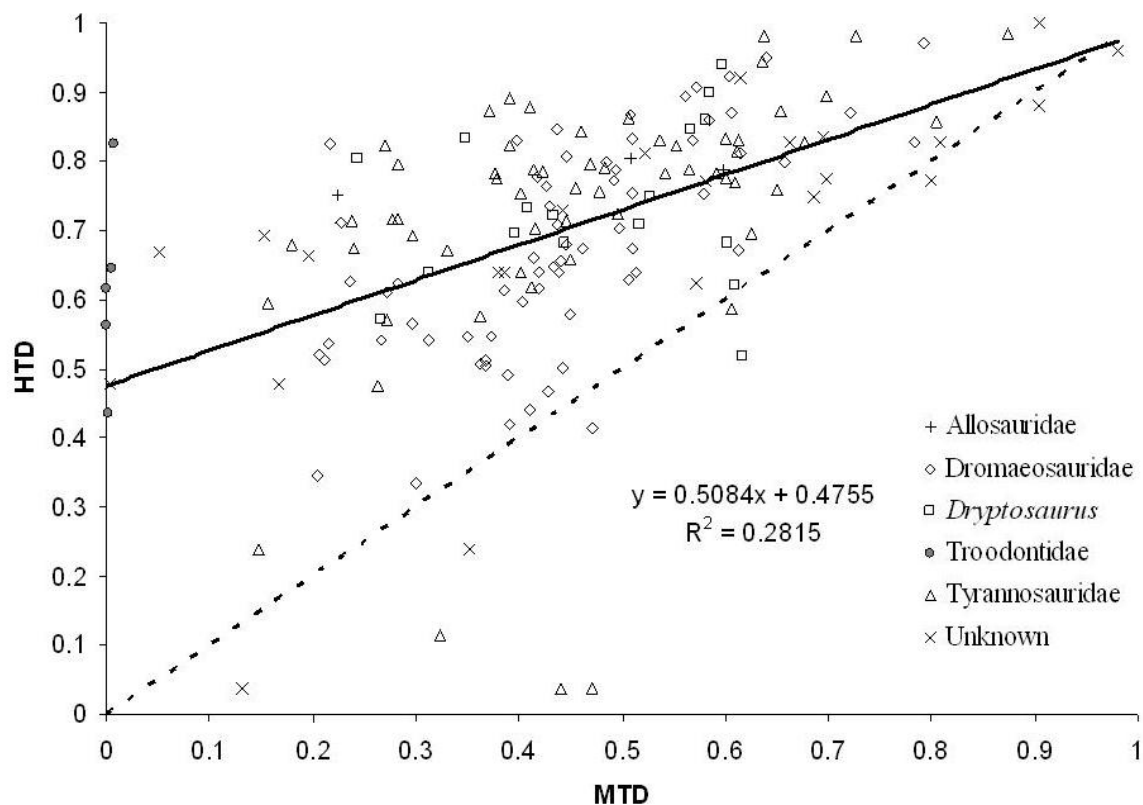
Figure 4.6: The height of the apex (CA), and the relative heights of the mesial terminal denticle (MTD), distal terminal denticle (DTD), and hypothetical terminal denticle (HTD), plotted against the angle of the line of action (LOA˚). CA is in Bookstein coordinates. MTD, DTD, and HTD are percentages of the CA.
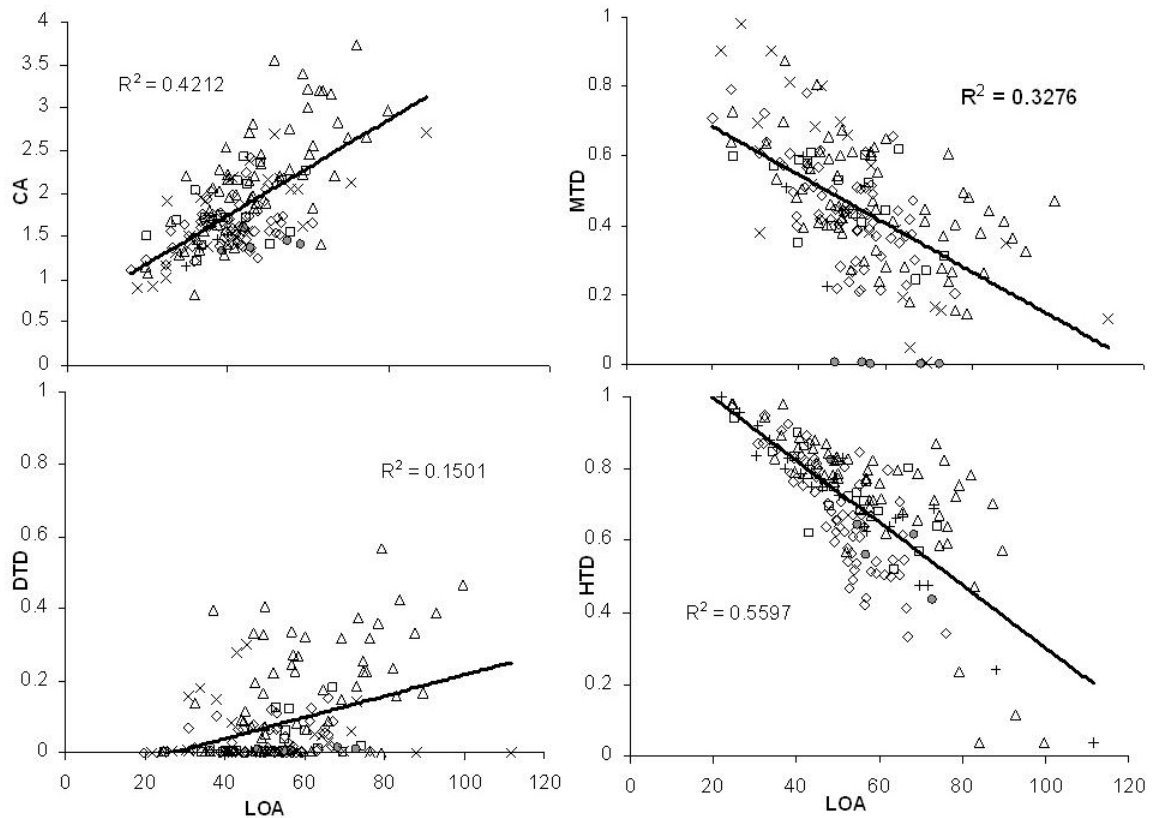
+ Allosauridae
◇ Dromaeosauridae
□ *Dryptosaurus*
● Troodontidae
△ Tyrannosauridae
× Unknown

Figure 4.7: The difference between the relative height of mesial (MTD) and distal terminal denticles (DTD) plotted against the angle of the line of action (LOA˚). (Scale= 5 mm)
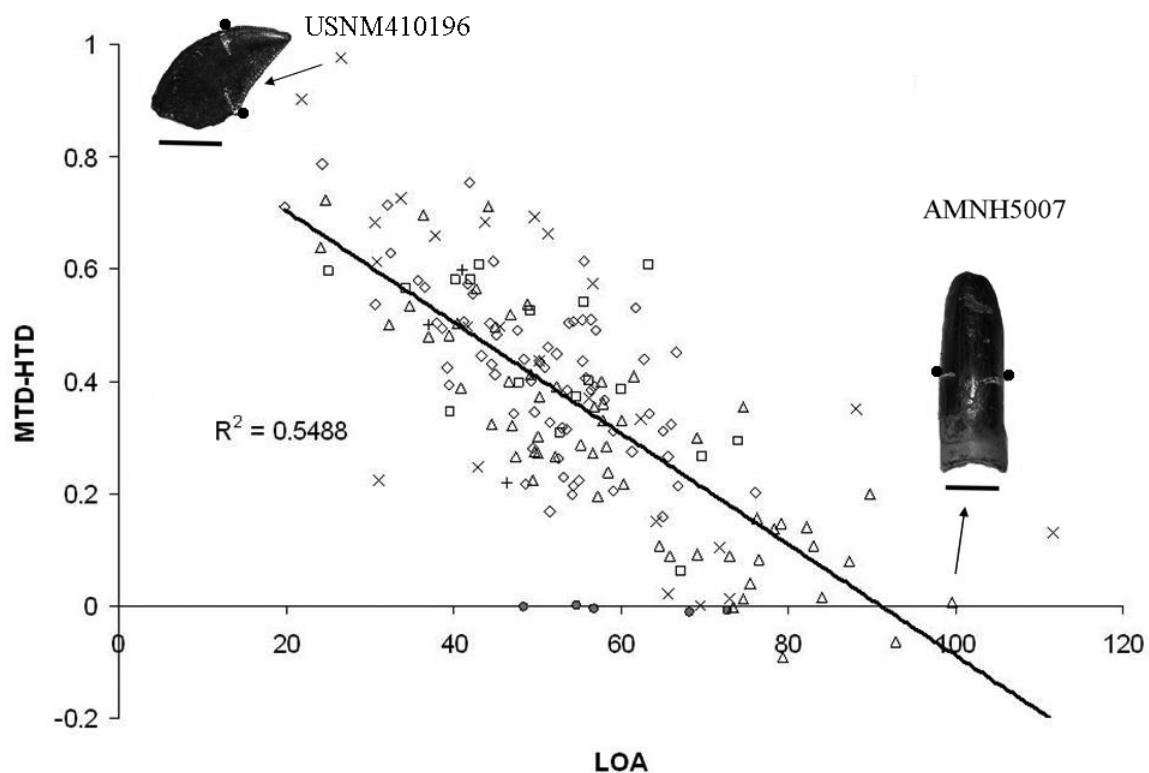
+ Allosauridae

◇ Dromaeosauridae

□ *Dryptosaurus*

• Troodontidae

△ Tyrannosauridae

× Unknown

Figure 4.8: The angle of the line of action (LOA°) and the relative height of the mesial (MTD) and hypothetical terminal denticle (HTD) plotted against tooth position. Dentary teeth are on the left and maxillary/premaxillary teeth are on the right. LOA° is in degrees and MTD and HDT are percentages of CA. For graphs representing the HTD/MTD, the MTD symbols are filled in gray.
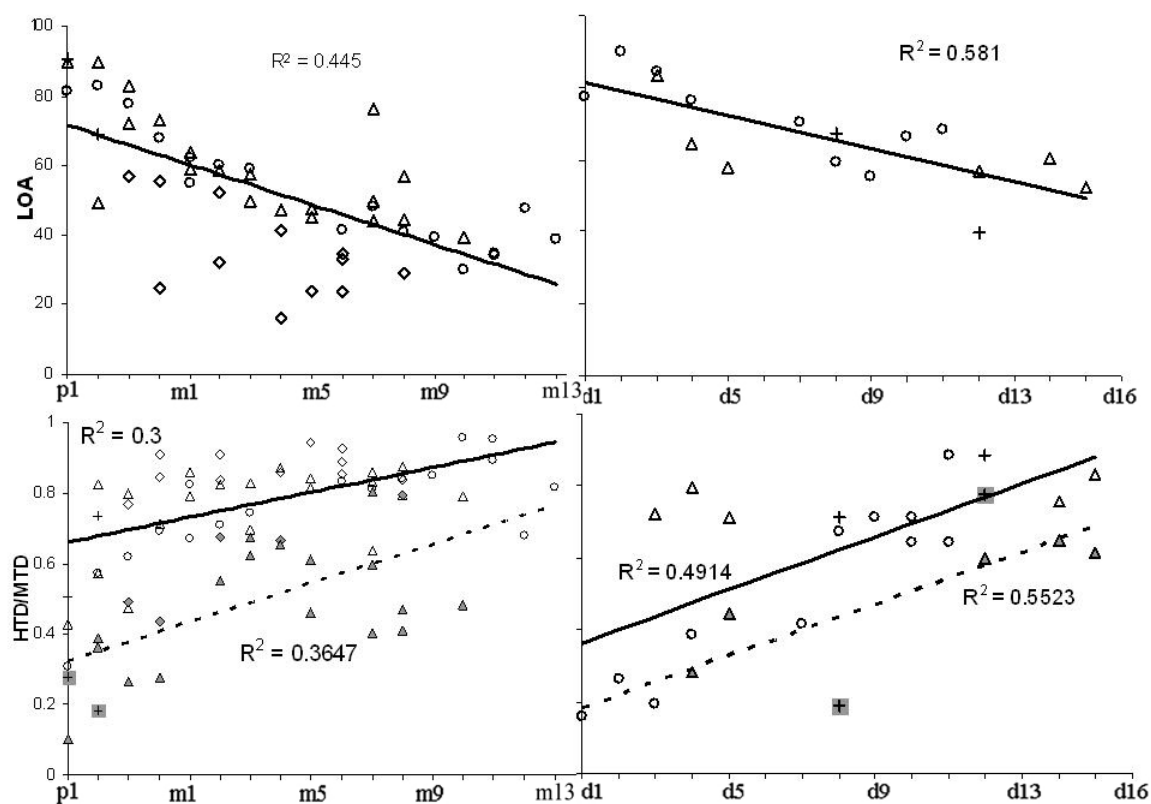
Figure 4.9: Principal component two (PC2) plotted against principal component one (PC1). Sample teeth depicting the morphometric variance along each axis are displayed. The mesial and distal terminal denticle landmarks are marked in red. All teeth have the specimen number (*above*) and component value (*below*). The distal face of each tooth is to the right. (Scale= 5mm)
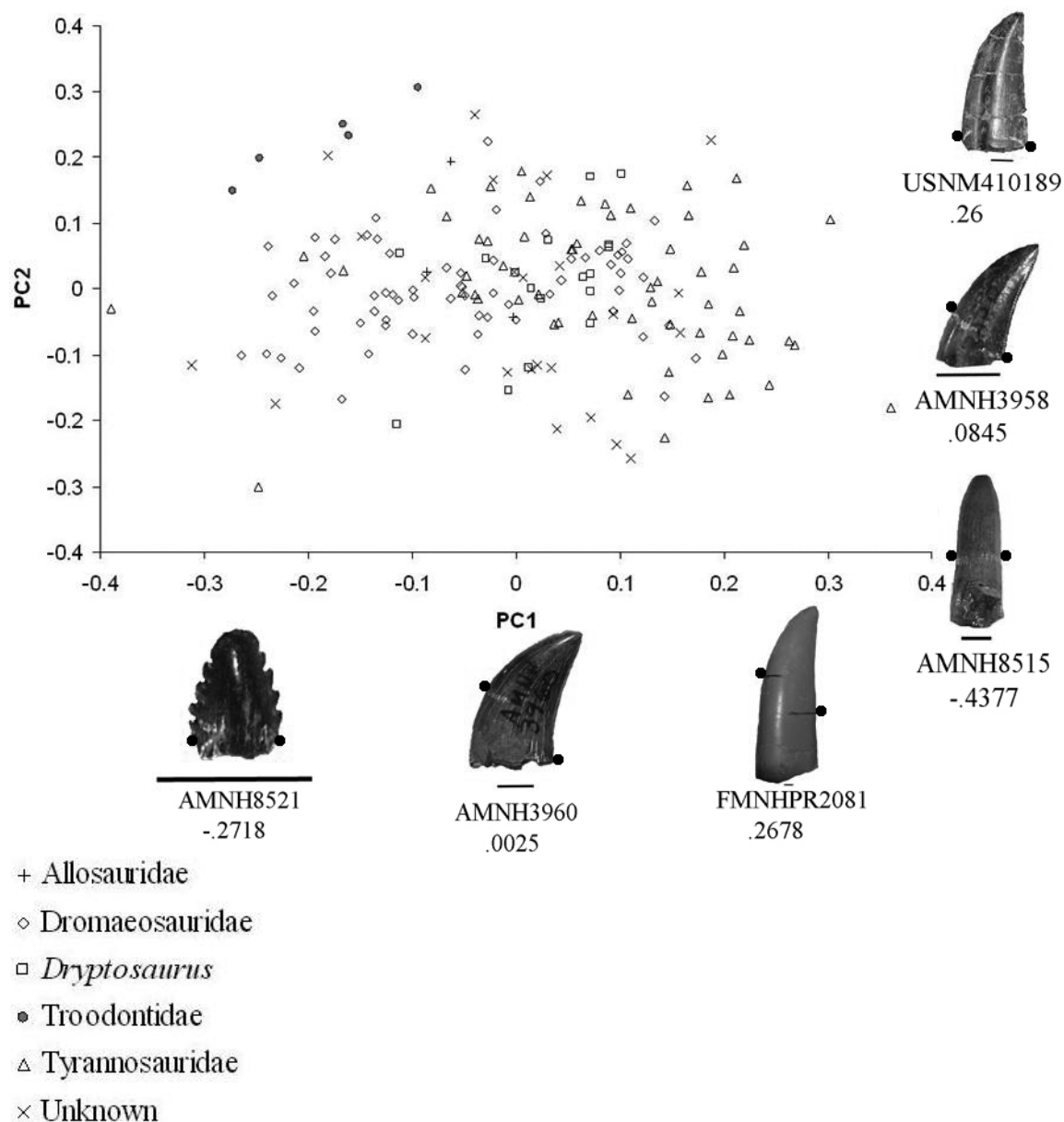
Figure 4.10: Principal component four (PC4) plotted against principal component three (PC3). Sample teeth depicting the morphometric variance along each axis are displayed. The mesial and distal terminal denticle landmarks are marked in red. All teeth have the specimen number (*above*) and component value (*below*). The distal face of each tooth is to the right. (Scale= 5 mm)
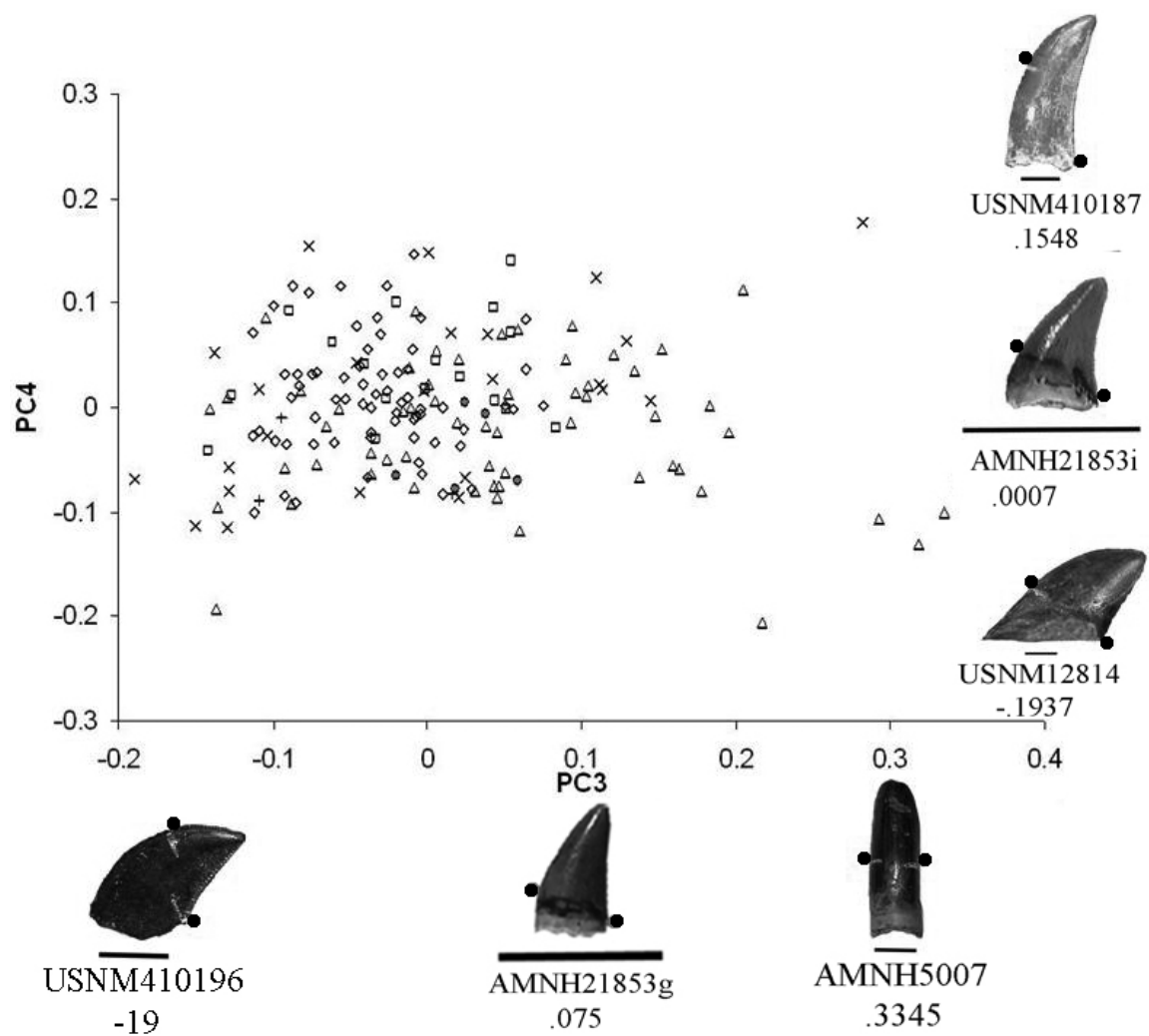
+ Allosauridae

◇ Dromaeosauridae

□ *Dryptosaurus*

● Troodontidae

△ Tyrannosauridae

✕ Unknown

Figure 4.11: Straight and curved lines of action for a range of teeth. The top row is the line of action as determined by the model proposed here, factoring out rotation. The dead space produced underestimates the extent of denticulation. The middle row displays a curved line of action when rotation is considered. The rotation results in more of the mesial margin contacting the substrate. The bottom row is actual teeth from the sample. (Scale= 5mm)

AMNH5007   AMNH21853g   USNM410196
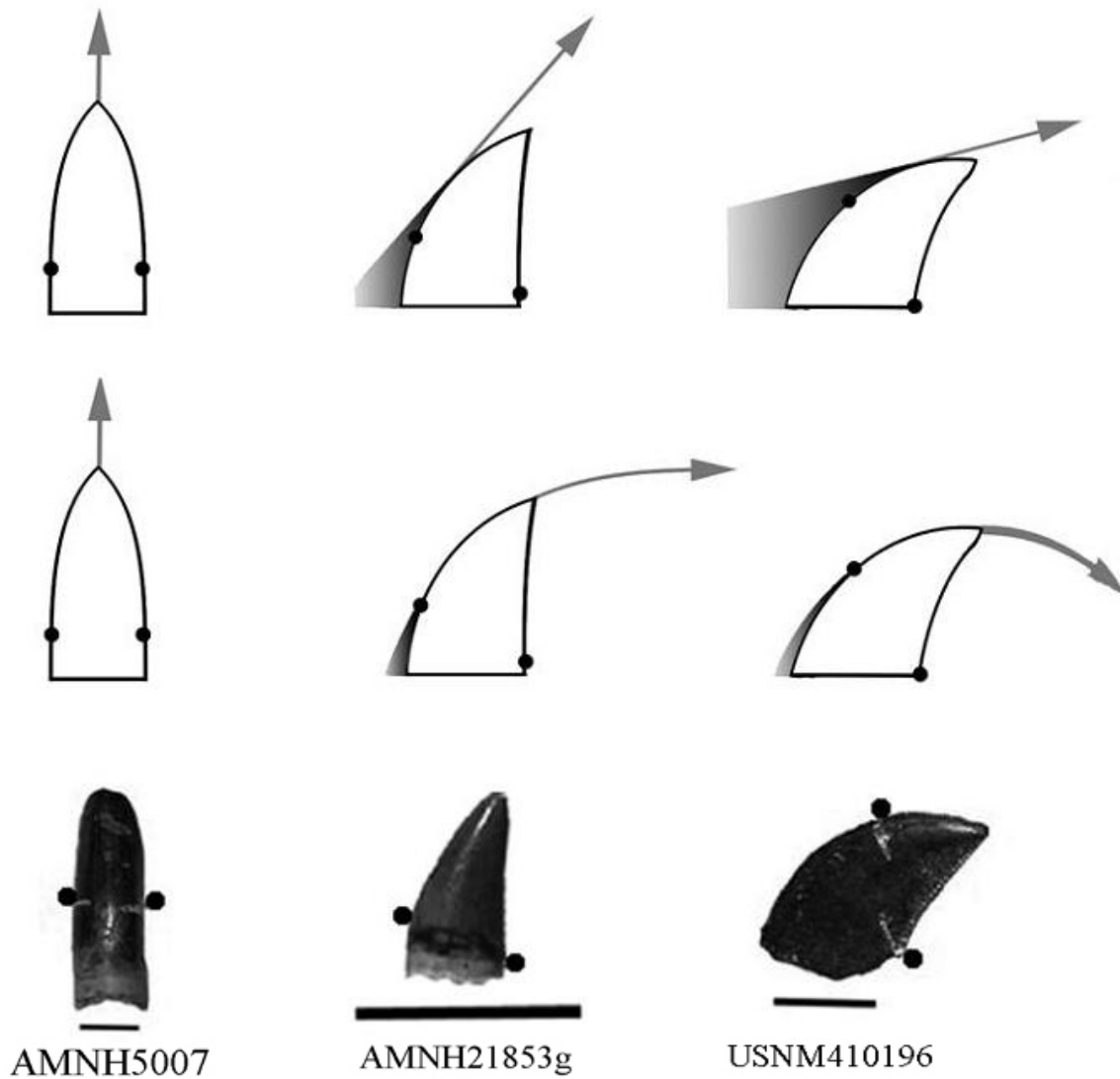
Figure 4.12: Apex curvature versus position along the dental arcade. Tooth '3' has a high degree of distal curvature and makes apical contact with the substrate at point A. Tooth '2' must have less of a curved apex in order for it to strike properly at point B. Tooth '1' shows very little distal curvature, and strikes the substrate at the least acute angle at point C. All teeth achieve axial loading. All teeth have also rotated the same number of degrees between A. and C., but because tooth '3' is closest to the hinge it will undergo the most rotation during its movement through the substrate.
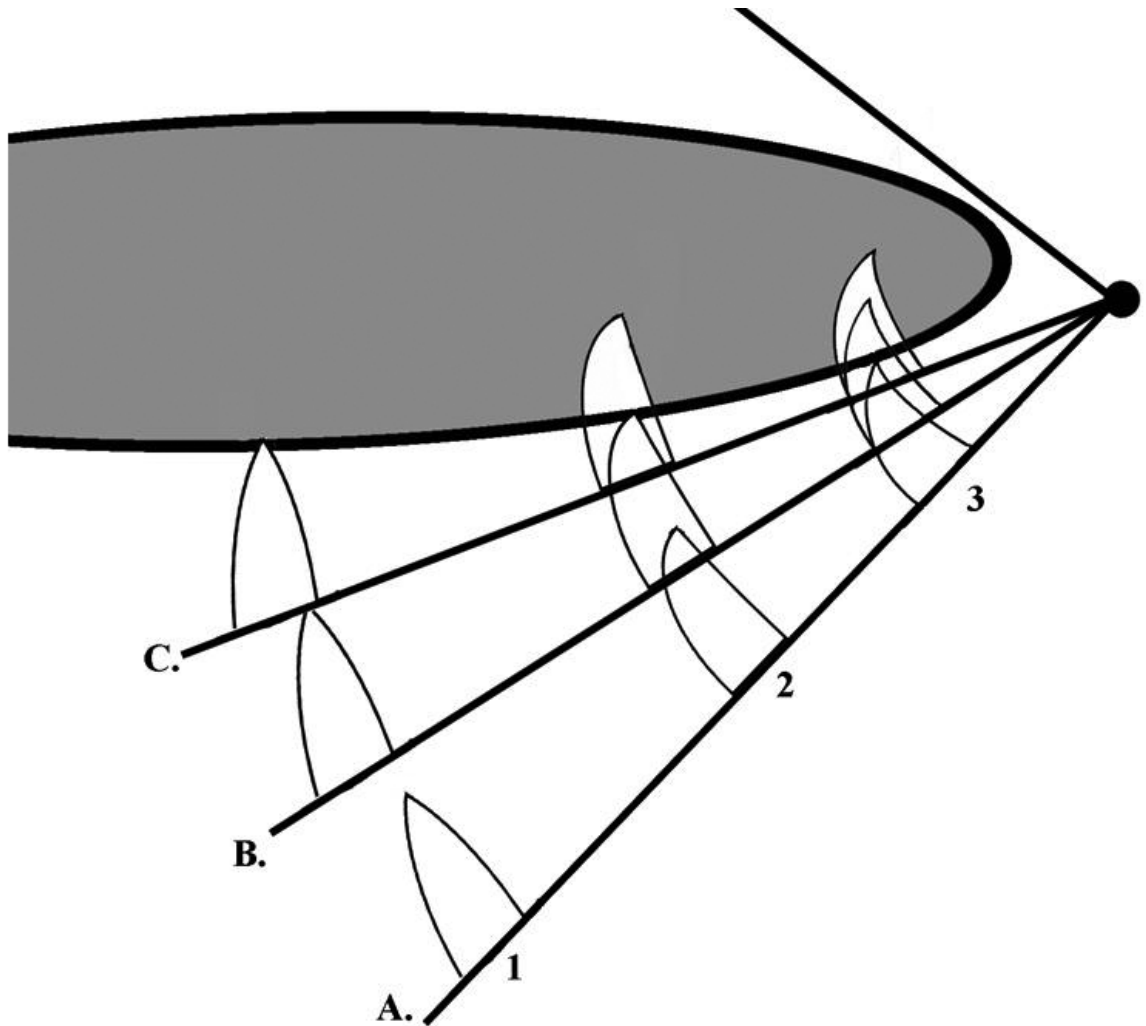
CHAPTER 5: General discussion

Theropod dinosaurs were the major terrestrial predators for most of the Mesozoic. Due in part to their large size and structural features, there is a great deal of interest in the feeding dynamics of these animals. Most research investigating dinosaur carnivory has been based on functional models, including cranial structuring, musculature, and kinesis (Busbey, 1995; Henderson, 1998, 2002; Mazzetta et al., 1998; Molnar, 1998; Rayfield et al, 2001, 2007; Rayfield, 2004), forelimb and hind limb structure (Ostrom, 1969a; Sereno, 1993; Holtz, 2002; Tykoski and Rowe, 2004), and general size and body dimensions (Farlow et al., 1995; Larson, 1997; Fastovsky and Smith, 2004; Seller and Manning, 2007). Significantly less research has been concerned with the structure and function characteristic of theropod ziphodont dentition. Ichnological and taphonomic evidence, such as coprolites (Chin et al, 1998), tooth marks (Fiorillo 1991; Jacobsen 1995, 1998; Erickson and Olson 1996; Rogers et al. 2003; Fowler & Sullivan 2006), isolated teeth (Buffetaut & Suteethorn, 1989; Horner and Lessem, 1994; Maxwell and Ostrom, 1995), etc., have also been used to expand upon theropod feeding ecology. Very few of the conclusions drawn based on this evidence have been authenticated by experimental evidence with an appropriate modern analogue.

The major goal of this dissertation is to develop novel techniques to further elaborate upon carnivorous dinosaur feeding dynamics. I focus on dental functional morphology, behavior as it relates to tooth use, and taphonomic traces resulting from tooth use in ziphodont carnivores. Actualistic experimentation with a modern dental analogue, the Komodo monitor (*Varanus komodoensis*), is used to draw rigorous

conclusions about feeding behavior and tooth mark production. I evaluate the function of

theropod teeth through the morphometric analysis of functionally relevant characteristics

such as denticulation. I also develop criteria to allow for the determination of the size of

a ziphodont consumer based on tooth mark striations. The techniques used in this

research, as well as new approaches to the systems investigated here, may be applied to

future research endeavors to further understand the paleoecology of carnivory.

Research Summary:

Actualistic feeding studies investigated the defleshing behavior characteristic of a

ziphodont consumer for the first time. Aside from outlining the unique feeding behavior

of *V. komodoensis* in detail, I was also able to display how this behavior related to

ziphodont tooth function. When defleshing, lateral rotation of the rostrum moves it

medial in reference to the mid-line of the body, while neck and forelimb movements

bring the rostrum caudal to its starting position. This results in an arching motion termed

the 'medial-caudal arc.' The teeth are drawn distally through the substrate, and are then

withdrawn and the process is repeated. This allows *V. komodoensis* to use its ziphodont

teeth to cut through flesh and section off pieces, which are then swallowed via inertial

feeding. Ziphodonty is ideal for the removal of flesh as seen here by distally drawing

teeth. There is no evidence of bone crushing, and skeletal elements are swallowed whole

when possible.

This is the first study to outline actualistically derived tooth marks from a

ziphodont consumer and explain their morphology through feeding behavior. Tooth

marks on bone surfaces reflect the unique feeding behavior of *V. komodoensis*. The

majority of marks are scores produced by the distal dragging of apices across bone

surfaces. Pits represent apical contact but a lack of distal motion, and are therefore much more rare. Edge marks are unique to ziphodonty because they reflect contact between the distal margins of teeth with the bone surface. Because little bone crushing is seen, few marks enter cancellous bone. Half of the marks display curvature, which reflects the motion of the rostrum during the medial-caudal arc. Marks are frequently parallel, which either represents simultaneous contact with multiple teeth or reflect the repetitive motions seen during defleshing.

A provisional comparison is also made between *V. komodoensis* marks and published accounts of supposed fossil theropod marks. This comparison is useful in yielding inferences about the nature of theropod feeding behavior and bone modification. Parallel scoring characteristic of theropod tooth marks may represent the repetitive distal dragging of tooth apices across bone surfaces, and the lack of curvature reflects less lateral movement during defleshing. Deep puncturing found suggests a bite force larger than that of *V. komodoensis*. Mark production in theropods may also be higher than previously thought, and is underrepresented due to taphonomic or collecting biases.

Data about tooth function is also quantitatively derived from the extent of denticulation in ziphodont teeth. For the first time I expand upon the morphological condition of denticulated carinae, as well as propose a functional model for this condition. The mesial margin tends to be partially denticulated in theropods. The model explains this by proposing that the area of a tooth that does not contact the substrate will not be denticulated. When a tooth is drawn through the substrate, a portion of the mesial margin does not contact the substrate. This area is defined as the tooth's dead-space, and the direction of tooth movement is the line of action. Teeth with an acute line of action

tend to have larger dead spaces, and consequently have less denticulated mesial margins than their less acute counterparts. The distal margin is extensively denticulated because it almost always contacts the substrate. Dental serial homology reflects decreasing mesial denticulation as one moves distal in position along the dental arcade. This is a reflection of the distance between each tooth and the hinge(s) that the jaw rotates around.

A link between tooth morphology and the behaviors witnessed in modern ziphodont consumers was made for the first time. The acute lines of action seen in many theropod teeth suggest that there was additional distal movement during defleshing then what could be produced solely by adduction. Theropods may have drawn their teeth distally through the substrate in a similar fashion to the medial-caudal arc witnessed in *V. komodoensis*. These teeth would consequently cut flesh through a distally oriented puncture.

Striated tooth marks produced by ziphodont carnivores are believed to reflect the width of the denticles of the consumer (Rogers et al., 2003). Although postulated by previous researchers, I tested this theory by comparing actualistically produced striated tooth marks with the denticles of similar sized individuals.   Striated tooth marks can underestimate, but never overestimate, denticle widths. The mark on a carcass with the maximum striation width usually reflected the size of the consumer accurately. In addition, I make a correlation between denticle size and body size in both *V. komodoensis* and theropods. Due perhaps to similar tooth function, these taxonomically distant groups plot along very similar allometric curves. Therefore, the size of a ziphodont consumer may be determined solely from tooth mark striations. Due to the allometric curve, the accuracy of this system is reduced as body size increases.

In summary, all the techniques developed here yield reliable conclusions that can be applied to extinct systems to better understand ziphodont paleobiology. The feeding behavior of a ziphodont consumer is observed and evaluated. Evidence of these behaviors in the form of tooth marks can be used to further corroborate similar behaviors in extinct taxa. The functional morphology of ziphodont denticulation is addressed and evaluated, and is further explained by behaviors witnessed in living ziphodont consumers. Last, tooth marks may also be used to identify predators, allowing for the construction of more refined models of trophic interactions in extinct systems.

<u>Future research:</u>

Although the research presented here has increased our understanding of the nature of ziphodonty, there is huge potential for further research. These techniques may be applied to further answering questions concerning ziphodont paleoecology. In addition, new techniques may be incorporated to further evaluate the systems approached in this investigation.

The range of taxa sampled should be increased. Ziphodonty is defined several times in this dissertation, yet little work has gone into the degree of ziphodonty among groups of taxa. The range of ziphodont taxa sampled in the literature (and this dissertation) tends to consist of mostly coelurosaurs. Future studies should investigate as large a sample of ziphodont and ziphodont-like taxa as possible. This should include a wide range of varanids, pelycosaurs, and archosaurs.

In this dissertation the morphology of ziphodont teeth was only partially investigated to answer the specific questions posed. Future research should focus on more in depth morphometric analyses of ziphodont structures. Previous morphometric

studies of theropod teeth have been limited to simple Euclidean distances to describe teeth. More advanced techniques such as geometric morphometric software and computer tomographic scanning, as well as positioning and jaw structure, should be incorporated. These techniques will not only better reveal dental variability among theropods, but also between theropods and other ziphodont taxa. The latter is especially important. *V. komodoensis* has been frequently compared to theropods. These advanced techniques can determine how similar these two groups are, and to which theropods *V. komodoensis* is most similar. Both Theropoda and Varanidae also have significant degrees of morphometric variation along the tooth row (personal observation), and the morphometric techniques mentioned above should be applied to determine the degree of heterodonty.

More in depth morphometric analyses will allow for digital modeling of ziphodont teeth. From this, finite element analysis can be used to determine how forces influence tooth structuring. This analysis can determine the direction a tooth can best resist the forces applied by the substrate. A line of action may be produced from this, and feeding behaviors can be implied. This may be conducted on a range of modern varanids. These data can be compared to prey type to produce a functional explanation for the results observed. Theropods can then be compared to the varanids, and behavior conclusions may be drawn based on analogy.

Although both the extent of denticulation and the denticle widths were investigated in detail in this dissertation, many aspects of denticle characters need further consideration. The mesial carina curves lingually in many theropod taxa (Farlow and Pianka, 2002), yet the extent, variability, or purpose of this has not been addressed. The

morphology of the denticles themselves has only been addressed from the perspective of tooth identification (Currie et al., 1990), and denticle dimensions and their functional significance should be investigated further.

Modifying actual substrate with mechanical models of teeth will also test the conclusions proposed here. Following Abler (1992), experimental systems may be set up with artificial teeth to test whether morphology affects the efficiency of a puncture. This can be done to produce actual dead spaces in the substrate, as well as allude to the line of action. Also, Spinosairidae and Troodontidae have unique dental morphology, and are believed to modify different substrate types than the typical theropod. Modeled teeth from a range of theropod taxa should be tested against a variety of substrates to determine tooth performance.

Other dental characters should also be considered in future studies. Tooth wear and wear facet data have indicated tooth movement in many herbivorous taxa (Weishampel, 1981), and have also alluded to ziphodont movement through flesh on occasion (Schubert and Ungar, 2005). Since the line of action was a major focus of this research, wear may provide an indicator of the direction of tooth movement of a tooth through the substrate.

This dissertation outlines the morphology and functional implications of *V. komodoensis* tooth marks, but more data can be collected from similar controlled assemblages. For example, the position of a mark on a particular skeletal element, as well as a mark's position relative to the entire carcass, may be considered. Looking at marks in reference to carcass characteristics can give insight into the defleshing strategy of *V. komodoensis*. Quantitative measurements of muscle masses may also help

determine where on a carcass *V. komodoensis* is more inclined to feed. If marks are supportive in determining higher-level behaviors such as these, then the principles derived can be applied to fossil assemblages.

Although tooth mark morphology has been successfully determined from a modern ziphodont carnivore, it has only been indirectly applied to taphonomic traces from Mesozoic assemblages. Few studies have systematically gone through collections of Mesozoic tooth marks specifically to identify taphonomic traces on bone surfaces (examples in Fiorillo, 1991; Jacobsen, 1995; 1998). In order for direct comparisons to be made, it is essential that fossils with taphonomic traces be identified and catalogued.

Once fossil assemblages with marks have been identified, the *V. komodoensis* controlled assemblages should be directly compared to them to test their validity and draw further behavioral and paleoecological conclusions about theropod feeding dynamics. Researchers documenting fossil tooth marks must have extensive experience with modern control collections, such as the ones produced here. They should "pass" blind tests of identification accuracy, and demonstrate high intra- and inter-analyst correspondence in mark identification (Blumenschine et al., 1996). The controlled assemblages produced here can be made available so researches can gain such experience. Fossil collections should be examined using similar technique to those proposed in this dissertation research. In addition, many of the techniques used here are quantitative. Statistics may therefore be incorporated to determine if there is a significant similarity between the two sets of marks. This will achieve two functions. First, this will authenticate that a ziphodont consumer made the mark, as opposed to trampling, diagenesis, etc. Second, similarities and differences in tooth function and behaviors can

be derived from these comparisons. For example, curvature in *V. komodoensis* tooth marks results from lateral head motion during feeding. Fossil mark curvature should indicate the general direction of theropod head movement as well.

V. komodoensis striated marks were shown to reflect the size of the consumer, so Mesozoic assemblages should be investigated specifically for striated marks. This will narrow down the list of potential consumers, and help recreate more refined secondary consumer level interactions. Because striation width is not a perfect indicator, other lines of taphonomic evidence narrowing down potential consumers, such as breakage patterns, skeletal part profiles, and electron microscopy, should also be applied to marked assemblages (see Pobiner and Blumenschine, 2003; Drumheller et al., 2007). These multiple lines of evidence will dramatically increase the reliability in identifying potential assemblage accumulator.

Although using captive *V. komodoensis* specimens for actualistic research has been very insightful, this methodology has several limits. Captive feeding trials deviate from natural circumstances in many ways, and further actualistic experimentation with *V. komodoensis* in a natural setting would allow for more in depth conclusions about this species' feeding habits and about ziphodonty in general. Nature would allow for a larger sample size, which would allow one to control for size, age, or sex. This would also allow for prey size/species to be considered as a variable. The artificially sectioned carcasses used here may have influenced mark production, and using unmodified carcasses in the future is encouraged. Last, competitive group feeding characterizes wild *V. komodoensis*. A natural setting would allow for this behavior to be observed and determine if it affect tooth mark production.

Feeding experiments with *V. komodoensis* can also yield interesting data outside of taphonomy. Carcass consumption sequences of mammals have shown how feeding on prey is determined by the efficiency of calorie intake (Blumenschine, 1986). Within bone nutrients play a major role in carcass processing, and mammalian carnivores tend to be limited by their bone crushing ability. Within bone nutrients are acquired via swallowing bones in *V. komodoensis* as opposed to crushing. It would be interesting to see if the carcass consumption sequence of *V. komodoensis* differs drastically from that of a typical mammalian carnivore.

Bite force is considered to be linked with cranio-dental structuring in theropods. With the exception of tyrannosaurids, theropods are believed to have low bite forces for their body size. Laterally compressed, denticulate teeth supposedly do not need a large bite force because they are optimally built for puncturing and cutting (Huber & Motta, 2004). Therefore the bite force of *V. komodoensis* is of great interest to the paleontological community, yet it has not been directly measured. *V. komodoensis* bite forces estimates have been based on morphometrics, and have been used as models for the determination of theropod bite forces (Weishampel et al., 2004; Therrian et al., 2005). Finite element data has indicated that the skull of *V. komodoensis* would not generate large bite force values (Moreno et al., 2008). Bite force data collected directly from live animals will not only reveal if these models are accurate, but also allow for establishment of more robust models in the future.

Bite force only analyzes force unidirectionally, but as shown in this dissertation there is a large amount of lateral and distal repositioning of the rostrum. The medial-caudal arc shows dramatic movement of the head, neck and forelimbs when defleshing.

This most definitely applies force to its food in a direction other than that of adduction. Finite element analysis has also indicated that the skull is well built to handle stresses in the lateral and caudal directions (Moreno et al., 2008). Measuring the strength of the medial-caudal arc by using a pull gauge should give a more complete picture of ziphodont function.

Last, the medial-caudal arc is described in moderate detail here, but the direction of rostral movement has not been quantified. Cinematography may be used to map the direction of the rostrum from multiple angles. Mapping movement from the dorsal perspective can elaborate upon the degree the rostrum is repositioned during a typical stoke. In this dissertation I determine the line of action of a ziphodont tooth based on its morphology, but in the future laterally positioned cameras can measure adduction and distal tooth motion to determine the line of action with actual behavior. This can then be compared to morphology analyses of *V. komodoensis* teeth to authenticate the functional model proposed here for theropod tooth function, denticulation, and dead-space.

APPENDICES

Appendix 1A: A listing of all striated tooth marks collected. All marks for each *Varanus komodoensis* specimen (left column) resulted from a single feeding trial. Only one of each type of skeletal element was present per feeding. An asterisk represents measurements were taken directly from the bone surface rather than from a mold. 'Cervical', 'thoracic', and 'lumbar' all indicate vertebral elements. 'Sub' is shorthand for sub-parallel. (Straitions=number of striations per mark; Width= width of the entire mark; SW=Striation width)

Name	Number	Location	Element	Mark type	Striations	Width	Regularity	Divergence	SW
Castor	940339	Denver	2nd Rib	score	2	0.31	regular	sub	0.16
			2nd Rib	score	3	0.53	regular	parallel	0.18
			2nd Rib	score	3	0.75	regular	parallel	0.25
			Humerus	score*	7	0.68	regular	parallel	0.1
Nadia	98R046	Miami Metro	Tibia	score*	2	0.25	regular	branched	0.13
			Tibia	score	3	0.44	regular	parallel	0.15
Hannibell	98R068	Miami Metro	12th Rib	score	3	0.28	regular	parallel	0.09
			13th Rib	edge	2	0.13	regular	parallel	0.06
			13th Rib	score	3	0.25	irregular	parallel	0.08
			13th Rib	edge	3	0.44	regular	parallel	0.15
			13th Rib	edge	2	0.34	regular	sub	0.17
			13th Rib	score	2	0.4	regular	sub	0.2
			13th Rib	edge	3	0.61	regular	parallel	0.2
			13th Rib	edge	2	0.5	irregular	parallel	0.25
			13th Rib	edge	unclear	unclear	unclear	unclear	unclear
			Lumbar 3	score	2	0.19	regular	sub	0.09

Name	Number	Location	Element	Mark type	Striations	Width	Regularity	Divergence	SW
Hannibell	98R068	Miami Metro	Lumbar 3	score	6	0.68	regular	parallel	0.11
			Lumbar 3	score	7	1	regular	parallel	0.14
			Lumbar 5	score	3	0.52	regular	parallel	0.17
			Lumbar 5	score	3	0.53	regular	parallel	0.18
			Thoracic 5	score	2	0.13	irregular	sub	0.06
			Thoracic 5	score	2	0.19	regular	parallel	0.09
			Thoracic 5	score	3	0.56	regular	parallel	0.19
			Thoracic 6	score	6	0.5	irregular	parallel	0.08
			Thoracic 6	score*	3	0.31	regular	branched	0.1
			Thoracic 6	score*	3	0.34	regular	parallel	0.11
			Thoracic 6	score	3	0.5	regular	sub	0.17
			Thoracic 6	score	2	0.34	regular	sub	0.17
			Thoracic 6	score	3	0.53	regular	parallel	0.18
Kaos	98R069	Miami Metro	Scapula	score	2	0.34	regular	branched	0.17
			Scapula	score	2	0.4	regular	branched	0.2
Satu	A02439	Denver	7th Thoracic	score*	10	0.38	irregular	sub	0.04
			13th Rib	score	2	0.16	regular	parallel	0.08
			13th Rib	score	6	0.69	regular	parallel	0.11
			13th Rib	score	3	0.63	regular	parallel	0.21
			13th Rib	score	4	0.88	regular	parallel	0.22
			13th Rib	furrow	5	1.25	regular	parallel	0.25
Ramah	A02440	Denver	Femur	score	2	0.31	regular	sub	0.16
Jack	H00957	Miami Metro	1st Rib	score	3	0.5	regular	parallel	0.17
			1st Rib	score	4	0.68	regular	branched	0.17
			1st Rib	edge	3	0.53	regular	parallel	0.18

Name	Number	Location	Element	Mark type	Striations	Width	Regularity	Divergence	SW
Jack	H00957	Miami Metro	1st Thoracic	score	7	0.5	irregular	parallel	0.07
			1st Thoracic	score	10	1	irregular	parallel	0.1
			1st Thoracic	score	3	0.38	regular	branched	0.13
			1st Thoracic	score	3	0.44	regular	parallel	0.15
			1st Thoracic	score	unclear	unclear	unclear	unclear	unclear
			2nd Rib	score	5	0.94	regular	parallel	0.19
			5th Cervical	score	3	0.56	regular	parallel	0.19
Lubier	H00958	Miami Metro	4th Lumbar	score*	3	0.31	regular	parallel	0.1
			4th Lumbar	score*	2	0.28	regular	branched	0.14
			4th Lumbar	score*	2	0.31	regular	branched	0.16
			4th Lumbar	score*	4	0.69	regular	sub	0.17
			4th Lumbar	score*	2	0.38	regular	branched	0.19
			13th Thoracic	score	8	1.66	regular	parallel	0.21

Appendix 1B: Tooth morphometrics for *Varanus komodoensis* dry skull specimens.
'Location' represents the housing bone where the tooth is attached. 'Position' depicts the location of the tooth in reference to other teeth on the same housing bone. Larger numbers indicate a more distal positioning. All morphometrics are in millimeters.

Specimen	Side	Location	Position	d. DW	m. DW	CBL
AMNH 109498	left	Maxilla	5	0.22	0.19	4.96
AMNH 109498	left	Maxilla	6	0.23	0.22	5.11
AMNH 109498	left	Maxilla	7	0.23	-	5.53
AMNH 109498	left	Maxilla	8	0.24	0.2	5.24
AMNH 109498	right	Maxilla	8	0.23	-	5.32
AMNH 109498	left	Maxilla	9	0.22	0.23	5.26
AMNH 109498	right	Maxilla	10	0.21	-	4.92
AMNH 109498	left	Maxilla	11	0.19	0.18	4.35
AMNH 109498	left	Maxilla	12	0.22	0.2	4.08
AMNH 109498	right	Maxilla	13	0.18	-	3.25
AMNH 109498	right	Dentary	4	0.18	0.24	4.42
AMNH 109498	right	Dentary	6	0.25	0.2	5.3
AMNH 109498	left	Dentary	7	0.24	0.24	5.56
AMNH 109498	right	Dentary	7	0.23	-	5.5
AMNH 109498	left	Dentary	9	0.23	0.22	5.18
AMNH 109498	left	Dentary	11	0.24	0.23	5.12
AMNH 109498	right	Dentary	11	0.28	0.24	5.33
AMNH 109498	left	Dentary	12	0.22	0.22	5.33
AMNH 109498	left	Dentary	13	0.22	0.2	4.57
AMNH 109498	right	Dentary	13	0.22	0.21	4.31
AMNH 37908	left	Premaxilla	3	0.12	-	1.51
AMNH 37908	right	Maxilla	2	0.15	-	3
AMNH 37908	left	Maxilla	5	0.21	0.18	4.03
AMNH 37908	right	Maxilla	6	0.18	-	3.6
AMNH 37908	left	Maxilla	7	0.19	0.14	3.73
AMNH 37908	right	Maxilla	8	0.19	-	3.59
AMNH 37908	left	Maxilla	9	0.18	0.16	3.68
AMNH 37908	right	Maxilla	10	0.18	-	3.26
AMNH 37908	left	Maxilla	11	0.16	0.15	3.08
AMNH 37908	right	Maxilla	11	0.17	0.15	3.08
AMNH 37908	left	Maxilla	12	0.17	-	2.85

Specimen	Side	Location	Position	d. DW	m. DW	CBL
AMNH 37908	right	Maxilla	12	0.18	0.15	2.85
AMNH 37908	left	Maxilla	13	0.15	0.15	2.24
AMNH 37908	right	Maxilla	13	0.16	0.17	2.24
AMNH 37908	right	Dentary	2	0.18	-	2.16
AMNH 37908	right	Dentary	3	0.19	0.19	2.58
AMNH 37908	left	Dentary	4	0.19	0.12	2.76
AMNH 37908	right	Dentary	4	0.19	0.16	2.75
AMNH 37908	right	Dentary	5	0.22	0.16	3.79
AMNH 37908	left	Dentary	6	0.18	0.14	3.51
AMNH 37908	right	Dentary	7	0.21	0.16	3.79
AMNH 37908	left	Dentary	8	0.2	0.16	3.83
AMNH 37908	left	Dentary	10	0.2	0.15	3.79
AMNH 37908	right	Dentary	10	0.2	0.17	3.69
AMNH 37908	right	Dentary	11	0.21	-	3.64
AMNH 37908	left	Dentary	12	0.19	0.16	3.28
AMNH 37908	right	Dentary	12	0.19	0.2	3.21
AMNH 37908	right	Dentary	13	0.17	0.16	2.7
AMNH 37909	left	Maxilla	5	0.24	0.23	6.53
AMNH 37909	right	Maxilla	6	0.23	0.2	6.34
AMNH 37909	left	Maxilla	7	0.23	0.19	6.53
AMNH 37909	right	Maxilla	7	0.24	0.21	6.46
AMNH 37909	left	Maxilla	8	0.22	0.19	6.4
AMNH 37909	right	Maxilla	8	0.25	0.23	6.82
AMNH 37909	right	Maxilla	9	0.24	0.21	6.33
AMNH 37909	right	Maxilla	11	0.25	0.21	5.77
AMNH 37909	left	Dentary	6	0.24	0.22	5.89
AMNH 37909	right	Dentary	6	0.25	-	6.09
AMNH 37909	left	Dentary	7	0.24	0.23	6.34
AMNH 37909	right	Dentary	7	0.24	0.23	6.33
AMNH 37909	right	Dentary	9	0.24	0.22	6.36
AMNH 37909	right	Dentary	11	0.24	0.22	5.92
AMNH 37909	right	Dentary	12	0.24	0.2	5.66
AMNH 37909	left	Dentary	13	0.24	0.24	5.25
AMNH 37910	left	Maxilla	3	0.21	0.16	4.26
AMNH 37910	left	Maxilla	5	0.21	0.18	4.93
AMNH 37910	right	Maxilla	6	0.13	0.18	5.05
AMNH 37910	left	Maxilla	7	0.22	0.17	5.18
AMNH 37910	right	Maxilla	7	0.2	0.19	4.79

Specimen	Side	Location	Position	d. DW	m. DW	CBL
AMNH 37910	right	Maxilla	8	0.21	0.19	4.55
AMNH 37910	left	Maxilla	9	0.21	0.19	4.62
AMNH 37910	right	Maxilla	9	0.21	0.19	4.55
AMNH 37910	right	Maxilla	10	0.2	0.18	3.96
AMNH 37910	left	Maxilla	11	0.19	0.18	4.12
AMNH 37910	right	Maxilla	11	0.21	0.16	3.96
AMNH 37910	left	Maxilla	12	0.19	0.18	3.63
AMNH 37910	right	Maxilla	12	0.18	0.18	3.67
AMNH 37910	right	Maxilla	13	0.16	0.17	2.91
AMNH 37911	right	Maxilla	5	0.25	0.25	6.3
AMNH 37911	left	Maxilla	6	0.24	0.22	6.17
AMNH 37911	right	Maxilla	6	0.25	0.24	6
AMNH 37911	left	Maxilla	7	0.25	0.22	6.8
AMNH 37911	right	Maxilla	7	0.25	0.25	6.61
AMNH 37911	left	Maxilla	9	0.26	-	5.94
AMNH 37911	right	Maxilla	9	0.24	0.2	6.1
AMNH 37911	left	Maxilla	11	0.22	0.21	5.2
AMNH 37911	right	Maxilla	11	0.21	0.23	5.25
AMNH 37911	left	Maxilla	12	0.23	0.2	4.6
AMNH 37911	right	Maxilla	13	0.19	0.21	4.02
AMNH 37911	left	Dentary	5	0.26	0.26	5.35
AMNH 37911	right	Dentary	6	0.25	0.22	6
AMNH 37911	left	Dentary	7	0.17	0.23	6.16
AMNH 37911	left	Dentary	9	0.25	0.24	6.37
AMNH 37911	right	Dentary	9	0.28	0.26	6.52
AMNH 37911	left	Dentary	11	0.24	0.22	6.06
AMNH 37911	right	Dentary	11	0.25	0.22	6.05
AMNH 37911	left	Dentary	12	0.25	0.25	5.85
AMNH 37911	left	Dentary	13	0.23	0.23	5.05
AMNH 37911	right	Dentary	13	0.22	0.21	4.6
AMNH 37912	right	Maxilla	5	0.26	0.23	5.78
AMNH 37912	left	Maxilla	6	0.24	0.22	5.86
AMNH 37912	right	Maxilla	6	0.25	0.22	5.99
AMNH 37912	left	Maxilla	7	0.23	0.21	5.91
AMNH 37912	left	Maxilla	8	0.23	0.2	6.38
AMNH 37912	right	Maxilla	8	0.24	0.22	5.93
AMNH 37912	left	Maxilla	9	0.22	0.2	5.36
AMNH 37912	left	Maxilla	10	0.21	0.21	5.51

Specimen	Side	Location	Position	d. DW	m. DW	CBL
AMNH 37912	left	Maxilla	13	0.19	0.21	3.97
AMNH 37912	left	Dentary	5	0.26	0.23	5.32
AMNH 37912	right	Dentary	7	0.24	0.23	5.88
AMNH 37912	left	Dentary	8	0.25	0.25	6.34
AMNH 37912	right	Dentary	8	0.24	0.23	5.66
AMNH 37912	right	Dentary	9	0.25	0.22	5.7
AMNH 37912	left	Dentary	10	0.25	0.24	6.17
AMNH 37912	right	Dentary	10	0.24	0.21	5.59
AMNH 37912	right	Dentary	11	0.24	0.23	5.06
AMNH 37912	left	Dentary	12	0.24	0.25	5.71
AMNH 37912	right	Dentary	12	0.24	0.22	5.19
AMNH 37912	left	Dentary	13	0.2	0.21	5.06
AMNH 37912	right	Dentary	13	0.22	0.22	4.86
AMNH 37913	right	Maxilla	5	0.25	0.19	6.04
AMNH 37913	left	Maxilla	6	0.22	0.19	5.53
AMNH 37913	right	Maxilla	6	0.21	-	5.59
AMNH 37913	right	Maxilla	7	0.23	-	5.81
AMNH 37913	left	Maxilla	8	0.21	0.16	5.52
AMNH 37913	right	Maxilla	8	0.22	0.19	5.95
AMNH 37913	right	Maxilla	9	0.23	0.2	5.86
AMNH 37913	left	Maxilla	10	0.22	0.18	5.42
AMNH 37913	right	Maxilla	10	0.23	0.19	5.47
AMNH 37913	left	Maxilla	12	0.22	0.22	4.54
AMNH 37913	right	Maxilla	12	0.21	0.21	4.51
AMNH 37913	right	Maxilla	13	0.18	0.2	3.87
AMNH 74606	left	Maxilla	6	0.22	0.21	5.61
AMNH 74606	right	Maxilla	7	0.23	0.22	6.27
AMNH 74606	left	Maxilla	8	0.22	0.21	5.57
AMNH 74606	right	Maxilla	8	0.23	0.22	5.92
AMNH 74606	right	Maxilla	9	0.23	0.21	5.87
AMNH 74606	left	Maxilla	10	0.22	0.2	5.2
AMNH 74606	right	Maxilla	10	0.22	0.21	5.3
AMNH 74606	left	Maxilla	11	0.22	0.19	5.26
AMNH 74606	left	Maxilla	12	0.21	0.2	4.69
AMNH 74606	right	Maxilla	13	0.19	0.18	3.78
AMNH 74606	left	Dentary	1	0.19	-	2.55
AMNH 74606	right	Dentary	1	0.21	-	2.65
AMNH 74606	left	Dentary	2	0.24	0.21	3.65

Specimen	Side	Location	Position	d. DW	m. DW	CBL
AMNH 74606	right	Dentary	3	0.24	0.23	4.28
AMNH 74606	right	Dentary	5	0.23	0.23	5.42
AMNH 74606	left	Dentary	6	0.24	0.2	5.73
AMNH 74606	right	Dentary	6	0.23	0.21	5.33
AMNH 74606	left	Dentary	7	0.23	0.2	5.94
AMNH 74606	right	Dentary	8	0.23	0.21	5.72
AMNH 74606	left	Dentary	9	0.23	0.21	6.14
AMNH 74606	right	Dentary	10	0.23	0.23	5.6
AMNH 74606	left	Dentary	11	0.22	0.21	5.92
AMNH 74606	right	Dentary	12	0.21	0.18	4.96
AMNH 74606	left	Dentary	13	0.21	0.19	4.15
AMNH 74606	right	Dentary	13	0.21	0.21	4.13
FMNH 22200	left	Maxilla	4	0.24	0.18	4.98
FMNH 22200	right	Maxilla	4	0.18	0.15	3.86
FMNH 22200	right	Maxilla	5	0.21	-	4.59
FMNH 22200	left	Maxilla	6	0.21	0.13	4.82
FMNH 22200	right	Maxilla	6	0.22	0.13	4.93
FMNH 22200	right	Maxilla	7	0.21	0.17	4.77
FMNH 22200	left	Maxilla	8	0.21	0.18	4.72
FMNH 22200	right	Maxilla	8	0.2	-	4.63
FMNH 22200	right	Maxilla	9	0.22	-	4.73
FMNH 22200	left	Maxilla	10	0.21	-	4.37
FMNH 22200	left	Maxilla	11	0.19	-	3.98
FMNH 22200	left	Maxilla	12	0.18	0.14	3.67
FMNH 22200	left	Dentary	1	0.15	-	1.9
FMNH 22200	right	Dentary	2	0.21	-	2.83
FMNH 22200	left	Dentary	3	0.22	0.21	3.5
FMNH 22200	right	Dentary	3	0.23	0.14	3.51
FMNH 22200	left	Dentary	4	0.22	0.18	3.68
FMNH 22200	right	Dentary	5	0.22	0.18	4.06
FMNH 22200	left	Dentary	6	0.22	0.16	4.56
FMNH 22200	right	Dentary	7	0.22	0.2	4.98
FMNH 22200	left	Dentary	8	0.21	-	4.82
FMNH 22200	left	Dentary	10	0.22	0.13	4.59

Appendix 2: All theropod teeth measured. 'Position' is the location of the tooth on the housing bone, with numbers increasing with distal positioning. The angle of the line of action (LOA) is in degrees and the height of the tooth apex (CA) is in Bookstein coordinates. The mesial (MTD), distal (DTD), and hypothetical terminal denticle (HTD) heights are all percentages of the CA. (Institutional Abbreviations; AMNH, American Museum of Natural History; FMNH, Field Museum of Natural History; USNM; National Museum of Natural History)

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
FMNHPR2100	Abelisauridae	Maxilla	4	59.53	1.53	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Maxilla	6	66.31	1.68	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Premaxilla	1	77.41	1.28	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Premaxilla	2	89.91	1.53	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Premaxilla	3	84.45	1.36	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Premaxilla	4	76.17	1.32	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	15	34.28	1.31	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	14	30.08	1.09	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	13	39.40	1.21	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	12	41.17	1.28	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	7	59.20	1.76	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	5	55.11	1.89	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	1	81.24	1.61	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Maxilla	3	70.27	1.27	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Maxilla	5	55.52	1.41	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Maxilla	7	68.21	1.52	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	2	83.06	1.82	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	3	77.93	1.58	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	4	68.08	1.53	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	5	62.01	1.46	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	6	60.20	1.70	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	10	41.26	1.61	-	-	-	-	-	-	-	-

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
FMNHPR2100	Abelisauridae	Dentary	11	48.44	1.61	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	15	34.96	1.91	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	16	47.84	1.24	-	-	-	-	-	-	-	-
FMNHPR2100	Abelisauridae	Dentary	17	38.92	0.63	-	-	-	-	-	-	-	-
AMNH507	Allosauridae	Maxilla	8	39.52	2.05	-	-	-	-	-	-	-	-
AMNH5789	Allosauridae	Isolated	-	46.50	1.45	0.22	0.00	0.75	0.22	-0.06	0.19	0.02	-0.08
AMNH5759	Allosauridae	Isolated	-	37.07	1.15	0.51	0.01	0.80	0.50	-0.09	0.03	-0.11	-0.09
AMNH5759	Allosauridae	Isolated	-	41.03	1.36	0.60	0.00	0.79	0.60	0.00	-0.04	-0.09	-0.01
AMNH851	Allosauridae	Maxilla	4	67.24	1.95	-	-	-	-	-	-	-	-
AMNH851	Allosauridae	Dentary	1	90.75	2.46	-	-	-	-	-	-	-	-
AMNH851	Allosauridae	Dentary	2	68.89	2.25	-	-	-	-	-	-	-	-
AMNH21816b	Dromaeosauridae	Isolated	-	59.10	1.25	0.31	0.00	0.54	0.31	-0.21	0.01	-0.07	-0.01
AMNH21816c	Dromaeosauridae	Isolated	-	57.98	1.55	0.37	0.00	0.51	0.37	-0.19	-0.04	-0.01	-0.01
AMNH21816d	Dromaeosauridae	Isolated	-	59.04	1.79	0.21	0.01	0.51	0.21	-0.17	0.08	0.06	0.00
AMNH21816e	Dromaeosauridae	Isolated	-	50.23	1.51	0.44	0.01	0.64	0.43	-0.11	-0.02	-0.06	0.01
AMNH21816f	Dromaeosauridae	Isolated	-	51.46	1.59	0.24	0.07	0.63	0.17	-0.13	0.11	0.03	-0.08
AMNH21816h	Dromaeosauridae	Isolated	-	53.52	1.61	0.38	0.07	0.61	0.32	-0.10	0.00	-0.02	0.00
AMNH21816i	Dromaeosauridae	Isolated	-	54.12	1.40	0.21	0.01	0.52	0.20	-0.24	0.06	-0.01	-0.05
AMNH21816j	Dromaeosauridae	Isolated	-	50.93	1.55	0.44	0.01	0.71	0.42	-0.05	0.02	-0.05	0.01
AMNH21816k	Dromaeosauridae	Isolated	-	54.31	1.62	0.22	0.00	0.54	0.22	-0.19	0.08	0.02	-0.02
AMNH21816l	Dromaeosauridae	Isolated	-	39.48	1.49	0.40	0.00	0.83	0.39	-0.02	0.12	-0.06	-0.03
AMNH21816m	Dromaeosauridae	Isolated	-	64.96	2.11	0.23	0.07	0.71	0.16	0.02	0.16	0.06	0.04
AMNH21816n	Dromaeosauridae	Isolated	-	52.57	1.55	0.27	0.00	0.54	0.26	-0.18	0.05	0.02	-0.04
AMNH21816o	Dromaeosauridae	Isolated	-	51.60	2.00	0.45	0.12	0.81	0.33	0.08	0.06	-0.01	0.01
AMNH21816p	Dromaeosauridae	Isolated	-	64.92	1.55	0.37	0.06	0.50	0.31	-0.15	-0.05	-0.01	0.04
AMNH21816q	Dromaeosauridae	Isolated	-	76.09	1.65	0.20	0.00	0.34	0.20	-0.23	-0.01	0.06	0.08
AMNH21816r	Dromaeosauridae	Isolated	-	55.06	1.60	0.27	0.05	0.61	0.22	-0.13	0.08	0.00	-0.03

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
AMNH21816s	Dromaeosauridae	Isolated	-	48.36	1.67	0.45	0.01	0.68	0.44	-0.05	0.00	-0.03	0.02
AMNH21816t	Dromaeosauridae	Isolated	-	53.10	1.45	0.30	0.07	0.57	0.23	-0.18	0.02	0.00	-0.06
AMNH21816v	Dromaeosauridae	Isolated	-	41.65	1.61	0.58	0.01	0.75	0.57	-0.03	-0.04	-0.08	0.02
AMNH21816w	Dromaeosauridae	Isolated	-	44.83	2.03	0.61	0.00	0.81	0.61	0.09	-0.03	-0.08	0.11
AMNH21816x	Dromaeosauridae	Isolated	-	56.36	1.32	0.39	0.01	0.42	0.38	-0.26	-0.10	-0.04	-0.02
AMNH21816y	Dromaeosauridae	Isolated	-	49.58	1.69	0.41	0.07	0.66	0.35	-0.05	0.00	0.00	-0.01
AMNH21816z	Dromaeosauridae	Isolated	-	38.72	1.39	0.49	0.00	0.79	0.49	-0.07	0.03	-0.09	-0.04
AMNH21644	Dromaeosauridae	Isolated	-	55.77	1.59	0.43	0.03	0.65	0.41	-0.06	-0.01	-0.04	0.04
AMNH21644	Dromaeosauridae	Isolated	-	61.82	2.04	0.66	0.12	0.80	0.53	0.17	-0.11	-0.06	0.12
AMNH21853a	Dromaeosauridae	Isolated	-	47.16	1.38	0.42	0.08	0.64	0.34	-0.12	-0.01	-0.04	-0.07
AMNH21853b	Dromaeosauridae	Isolated	-	65.64	1.73	0.42	0.15	0.62	0.26	-0.03	-0.04	0.01	0.00
AMNH21853d	Dromaeosauridae	Isolated	-	51.25	1.41	0.46	0.00	0.67	0.46	-0.10	-0.01	-0.09	0.01
AMNH21853f	Dromaeosauridae	Isolated	-	61.36	1.91	0.36	0.09	0.51	0.28	-0.13	-0.05	0.05	0.00
AMNH21853g	Dromaeosauridae	Isolated	-	66.90	1.74	0.30	0.09	0.33	0.21	-0.24	-0.10	0.08	0.00
AMNH21853h	Dromaeosauridae	Isolated	-	63.29	1.69	0.35	0.01	0.55	0.34	-0.13	-0.01	-0.01	0.06
AMNH21853i	Dromaeosauridae	Isolated	-	56.93	1.37	0.41	0.02	0.44	0.39	-0.23	-0.10	-0.04	0.00
AMNH21853j	Dromaeosauridae	Isolated	-	66.54	1.67	0.47	0.02	0.41	0.45	-0.17	-0.17	0.00	0.09
AMNH3958	Dromaeosauridae	Isolated	-	47.66	1.77	0.50	0.01	0.70	0.49	-0.01	-0.02	-0.04	0.06
AMNH3958	Dromaeosauridae	Isolated	-	50.19	1.70	0.44	0.01	0.66	0.44	-0.05	-0.01	-0.02	0.03
AMNH3958	Dromaeosauridae	Isolated	-	44.42	1.71	0.57	0.07	0.83	0.50	0.10	0.00	-0.04	0.00
AMNH3958	Dromaeosauridae	Isolated	-	24.40	1.23	0.79	0.01	0.97	0.79	0.15	-0.06	-0.11	-0.02
AMNH3958	Dromaeosauridae	Isolated	-	19.77	1.10	0.71	0.00	1.02	0.71	0.10	0.06	-0.08	-0.09
AMNH3958	Dromaeosauridae	Isolated	-	41.34	1.69	0.51	0.00	0.83	0.51	0.07	0.05	-0.05	0.03
AMNH3958	Dromaeosauridae	Isolated	-	44.89	1.70	0.42	0.00	0.78	0.41	0.03	0.08	0.00	0.00
AMNH3958	Dromaeosauridae	Isolated	-	45.25	1.76	0.48	0.00	0.80	0.48	0.05	0.04	-0.03	0.03
AMNH3958	Dromaeosauridae	Isolated	-	42.40	1.69	0.56	0.01	0.89	0.55	0.11	0.05	-0.07	0.03
AMNH3958	Dromaeosauridae	Isolated	-	35.71	1.36	0.58	0.00	0.86	0.58	0.04	0.01	-0.07	-0.03

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
AMNH3958	Dromaeosauridae	Isolated	-	32.06	1.56	0.72	0.01	0.87	0.71	0.12	-0.07	-0.07	0.03
AMNH3958	Dromaeosauridae	Isolated	-	32.57	1.37	0.64	0.01	0.95	0.63	0.09	0.04	-0.11	-0.03
AMNH28494	Dromaeosauridae	Isolated	-	52.38	1.51	0.45	0.00	0.58	0.45	-0.13	-0.06	-0.03	0.01
AMNH28494	Dromaeosauridae	Isolated	-	48.68	1.49	0.22	0.00	0.83	0.22	-0.03	0.22	-0.04	-0.03
AMNH28494	Dromaeosauridae	Isolated	-	53.47	1.50	0.39	0.00	0.49	0.38	-0.19	-0.06	-0.02	0.00
AMNH28494	Dromaeosauridae	Isolated	-	39.29	1.20	0.43	0.00	0.76	0.42	-0.12	0.05	-0.09	-0.08
AMNH28494	Dromaeosauridae	Isolated	-	55.36	1.73	0.51	0.00	0.75	0.51	0.03	-0.01	-0.09	0.12
AMNH28494	Dromaeosauridae	Isolated	-	52.97	1.43	0.43	0.11	0.47	0.32	-0.21	-0.12	0.01	-0.08
AMNH28494	Dromaeosauridae	Isolated	-	66.03	1.51	0.37	0.05	0.55	0.32	-0.14	-0.03	-0.03	0.03
AMNH28494	Dromaeosauridae	Isolated	-	54.43	1.39	0.51	0.00	0.63	0.51	-0.10	-0.07	-0.08	0.03
AMNH28494	Dromaeosauridae	Isolated	-	49.53	1.55	0.28	0.00	0.62	0.28	-0.14	0.08	-0.01	-0.03
AMNH28494	Dromaeosauridae	Isolated	-	49.21	1.55	0.40	0.00	0.60	0.40	-0.14	-0.01	-0.02	-0.01
AMNH28494	Dromaeosauridae	Isolated	-	38.09	1.49	0.60	0.10	0.92	0.50	0.10	0.02	-0.10	-0.03
AMNH28494	Dromaeosauridae	Isolated	-	62.79	1.57	0.44	0.00	0.50	0.44	-0.14	-0.10	-0.03	0.07
AMNH23643	Dromaeosauridae	Isolated	-	54.03	2.08	-	-	-	-	-	-	-	-
AMNH23643	Dromaeosauridae	Isolated	-	53.70	1.87	0.51	0.01	0.67	0.50	0.00	-0.05	-0.03	0.09
AMNH23643	Dromaeosauridae	Isolated	-	50.69	1.45	-	-	-	-	-	-	-	-
AMNH21609	Dromaeosauridae	Isolated	-	43.34	1.93	0.51	0.06	0.87	0.45	0.11	0.07	-0.04	0.02
AMNH22670	Dromaeosauridae	Isolated	-	30.72	1.18	0.61	0.07	0.87	0.54	-0.02	-0.01	-0.11	-0.10
AMNH22670	Dromaeosauridae	Isolated	-	41.84	1.76	0.78	0.03	0.83	0.75	0.14	-0.16	-0.10	0.10
AMNH22670	Dromaeosauridae	Isolated	-	36.54	1.65	0.57	0.00	0.91	0.57	0.10	0.05	-0.09	0.03
AMNH22670	Dromaeosauridae	Isolated	-	55.53	1.45	0.61	0.00	0.67	0.61	-0.05	-0.12	-0.11	0.07
AMNH22670	Dromaeosauridae	Isolated	-	21.79	1.14	-	-	-	-	-	-	-	-
AMNH22670	Dromaeosauridae	Isolated	-	48.83	1.38	-	-	-	-	-	-	-	-
AMNH22670	Dromaeosauridae	Isolated	-	56.51	1.73	0.51	0.00	0.64	0.51	-0.04	-0.07	-0.05	0.08
AMNH8516	Dromaeosauridae	Isolated	-	44.53	1.64	0.43	0.00	0.74	0.43	-0.02	0.04	-0.01	-0.01
AMNH30556	Dromaeosauridae	Dentary	8	41.29	2.04	-	-	-	-	-	-	-	-

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
AMNH30556	Dromaeosauridae	Dentary	10	33.12	1.91	-	-	-	-	-	-	-	-
AMNH30556	Dromaeosauridae	Dentary	12	28.92	1.25	-	-	-	-	-	-	-	-
AMNH5356	Dromaeosauridae	Dentary	3	56.94	2.41	0.49	0.00	0.77	0.49	0.12	0.02	-0.01	0.15
AMNH5356	Dromaeosauridae	Dentary	4	55.33	2.25	0.44	0.00	0.85	0.44	0.13	0.10	-0.03	0.12
AMNH5356	Dromaeosauridae	Dentary	6	52.39	2.02	-	-	-	-	-	-	-	-
AMNH6518	Dromaeosauridae	Dentary	4	24.75	1.13	-	-	-	-	-	-	-	-
AMNH6518	Dromaeosauridae	Dentary	6	31.91	1.28	-	-	-	-	-	-	-	-
AMNH6518	Dromaeosauridae	Dentary	10	34.93	1.18	-	-	-	-	-	-	-	-
AMNH30556	Dromaeosauridae	Dentary	8	16.27	1.25	-	-	-	-	-	-	-	-
AMNH30556	Dromaeosauridae	Dentary	9	23.64	1.19	-	-	-	-	-	-	-	-
AMNH30556	Dromaeosauridae	Dentary	10	24.04	1.08	-	-	-	-	-	-	-	-
AMNH5456	*Dryptosaurus*	Isolated	-	55.58	1.72	0.60	0.06	0.68	0.54	0.01	-0.12	-0.06	0.06
AMNH3957	*Dryptosaurus*	Isolated	-	42.06	1.38	0.58	0.00	0.86	0.58	0.01	0.00	-0.13	0.01
AMNH3937	*Dryptosaurus*	Isolated	-	63.41	1.41	0.62	0.01	0.52	0.61	-0.11	-0.21	-0.09	0.09
AMNH3937	*Dryptosaurus*	Isolated	-	40.26	1.22	0.59	0.01	0.90	0.58	0.00	0.02	-0.14	-0.04
AMNH5734	*Dryptosaurus*	Isolated	-	47.83	1.73	0.40	0.00	0.70	0.40	-0.03	0.05	0.00	0.02
AMNH5734	*Dryptosaurus*	Isolated	-	69.62	1.54	0.27	0.00	0.57	0.27	-0.11	0.05	-0.02	0.10
AMNH3968	*Dryptosaurus*	Isolated	-	39.74	2.03	0.35	0.00	0.83	0.35	0.07	0.17	0.04	0.01
AMNH3968	*Dryptosaurus*	Isolated	-	54.80	2.43	0.41	0.04	0.73	0.37	0.09	0.06	0.05	0.07
AMNH3967	*Dryptosaurus*	Isolated	-	25.10	1.51	0.60	0.00	0.94	0.60	0.09	0.07	-0.03	-0.03
AMNH3967	*Dryptosaurus*	Isolated	-	74.01	2.27	0.31	0.02	0.64	0.29	0.03	0.07	0.05	0.14
AMNH3967	*Dryptosaurus*	Isolated	-	34.37	1.68	0.57	0.00	0.85	0.57	0.07	0.02	-0.03	0.01
AMNH3967	*Dryptosaurus*	Isolated	-	49.36	1.72	0.53	0.00	0.75	0.53	0.02	-0.02	-0.04	0.04
AMNH3962	*Dryptosaurus*	Isolated	-	67.21	2.15	0.24	0.18	0.80	0.06	0.10	0.18	0.08	-0.02
AMNH3966	*Dryptosaurus*	Isolated	-	60.05	2.36	0.44	0.06	0.68	0.38	0.07	-0.01	0.04	0.10
AMNH3966	*Dryptosaurus*	Isolated	-	56.21	2.10	0.52	0.12	0.71	0.40	0.07	-0.05	0.02	0.03
AMNH3969	*Dryptosaurus*	Isolated	-	52.84	2.14	0.43	0.13	0.72	0.31	0.07	0.02	0.05	0.00

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
AMNH3961	*Dryptosaurus*	Isolated	-	43.08	1.72	0.61	0.00	0.62	0.61	-0.01	-0.16	0.01	0.04
AMNH22669	Troodontidae	Isolated	-	75.59	1.80	-	-	-	-	-	-	-	-
AMNH8519	Troodontidae	Isolated	-	54.84	1.59	0.00	0.00	0.65	0.00	-0.17	0.25	0.06	-0.07
AMNH8521	Troodontidae	Isolated	-	56.87	1.36	0.00	0.01	0.56	-0.01	-0.25	0.20	0.02	-0.08
AMNH8521	Troodontidae	Isolated	-	72.81	1.41	0.00	0.01	0.43	-0.01	-0.27	0.15	0.04	-0.01
AMNH8521	Troodontidae	Isolated	-	48.51	1.33	0.01	0.01	0.82	0.00	-0.09	0.31	-0.02	-0.07
AMNH8521	Troodontidae	Isolated	-	68.28	1.45	0.00	0.01	0.62	-0.01	-0.16	0.23	0.02	0.01
AMNH28458	Troodontidae	Isolated	-	46.58	1.32	-	-	-	-	-	-	-	-
AMNH21873	Troodontidae	Isolated	-	56.71	1.93	-	-	-	-	-	-	-	-
AMNH21871	Troodontidae	Isolated	-	67.25	1.48	-	-	-	-	-	-	-	-
AMNH8521	Troodontidae	Isolated	-	32.13	1.26	-	-	-	-	-	-	-	-
AMNH8521	Troodontidae	Isolated	-	25.03	1.37	-	-	-	-	-	-	-	-
AMNH8521	Troodontidae	Isolated	-	49.45	1.46	-	-	-	-	-	-	-	-
AMNH21728	Tyrannosauridae	Isolated	-	46.80	1.65	0.59	0.07	0.78	0.52	0.04	-0.05	-0.06	0.00
AMNH5007	Tyrannosauridae	Isolated	-	99.47	2.97	0.47	0.46	0.04	0.01	-0.21	-0.47	0.33	-0.10
AMNH5395	Tyrannosauridae	Isolated	-	76.26	1.83	0.16	0.00	0.59	0.16	-0.08	0.15	0.06	0.07
AMNH5395	Tyrannosauridae	Isolated	-	58.52	1.89	0.24	0.00	0.71	0.24	-0.02	0.15	0.02	0.05
AMNH5395	Tyrannosauridae	Isolated	-	79.13	1.40	0.15	0.00	0.24	0.15	-0.39	-0.03	0.05	-0.06
AMNH5395	Tyrannosauridae	Isolated	-	46.52	1.76	0.40	0.00	0.75	0.40	0.01	0.08	0.00	0.01
AMNH21505	Tyrannosauridae	Isolated	-	87.38	2.66	0.41	0.33	0.70	0.08	0.18	-0.02	0.15	-0.01
AMNH9701	Tyrannosauridae	Isolated	-	74.54	3.22	0.61	0.25	0.59	0.35	0.14	-0.23	0.12	0.05
AMNH3960	Tyrannosauridae	Isolated	-	36.40	1.33	0.70	0.00	0.89	0.70	0.04	-0.05	-0.14	0.00
AMNH3960	Tyrannosauridae	Isolated	-	42.75	1.55	0.57	0.00	0.79	0.56	0.00	-0.02	-0.08	0.02
AMNH3960	Tyrannosauridae	Isolated	-	52.12	1.37	0.27	0.01	0.57	0.27	-0.20	0.05	-0.03	-0.05
AMNH3955	Tyrannosauridae	Isolated	-	55.19	1.61	0.30	0.01	0.69	0.29	-0.07	0.11	-0.01	0.00
AMNH3955	Tyrannosauridae	Isolated	-	57.95	1.84	0.33	0.00	0.67	0.33	-0.04	0.08	0.01	0.05
AMNH21638	Tyrannosauridae	Isolated	-	61.62	1.90	0.41	0.00	0.62	0.41	-0.04	-0.01	-0.01	0.09

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
AMNH21638	Tyrannosauridae	Isolated	-	48.82	1.29	0.54	0.01	0.78	0.54	-0.04	-0.02	-0.13	0.01
AMNH21638	Tyrannosauridae	Isolated	-	49.26	1.58	0.46	0.04	0.76	0.41	-0.01	0.03	-0.06	0.00
AMNH21638	Tyrannosauridae	Isolated	-	40.86	1.34	0.39	0.00	0.89	0.39	0.01	0.14	-0.07	-0.05
AMNH29066	Tyrannosauridae	Isolated	-	60.23	2.46	0.28	0.07	0.72	0.22	0.06	0.13	0.09	0.05
AMNH21554	Tyrannosauridae	Isolated	-	65.80	2.20	0.18	0.09	0.68	0.09	0.00	0.18	0.10	0.01
AMNH21554	Tyrannosauridae	Isolated	-	40.49	1.46	0.51	0.00	0.86	0.50	0.05	0.06	-0.07	-0.02
AMNH21554	Tyrannosauridae	Isolated	-	73.44	3.40	0.37	0.37	0.87	0.00	0.30	0.10	0.18	-0.08
AMNH21554	Tyrannosauridae	Isolated	-	69.14	2.76	0.41	0.32	0.79	0.09	0.21	0.03	0.14	-0.07
AMNH21715	Tyrannosauridae	Isolated	-	34.84	1.29	0.54	0.00	0.83	0.53	-0.05	0.02	-0.09	-0.06
AMNH27097	Tyrannosauridae	Isolated	-	82.14	3.17	0.38	0.24	0.78	0.14	0.22	0.07	0.13	0.04
AMNH27097	Tyrannosauridae	Isolated	-	75.47	2.46	0.27	0.23	0.82	0.04	0.17	0.16	0.10	0.01
AMNH21820	Tyrannosauridae	Isolated	-	56.64	2.14	0.61	0.34	0.77	0.27	0.15	-0.13	0.03	-0.08
AMNH27096	Tyrannosauridae	Isolated	-	24.71	1.08	0.73	0.01	0.98	0.72	0.02	-0.01	-0.14	-0.10
AMNH8513	Tyrannosauridae	Isolated	-	50.19	1.95	0.42	0.05	0.79	0.37	0.06	0.07	0.00	0.02
AMNH8515	Tyrannosauridae	Isolated	-	83.94	2.82	0.44	0.42	0.04	0.02	-0.25	-0.44	0.32	-0.13
AMNH8514	Tyrannosauridae	Isolated	-	78.29	3.19	0.50	0.36	0.72	0.14	0.22	-0.08	0.16	-0.06
AMNH3067	Tyrannosauridae	Isolated	-	24.21	1.15	0.64	0.00	0.98	0.64	0.05	0.06	-0.09	-0.09
AMNH27097	Tyrannosauridae	Isolated	-	92.76	2.65	0.32	0.39	0.11	-0.06	-0.25	-0.30	0.29	-0.11
AMNH9701	Tyrannosauridae	Isolated	-	79.35	3.19	0.48	0.57	0.76	-0.09	0.26	-0.08	0.22	-0.21
FMNHPR2081	Tyrannosauridae	Maxilla	1	57.78	2.80	0.45	0.08	0.71	0.36	0.14	0.01	0.09	0.08
FMNHPR2081	Tyrannosauridae	Isolated	-	36.90	2.21	0.87	0.39	0.98	0.48	0.36	-0.18	-0.01	-0.08
FMNHPR2081	Tyrannosauridae	Premaxilla	4	64.53	3.55	0.28	0.17	0.80	0.11	0.21	0.17	0.18	0.00
FMNHPR2081	Tyrannosauridae	Premaxilla	3	83.33	4.40	-	-	-	-	-	-	-	-
FMNHPR2081	Tyrannosauridae	Maxilla	8	56.83	2.71	0.60	0.25	0.77	0.35	0.20	-0.10	0.05	0.01
FMNHPR2081	Tyrannosauridae	Maxilla	11	52.26	2.00	0.61	0.22	0.83	0.39	0.18	-0.07	-0.02	0.00
FMNHPR2081	Tyrannosauridae	Maxilla	10	60.10	2.34	0.65	0.32	0.76	0.33	0.21	-0.16	0.05	-0.02
FMNHPR2081	Tyrannosauridae	Isolated	-	50.01	1.41	0.38	0.07	0.77	0.30	-0.03	0.07	-0.04	-0.06

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
FMNHPR2081	Tyrannosauridae	Isolated	-	32.37	1.68	0.64	0.14	0.94	0.50	0.18	0.02	-0.04	-0.04
FMNHPR2081	Tyrannosauridae	Dentary	1	89.84	2.27	-	-	-	-	-	-	-	-
FMNHPR2081	Tyrannosauridae	Dentary	2	49.40	2.54	0.39	0.17	0.82	0.22	0.17	0.11	0.09	-0.01
FMNHPR2081	Tyrannosauridae	Dentary	3	82.93	2.20	0.26	0.16	0.47	0.11	-0.05	-0.01	0.15	0.06
FMNHPR2081	Tyrannosauridae	Dentary	7	57.55	1.96	0.63	0.23	0.70	0.40	0.11	-0.16	0.02	-0.01
FMNHPR2081	Tyrannosauridae	Dentary	11	49.61	2.17	0.60	0.33	0.83	0.27	0.21	-0.07	0.05	-0.09
FMNHPR2081	Tyrannosauridae	Dentary	12	57.25	1.95	0.47	0.27	0.79	0.20	0.13	0.00	0.04	-0.08
FMNHPR2081	Tyrannosauridae	Dentary	2	89.65	3.73	0.36	0.16	0.57	0.20	0.13	-0.02	0.20	0.11
FMNHPR2081	Tyrannosauridae	Dentary	4	73.06	2.23	0.28	0.19	0.71	0.09	0.09	0.11	0.10	0.02
FMNHPR2081	Tyrannosauridae	Dentary	5	58.99	2.38	-	-	-	-	-	-	-	-
FMNHPR2081	Tyrannosauridae	Dentary	6	58.30	2.21	0.55	0.27	0.82	0.28	0.21	-0.04	0.04	-0.02
FMNHPR2081	Tyrannosauridae	Dentary	8	47.09	2.29	0.65	0.33	0.87	0.32	0.27	-0.09	0.05	-0.08
FMNHPR2081	Tyrannosauridae	Dentary	9	47.48	2.03	0.46	0.19	0.84	0.27	0.15	0.06	0.04	-0.06
FMNHPR2081	Tyrannosauridae	Dentary	11	76.36	2.56	0.40	0.32	0.64	0.08	0.11	-0.05	0.16	-0.06
FMNHPR2081	Tyrannosauridae	Dentary	12	44.58	1.67	0.41	0.09	0.88	0.32	0.09	0.13	-0.01	-0.05
USNM12814	Tyrannosauridae	Dentary	7	49.99	2.23	0.68	0.40	0.83	0.27	0.24	-0.15	0.06	-0.12
USNM12814	Tyrannosauridae	Dentary	9	44.99	2.06	0.61	0.11	0.81	0.50	0.15	-0.05	-0.01	0.04
USNM12814	Tyrannosauridae	Dentary	11	44.10	1.80	0.80	0.09	0.86	0.71	0.18	-0.17	-0.10	0.09
USNM12814	Tyrannosauridae	Dentary	14	39.43	0.82	0.48	0.00	0.79	0.48	-0.17	0.03	-0.14	-0.19
USNM203586	Tyrannosauridae	Isolated	-	69.05	2.29	0.45	0.15	0.66	0.30	0.07	-0.04	0.05	0.07
USNM7625	Tyrannosauridae	Isolated	-	74.54	3.01	0.24	0.23	0.67	0.01	0.11	0.12	0.20	-0.02
USNM12814	Tyrannosauridae	Dentary	3	72.10	2.25	-	-	-	-	-	-	-	-
AMNH21730	Unknown	Isolated	-	33.70	1.31	0.90	0.18	0.88	0.72	0.10	-0.24	-0.13	-0.06
AMNH3960	Unknown	Isolated	-	30.49	1.69	-	-	-	-	-	-	-	-
AMNH3960	Unknown	Isolated	-	39.61	1.50	-	-	-	-	-	-	-	-
AMNH21816a	Unknown	Isolated	-	56.28	1.56	0.38	0.01	0.64	0.37	-0.09	0.02	-0.05	0.04
AMNH3960	Unknown	Isolated	-	30.99	1.91	0.38	0.16	1.01	0.22	0.19	0.23	0.02	-0.09

Catalogue #	Family	Host Bone	Position	LOA	CA	MTD	DTD	HTD	MTD-DTD	PC1	PC2	PC3	PC4
USNM358255	Unknown	Isolated	-	111.60	2.71	0.13	0.00	0.04	0.13	-0.31	-0.12	0.28	0.18
USNM427789	Unknown	Isolated	-	42.96	1.90	0.52	0.27	0.81	0.25	0.16	-0.01	0.02	-0.07
USNM7260	Unknown	Isolated	-	88.06	2.12	0.35	0.00	0.24	0.35	-0.23	-0.17	0.11	0.12
USNM410187	Unknown	Isolated	-	56.63	2.38	0.57	0.00	0.62	0.57	0.03	-0.12	0.00	0.15
USNM410187	Unknown	Isolated	-	51.35	2.19	0.66	0.00	0.83	0.66	0.16	-0.07	-0.08	0.15
USNM410192	Unknown	Isolated	-	43.76	1.38	0.68	0.00	0.75	0.68	-0.01	-0.13	-0.11	0.02
USNM410192	Unknown	Isolated	-	37.83	1.50	0.81	0.15	0.83	0.66	0.07	-0.20	-0.10	-0.03
USNM410192	Unknown	Isolated	-	45.53	1.63	0.80	0.30	0.77	0.50	0.11	-0.26	-0.04	-0.08
USNM410189	Unknown	Isolated	-	62.44	2.16	0.39	0.05	0.64	0.33	0.01	0.02	0.04	0.07
USNM410189	Unknown	Isolated	-	65.70	2.19	0.05	0.03	0.67	0.02	-0.04	0.26	0.11	0.02
USNM410188	Unknown	Isolated	-	41.76	1.95	0.58	0.08	0.77	0.50	0.09	-0.04	0.00	0.02
USNM412502	Unknown	Isolated	-	64.19	2.69	0.20	0.04	0.66	0.15	0.03	0.17	0.13	0.06
USNM412502	Unknown	Isolated	-	69.54	2.06	0.00	0.00	0.48	0.00	-0.18	0.20	0.14	0.01
USNM412502	Unknown	Isolated	-	71.71	2.05	0.17	0.06	0.48	0.11	-0.15	0.08	0.11	0.02
USNM412502	Unknown	Isolated	-	78.70	2.42	-	-	-	-	-	-	-	-
USNM442398	Unknown	Isolated	-	73.03	1.62	0.15	0.14	0.69	0.01	-0.02	0.17	0.04	0.03
USNM442398	Unknown	Isolated	-	30.88	1.15	0.61	0.00	0.92	0.61	0.00	0.03	-0.13	-0.08
USNM508561	Unknown	Isolated	-	57.82	1.32	-	-	-	-	-	-	-	-
USNM358253	Unknown	Isolated	-	50.23	2.17	0.44	0.01	0.73	0.44	0.04	0.03	0.02	0.07
USNM410190	Unknown	Isolated	-	49.70	1.40	0.70	0.01	0.77	0.69	0.02	-0.12	-0.14	0.05
USNM410196	Unknown	Isolated	-	26.56	0.93	0.98	0.00	0.96	0.98	0.04	-0.21	-0.19	-0.07
USNM410196	Unknown	Isolated	-	30.56	1.01	0.69	0.01	0.84	0.68	-0.09	-0.07	-0.13	-0.11
USNM410188	Unknown	Isolated	-	21.86	0.90	0.90	0.00	1.00	0.90	0.02	-0.12	-0.15	-0.11

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