

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

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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 with tooth mark production. We also discuss the significance and limits of applying these data to fossil assemblages.

Goat carcasses were fed to 11 captive individuals. *V. komodoensis* modifies bone surfaces extensively. Individuals exhibit a “medial-caudal arc” 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 5% of all marks.

Both feeding behavior and tooth marks indicate that ziphodont crowns are ideal for defleshing by being drawn distally through a carcass. Crowns are poorly built for crushing, and within-bone nutrients are acquired through swallowing. Mark production is a by-product of the distal crown 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. Parallel clusters may result from repetitive defleshing strokes and/or from multiple crown contacts during a stroke.

These observations can be used to draw functional, behavioral, and taphonomic interpretations from fossil assemblages. When they are provisionally applied to theropod tooth marks, similar crown 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.

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Introduction

Throughout history, certain groups of tetrapods possessed a unique dentition known as ziphodont. Meaning “sword tooth,” it is characterized by labio-lingually compressed, distally curved, serrated crowns. The serrated carinae have a true series of individualized 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 an Eocene crocodylian (Langston 1975). Ziphodonty is a synapomor-

phy of Archosauria (Benton 2004), and although it has occurred in several Cenozoic crocodylians, it is predominantly found in the Mesozoic. The majority of carnivorous archosaurs throughout the Mesozoic era possessed it, including 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 occurs only in certain members of the squamate family Varanidae (Auffenberg 1981). These crowns

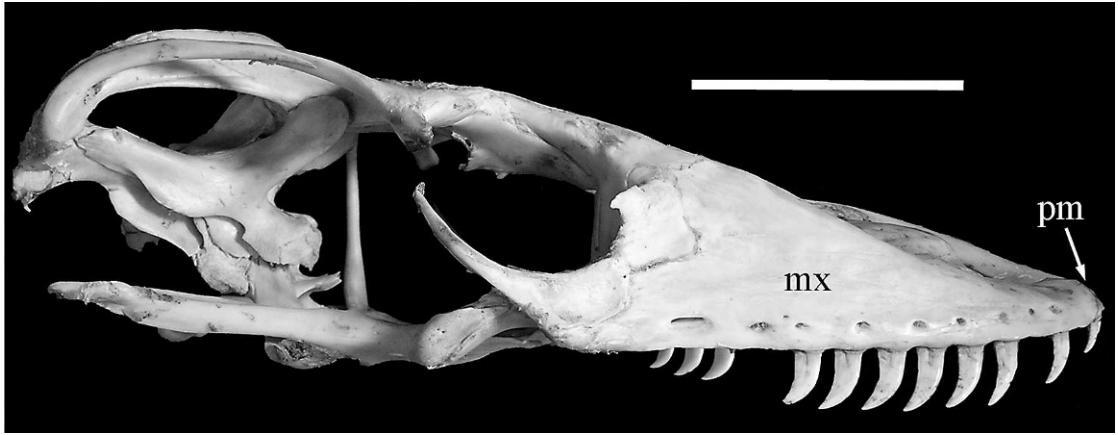


FIGURE 1. View of *Varanus komodoensis* cranium displaying both premaxillary (pm) and maxillary (mx) dentition (FMNH 22200, Field Museum of Natural History, Chicago). The distal carina is facing left in all crowns. Notice the convex profile formed by the crowns along the tooth row from this perspective. This specimen is missing its right quadrate element. (Scale, 50 mm.)

are morphologically very similar to their extinct counterparts, and excavators have confused isolated crowns of ziphodont crocodylians for large varanid teeth (Molnar 2004). The crowns of modern crocodylians and the canines of mammalian carnivores are robust and conical, and lack true denticles (Prasad and Lapparent de Broin 2002). Although several shark species possessed denticulate crowns, as did saber-tooth cats, we do not consider them ziphodont because of size and/or shape differences in the dentition (Akersten 1985; Farlow et al. 1991).

Although many feeding studies have investigated the kinetic cranium of varanids (e.g., Frazzetta 1962; Bolt and Ewer 1964; Smith 1982; Smith and Hylander 1985; Condon 1987; Moreno et al. 2007, 2008), only a few studies have actually investigated dental structure, function, and consequential feeding behaviors. Rieppel (1979) hypothesized that the curved crowns of *Varanus salvator* are effective because cranial kinesis reorients the apices so they contact prey first. The most in-depth accounts of varanid feeding behavior and dental function are in Auffenberg's (1972, 1978, 1981) seminal volumes. They discuss 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, the mouth of *V. komodoensis* is moved forward and to the

side over a portion of the carcass, and repetitively drawn back in an arcing motion. The ziphodont crowns are positioned along the margin of the rounded rostrum. The margin of the tooth row appears convex from the lateral perspective, and all crowns are believed to function in unison like one "curved scalpel blade" (Auffenberg 1981: p. 210) (Fig. 1). When the teeth are drawn back, a distally positioned crown apex makes initial contact and the longer, more mesially positioned crowns sequentially cut deeper than the preceding crown.

Concerning extinct ziphodont representatives, several approaches have been used to determine dental function. A small number of morphometric studies, mainly of theropods, have investigated this. Farlow et al. (1991) speculated on the function of denticulated crowns by applying serrated cutting mechanics as outlined by Frazzetta (1988). 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; Sweetman 2004; Smith 2005, 2007; Smith et al. 2005). In one of the few experiments on denticulated crown performance, Abler (1992) examined the forces involved in cutting and puncturing various substrates in tyrannosaurids.

Several conclusions about crown use are also drawn from the investigations of *V. komodoensis* discussed above. The teeth and skull morphology of large theropods suggest food processing similar to that of *V. komodoensis* (Paul 1988; Molnar and Farlow 1990; Rayfield et al. 2001). Several researchers have proposed that theropods may have cultivated bacteria between denticles (Abler 1992; Carpenter 1998), as was once believed for *V. komodoensis*. Certain dental similarities in basal archosaurs suggest that they were active predators (Senter 2003). Ziphodont crocodylians are thought to have had feeding behavior similar to that of *V. komodoensis* because of their similar crown 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 tooth marks 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 and Blumenschine 2003). Bone surface modifications ascribed to ziphodont tooth marks have been identified in many assemblages (Table 1), and from these, many behavioral reconstructions have been developed. Concerning crown function and feeding behavior, theropod tooth marks have a morphology and frequency that is argued to reflect a similar feeding technique, and consequently similar crown function, to that of *V. komodoensis*. Specifically, these marks reveal both the drawing back of the crowns through the flesh and a lack of bone gnawing (Fiorillo 1991a; Jacobsen 1995, 1998; Erickson and Olson 1996).

Unfortunately, modern ziphodont varanid studies are inappropriate 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, is used as a model for ziphodont function. The majority of the aforementioned conclusions about ziphodont archosaurs are based solely on Auffenberg's (1981) study, even though dental function was not his major focus. Virtually no studies have been conducted specifically 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 making strong functional/behavioral inferences. Although many intriguing ideas have been prompted by these Mesozoic traces (Table 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 neotaphonomically 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 whether these characters actually reveal meaningful information concerning ziphodont behavior or crown function. This casts doubt on prior interpretations drawn from fossil examples of

TABLE 1. A chronologically ordered account of published descriptions of marks identified as tooth marks believed to be produced by ziphodont theropods, including the interpretation of the mark provided in the account. Quotation marks indicate words taken directly from the text referenced. Superscripted numbers describe the same marked specimen/assemblage. An asterisk indicates a description that we derived from photographs published by the referenced author. Values in parentheses under "No. of marks" are traces that the author considers to be "questionable" tooth marks.

Reference	Marked taxon	Marked element(s)	No. of marks	Type of mark	Striated mark	Parallel clusters	Interpretation
Matthew 1908; Colbert 1961; Farlow 1976	<i>Apatosaurus (Brontosaurus)</i>	"several"	—	scores, fractures	—	—	<i>Allosaurus</i> feeding
Jensen 1968	<i>Camarasaurus</i>	—	"various"	"long, deep grooves"	—	—	scavenged and washed downstream <i>Gorgosaurus (Albertosaurus)</i> feeding
Dodson 1971	—	—	—	"grazing tooth marks"	—	subparallel*	
Currie et al. 1990 ¹	<i>Sauromitholestes</i>	—	—	"paired grooves"	yes	—	<i>Sauromitholestes</i> used carinae parallel to bone
Rogers 1990	<i>Eimiosaurus (Styracosaurus)</i>	4	—	"U-shaped grooves," punctures	—	—	—
Fiorillo 1991a ²	Cretaceous Dinosauria	18	—	"scores," scalloped surface"	—	—	Theropoda do not crush bones for within-bone nutrients
Fiorillo 1991b ²	Cretaceous Dinosauria	3	—	punctures	—	—	carcass scavenging and prey utilization
Sereno and Novas 1993	<i>Herrerasaurus</i>	2	3	punctures	—	—	perimortem <i>Saurosuchus</i> / intraspecific aggression
Hunt et al. 1994	<i>Apatosaurus</i>	>7	—	scores	—	parallel	early scavenging by <i>Torosaurus</i> or <i>Allosaurus</i>
Currie and Jacobsen 1995	<i>Quetzalcoatlus</i>	1	4	scores, imbedded tooth	no	not parallel	<i>Sauromitholestes</i> scavenging
Jacobsen 1995, 1997, 1998; Ryan et al. 2001 ³	ceratopsids	17	—	unspecified marks	yes	—	low mark frequency indicates mass death/ <i>Troodon</i> feeding
Jacobsen 1995, 1997, 1998	hadrosaurids	47	—	unspecified marks	yes	—	mark location on ends of long bones indicates low prey availability
Jacobsen 1995, 1997	ornithomimid	2	2	unspecified marks	—	—	<i>Sauromitholestes</i> feeding
Jacobsen 1995, 1997, 1998	tyrannosaurids	8	—	punctures, linear scoring	yes	parallel	—
Tanke and Currie 1995, 1998	<i>Sinraptor</i>	5	28	puncture, furrow	no	subparallel	perimortem intraspecific aggression
Tanke and Currie 1995, 1998	<i>Gorgosaurus (Albertosaurus)</i>	2	2	puncture, furrow / score, "disruptive texture"	no	—	perimortem intraspecific aggression
Varricchio 1995	Iguanodontoids, <i>Troodon</i>	12	"few"	—	—	—	assemblage accumulated through drought, botulism, or toxicosis
Erickson and Olson 1996	<i>Triceratops</i>	—	58 (+22)	furrows, fracture, punctures	yes	—	"puncture and pull" <i>Tyrannosaurus</i> feeding

TABLE 1. Continued.

Reference	Marked taxon	Marked element(s)	No. of marks	Type of mark	Striated mark	Parallel clusters	Interpretation
Erickson and Olson 1996	<i>Edmontosaurus</i>	1	5	furrows	no	subparallel*	"puncture and pull" <i>Tyrannosaurus</i> feeding
Bakker et al. 1997	camarasaur	"a few"	—	scores, furrows	—	parallel*	<i>Allosaurus</i> disarticulation and parental behavior
Jacobsen 1997, 1999, 2001 ¹	<i>Sauromitholestes</i>	1	3	"serration marks"	yes	—	<i>Tyrannosaurus</i> hunting or scavenging
Carpenter 1998	<i>Edmontosaurus</i>	5	3	"saddle shaped groove," pits	—	—	perimortem large theropod bite
Chure et al. 1998	<i>Allosaurus</i>	1	"series"	"grooves," fracture	no	subparallel	theropod scavenging
Chure et al. 1998	<i>Camarasaurus</i>	1	20	"grooves"	no	parallel	theropod "nipping" meat off carcass
Tanke and Currie 1998	<i>Daspletosaurus</i>	1	1	puncture	no	—	perimortem intraspecific aggression
Tanke and Currie 1998	<i>Monolophosaurus</i>	1	9	"raised blister-like lesions"	—	—	perimortem intraspecific aggression
Tanke and Currie 1998	<i>Tarbosaurus</i>	—	—	"toothstrike trauma"	—	—	perimortem intraspecific aggression
Tanke and Currie 1998	<i>Carcharodontosaurus</i>	—	—	"facebite lesions"	—	—	perimortem intraspecific aggression
Tanke and Currie 1998	<i>Tyrannosaurus</i>	—	—	score/furrow	—	—	perimortem intraspecific aggression
Jacobsen and Ryan 1999	<i>Edmontosaurus</i>	—	"a variety"	punctures, "serration drags"	yes	—	<i>Albertosaurus/Sauromitholestes</i> scavenging
Rogers et al. 2003	<i>Majungasaurus</i> (<i>Majungatholus</i>)	21	—	scores, "denticle drags"	yes	parallel	<i>Majungasaurus</i> cannibalism
Rogers et al. 2003	<i>Rapetosaurus</i>	1	—	scores/ furrows	no	subparallel	<i>Majungasaurus</i> predation
Carpenter et al. 2005	<i>Stegosaurus</i>	1	1	"U-shaped notch"	—	—	<i>Allosaurus</i> predation
Fowler and Sullivan 2006	ceratopsid	—	12 (+21)	punctures, scores	no	subparallel	<i>Daspletosaurus</i> scavenging
Gignac et al. 2007	<i>Tenontosaurus</i>	—	"numerous"	punctures	—	—	determined <i>Deinonychus</i> bite force from punctures

these marks. The tooth mark models developed from modern mammals and crocodylians 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 whether 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. We report on the general behavioral trends observed during these feedings, building and expanding upon the descriptions of previous researchers and evaluating dental function. We measured and categorized bone surface modifications produced during these controlled feedings, describing for the first time *V. komodoensis* feeding traces. We then determined whether and how these tooth marks represent ziphodont behavior and dental function. Last, we 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 molariform crowns. There are several examples of ziphodont varanids, including *V. salvator* and *V. varius* (Auffenberg 1981; D'Amore personal observation), but *V. komodoensis* is considered to be the "most" ziphodont. *V. komodoensis* crowns 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 crown morphology of this species and its extinct counterparts is very similar, especially between crowns of similar sizes (Farlow et al. 1991). *V. komodoensis* has been compared to 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; Van 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). Only adults were sampled because *V. komodoensis* feeding habits change ontogenetically. Juveniles occupy an arboreal feeding niche, but 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 of immature individuals may also be different from those of adults (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." These carcasses were obtained from a local butcher by the commissary of the housing zoo, and meat was used only at that location. All carcasses consisted of unmodified flesh and bones except for the caudal-most ribs having being sawn off distally, and

TABLE 2. *Varanus komodoensis* individuals used in this study. Abbreviations: 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 No.	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	♀

the vertebral and sternal elements halved mid-sagittally. A small number of marks on two carcasses, other than those associated with the sectioning process, resulted from the butchering, and 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 carcasses to have identical skeletal composition, the only available carcasses were artificially sectioned from different body regions. Three carcass types were available. "Upper forequarter" portions contain vertebrae from the axis to the fifth or sixth thoracic vertebra, ribs one through five or six, the scapula, and the most proximal 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 carcasses used ranged from 0.82 to >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 "match" carcasses with individuals on the basis of their ability to remove enough flesh to make bone-tooth contact before becoming satiated.

This assessment was based on the size of carcasses 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 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. Using these criteria, we sometimes removed excess flesh prior to feeding, taking care to prevent the butchering tool from making 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 at a time was in the enclosure during feeding. Each carcass was weighed before introduction and after retrieval to see how much flesh was consumed. A single carcass 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 a significant distance away from the researcher or out of the field of view. Individuals appeared to react to the tethered carcass as though it were fixed. This increased the willingness of individual to

remove flesh from the carcass and deterred attempts 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 an individual lost interest in feeding, the researcher would lightly tug on the tether to renew interest. The trial was considered complete when the individual no longer interacted with the carcass or at the request of the zoo staff.

Carcass Processing

After collection, the carcass 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 10× 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 that 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.—We 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" occur 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 12 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 a 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 possessed 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. These may run along the whole length of a mark or a portion of it. These striations are usually visible with only a hand lens or a dissecting microscope and may be regularly or irregularly spaced. All striations are included as one mark.

Morphometrics.—Two quantitative values taken for each tooth mark are length and width. 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

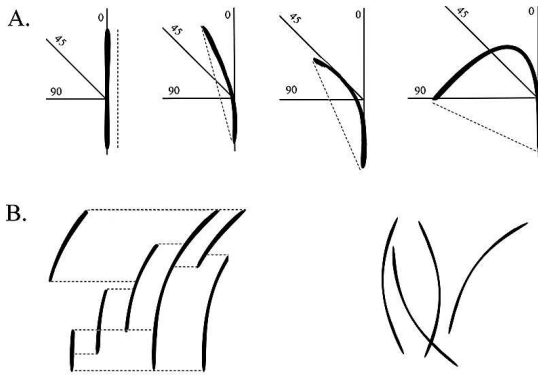


FIGURE 2. A, The curvature of an elongate mark is determined by the angle formed by the position of one end of a mark in relationship to the other end. From left to right; "straight," $<45^\circ$, $45-90^\circ$, and $>90^\circ$. Note that all marks represented have different curvatures, but the same "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.

perpendicular to the length and is the distance across the actual modification at its widest point. Digital calipers were used to measure all dimensions over 1.5 mm to the hundredth millimeter. All dimensions less than 1.5 mm were measured using a dissecting microscope ($20\times$) with an ocular scale bar to the nearest 0.053 mm. In a few cases ($<2\%$) marks were so faint that one or both of these dimensions could not be measured accurately. Lengths and widths were plotted in interquartile 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 (Fig. 2). If there is no bowing or bending, the mark is considered "straight." If the mark bends at more than one point along its length, it is considered "sinuous." Marks with a single curve fall into three major categories based on their curvature; $<45^\circ$, $45-90^\circ$, $>90^\circ$. 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 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" (Fig. 2). Marks must be next to one another and are considered parallel only if they occur on a similar area of the bone surface (e.g., 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, but two marks are considered parallel only if the portions that run alongside each other are parallel.

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 (e.g., there is no left versus right tenth 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 non-bony flesh were specified. Quantity of flesh was not directly measured, but was based on observation and accounts in the literature (Frandsen 1974). Elements that were 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 fasciae latae. A student's *t*-test was conducted to determine whether these elements differed significantly in number of marks from remaining elements.

Recording and Behavior Analysis

Nine of the 14 feeding bouts were recorded with a hand-held digital camera. The nature of the enclosure or the individual's unwillingness to feed with observers present prevented recording of the other five bouts. Out of these nine, eight were used in the following analysis. Because the *V. komodoensis* behavior

TABLE 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. "No. of marks" is the total number of tooth marks on one carcass from one trial. Trial length is in minutes. Abbreviations: UF, upper forequarter; TL, thoracic/lumbar; UH, upper hindquarter).

Individual	Trial	Filmed	Trial length	Section	Mass removed	Elements marked	No. 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
SD			30.31		0.25	5.25	104.1

we witnessed appeared to be so consistent, we do not believe that this sample excludes any significant behaviors. Although we tried to be consistent and record all behaviors, we had to stop the camera 13 times in order to replace film, to reposition the carcass, or to remove the carcass because so much flesh had been removed that underlying bones could have been swallowed. These portions were removed and the carcass was reintroduced. In only one instance did the carcass 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 trials were noted. Only the major behaviors associated with *V. komodoensis* carcass consumption are described here. We paid particular attention to the part of the carcass on which the individuals were feeding in a way that may have resulted bone-tooth contact. Marks were later referred back to these observations. We did not quantify the frequency or duration of behaviors, which although important characteristics, are beyond the scope of this study.

Results

Varanus komodoensis individuals fed on the introduced carcasses during all 14 feeding

trials. The duration of the included feeding trials was between 32 and 105 minutes with a median of about 66 minutes (Table 3). The rate of *V. komodoensis* flesh removal ranged from about 1.5 g/minute to over 13 g/minute. All skeletal elements were retrieved from the carcasses in all trials except for one. In this instance, the carcass 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 that we observed supports that reported by both Burden (1928) and Auffenberg (1978, 1981) for *V. komodoensis*. After the introduction of a carcass into an enclosure, all *V. komodoensis* individuals exhibit some sort of exploratory behavior prior to consumption. An individual would lower the head and either encircle the carcass or walk directly toward it. Tongue flicking either in the direction of or directly on the carcass would often occur. Individuals would also rub their rostrum back and forth on the carcass. Occasionally they would take small initial bites that involved a slight opening of the mouth.

Defleshing behavior is the most commonly observed and distinctive aspect of *V. komo-*

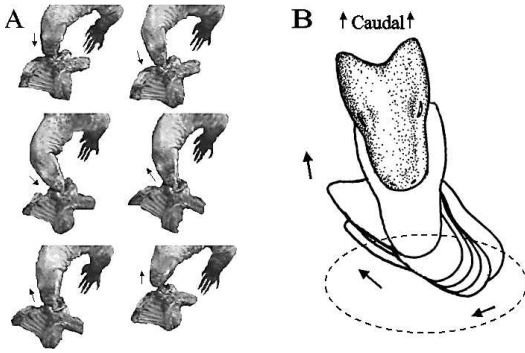


FIGURE 3. *Varanus komodoensis* demonstrating a single, medial-caudal defleshing stroke. The arrows represent the direction of head movement. A, Two sequences, top to bottom, showing that the rostrum is positioned over a portion of the carcass; the rostrum is then drawn back in a medial-caudal arc while 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 toward the top of the figure. Notice that motion starts mostly medial and ends mostly caudal, resulting in an arcing motion. Crowns of the right side of the rostrum are cutting in this particular stroke.

doensis feeding behavior. Defleshing is defined as any behavior by which an animal removes meat without attempting to swallow the carcass whole (Fig. 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 long axis of the rest of the body. This results in the head being medial and caudal to its starting position. 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, but eventually transitions to being almost exclusively caudal. At the end of a stroke the jaw is then reopened and repositioned for the next stroke, usually over the same location. Defleshing strokes may be repeated several times, either consecutively

toward one side or alternating between two sides. These movements are either slow and methodical, or quick and violent. The intensity of these movements is 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 while stepping backward with both the fore and hind limbs. If lateral movements of the head are quick, the carcass might be tossed from side to side.

Once a section of the carcass 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 whole. At first, an animal usually bites a portion of the carcass and elevates its head to provide inertia, or it 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), we saw this latter behavior often in certain individuals. When the carcass was elevated, several quick jerking head movements followed to help "force" the large item down. Attempts made to swallow the entire carcass were unsuccessful owing 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.

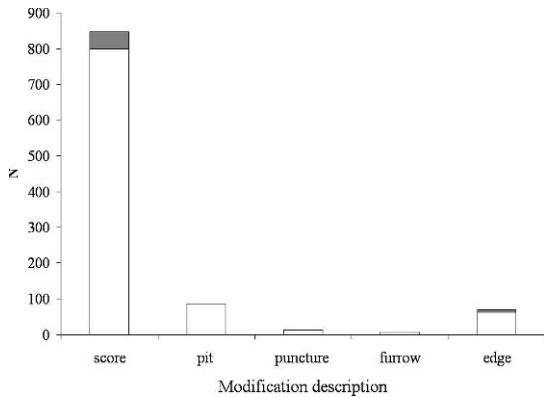


FIGURE 4. Number of tooth marks (N) in each class defined here that were produced on all introduced carcasses. Gray areas indicate portions of each mark that possess striations.

Portions of the carcass fed on first tend to bear large portions of intact, boneless flesh. Attempts to swallow the carcass whole started at the end that fit into the mouth most easily, and occurred in only three trials, persisting for several minutes. Few behaviors deviate from 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 whether it had any influence on feeding mechanics.

Certain areas of each carcass received the most attention in the form of defleshing and swallowing behaviors. For the upper fore-quarter portions, the dorsal-/cranialmost 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 caudalmost 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 artificial carcass. Bone-tooth contact did 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* crowns 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.—We recorded a total of 1024 tooth marks on 71 of the recovered bone elements (Table 3, Fig. 4). The remaining 153 elements, over two-thirds of the total sample, were 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 (Fig. 5); few (8%) are pits (Fig. 6), and punctures and furrows are rare (<1.5% each). Edge marks make up fewer than 7% of all marks. Only 5% of all marks display striations (Fig. 7). The majority of these striated marks are scores, but seven edge marks and one furrow also display striations (Fig. 4). 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 is not apparent relationship between the amount of flesh removed and the number of tooth marks produced.

Typical *V. komodoensis* tooth marks are narrow but may vary in length. The vast majority of all pits and scores are less than 1 mm wide. In all cases median lengths and widths are smaller than means, indicating an increased frequency at the lower values (Table 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 are less than 1 mm. Scores have less uniform lengths, with over half between 1 and 4 mm. Median lengths of

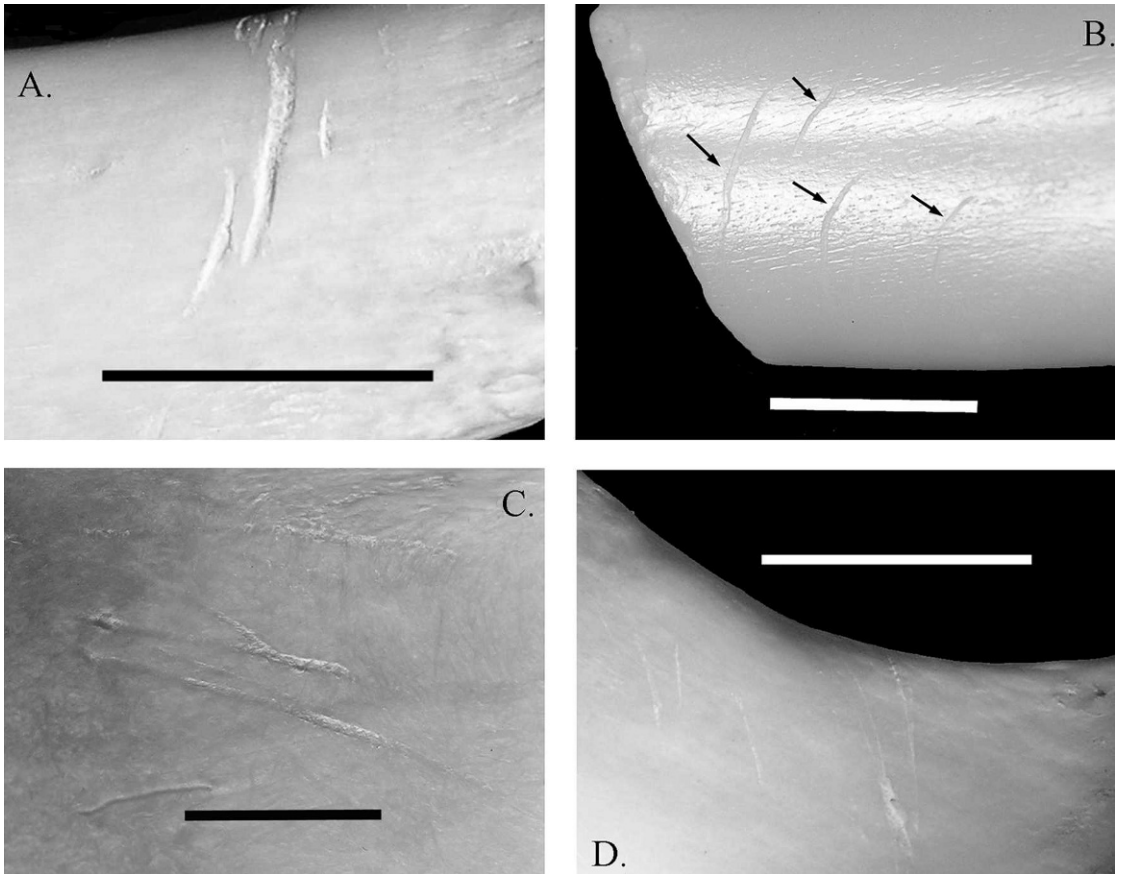


FIGURE 5. Clusters of parallel scores. A, C, and D consist of marks that are either straight or curved $<45^\circ$, and B depicts several marks curved $45\text{--}90^\circ$. Crushing of cortical layers is evident in all except B. (Scale, 10 mm.)

scores and furrows are more than five times greater than widths, whereas pits and punctures have a median length just over twice the width. Edge marks have median widths and

interquartile ranges greater than those of scores but they are substantially shorter (Fig. 8). The largest mark overall, a score, is over ten times wider and nine times longer

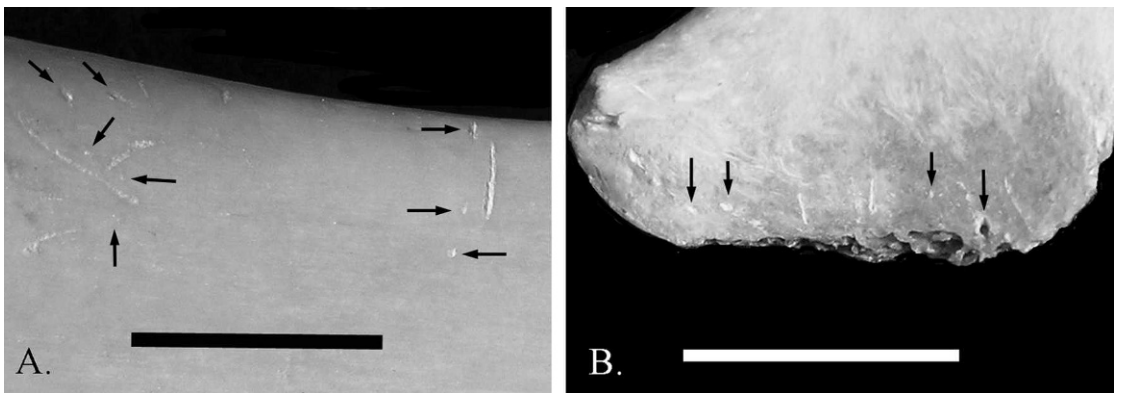


FIGURE 6. Pitting and puncturing (arrows) and scoring (not indicated) on a cranial rib (A) and lumbar vertebral process (B). All marks indicated by arrows are pits with the exception of the farthest right on B, which is a small puncture. Note the similar width between scores and pits. (Scale, 10 mm.)

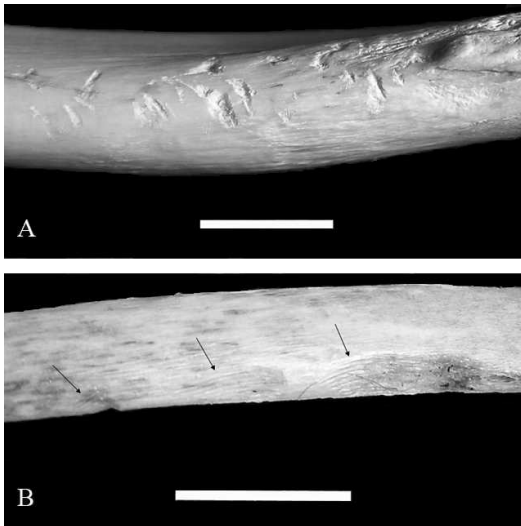


FIGURE 7. A, Clusters of parallel edge marks on the caudal edge of a proximal rib. Note the large width-to-length ratio. B, Curved striated marks on a caudal rib. The left two are scores and the far right one is a furrow because it entered cancellous bone. (Scale, 10 mm.)

than the mean. Such large marks are quite rare. When looked at separately, scores with 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.

Of the 71 marked bone elements, 34 have at least one cluster of parallel marks, with a maximum number of nine (Fig. 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. Most 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 $<45^\circ$, 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° .

In determining the frequency of tooth marks on various elements types, we discovered a significant difference in number of marks on elements with a "substantial" amount of proximal flesh (*t*-test: *p*-value < 0.00002 ; Table 5). The elements bearing or close to "substantial" amounts of flesh have an average of 8.6 marks per element type, as opposed to the remainder, which have an average of 1.3 marks. Only a few elements not considered proximal to a "substantial" amount of meat had a noticeably high number of marks. These were the axis in the cervical/thoracic portions and the cranial-most thoracic vertebrae and rib on the thoracic/lumbar portions.

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 per element. For the thoracic/lumbar portion, the most heavily tooth-

TABLE 4. Morphometrics of all tooth marks. Values are for all marks where length and/or width were measurable. All values are in millimeters. In a small number of cases, scores were too faint to obtain one or both of these values, and these cases were omitted in the calculations. Therefore, for scores "N" is lower than the actual number of scores observed.

	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
Mean	4.51	0.42	0.88	0.42	2.29	0.94	8.74	1.41	2.61	0.67
SD	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

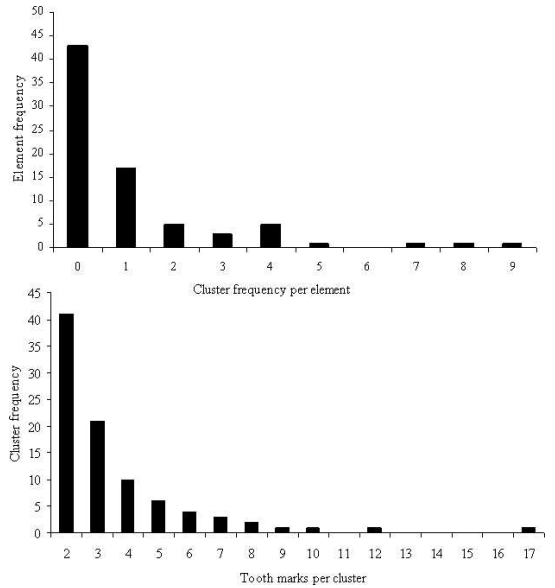
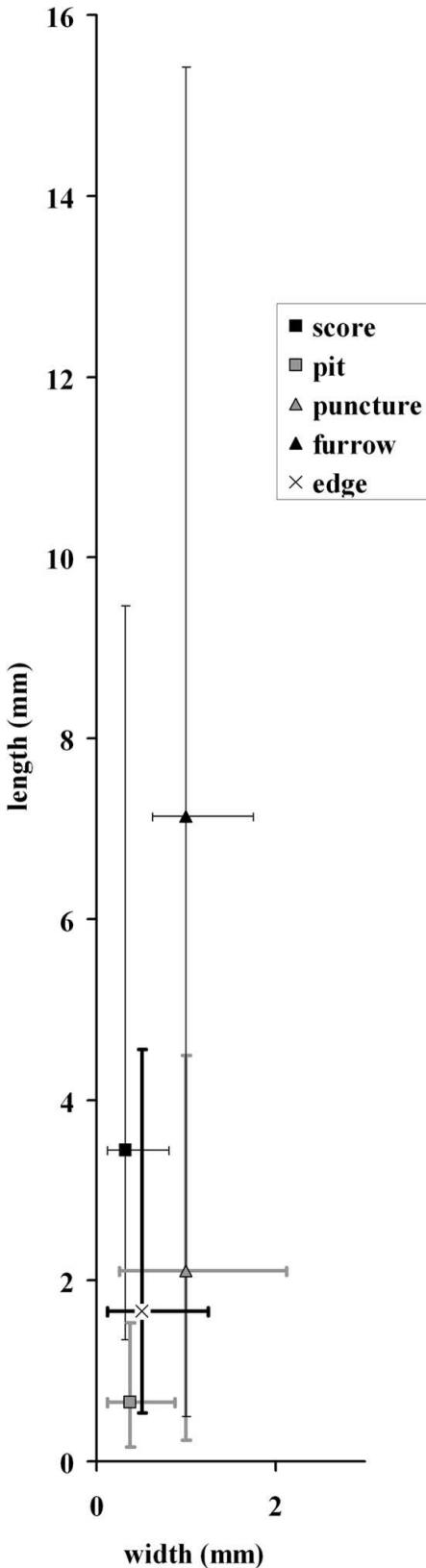


FIGURE 9. Characteristics of clusters of parallel marks. The top graph indicates the frequency of clusters of parallel marks on each marked element. Unmarked elements were not included. The bottom graph indicates the number of parallel tooth marks within each cluster independent of element.

marked rib is the caudalmost (rib 13). With the exception of lumbar vertebra 6, the cranialmost (thoracic vertebra 5) and caudalmost (lumbar vertebra 5) are most frequently tooth-marked, with progressively fewer 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 found only on ribs and vertebrae and were absent on the appendicular skeleton.

We were unable to determine which tooth row, the upper or lower, modified bone 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



FIGURE 8. Medians and interquartile ranges for the lengths and widths of the five mark types produced by *Varanus komodoensis*. For total ranges, see Table 4.

TABLE 5. The mean number of tooth marks by element type. 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 element fed to all *Varanus komodoensis* specimens. All introduced elements are included. "Thoracic," "Cervical," "Lumbar," "Caudal," and "Sacral" all refer to vertebral elements. "Sternum," "Sacral," and "Caudal" values represent all elements of that element type from all positions. A "+" under "proximal flesh" indicates a substantial amount of flesh adjacent to the element.

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

could have been produced by either row. Second, the carcass was flipped over frequently during almost all trials, making a single bone surface accessible for potential crown contact by either tooth row. Individuals fed on certain areas regardless of carcass orientation.

Discussion

Varanus komodoensis Feeding Behavior and Crown Function.—*Varanus komodoensis* shows a consistent set of behaviors when feeding. Because the behaviors in our sample are so uniform, we suggest that they are typical for the vast majority of *V. komodoensis* individuals, both wild and captive. These feeding methods support accounts of previous authors (Burden 1928; Auffenberg 1981), and correlate well with cranial structuring and the skull's ability to resist forces generated when *V. komodoensis* pulls in both lateral and caudal directions (Moreno et al. 2007, 2008). Additional inferences concerning dental function may be derived from the behaviors observed here that have not been previously proposed.

Defleshing behavior moves the head in a repetitive, "back and forth" motion, but we assert that defleshing is strictly unidirectional. As first discussed by Auffenberg (1981) and expanded upon here, ziphodont crowns function best when drawn distally—that is, with the distal carina leading through the substrate. When *V. komodoensis* feeds, the crowns contact and cut through flesh only when they are drawn distally during the medial-caudal movement. Once the crowns have been drawn distally, they are withdrawn. No cutting occurs when the rostrum is then brought forward over the carcass for a subsequent stroke. The crowns are usually reintroduced where the previous stroke started, allowing them to cut deeper with each stroke. This process is repeated until the flesh is entirely cut or the crowns 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 crowns on one side of the rostrum a large distance in an arcing direction (Fig. 3). This arcing motion conforms to the rounded shape of the rostrum to

ensure that the crowns on this side follow one another through flesh (Auffenberg 1981). The crowns on the opposite side move a shorter distance and not in such a way as to cut efficiently. The crowns moving along the arc are the only ones that cut during defleshing. If crowns 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, crown function is specialized for flesh removal in *V. komodoensis* (Burden 1928; Auffenberg 1978, 1981). Ziphodontology is ideally structured for distal movement through flesh, facilitated in this case by medial-caudal defleshing. Because the crowns are drawn distally, the highly curved crowns contact 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 the crown to move distally through the substrate more efficiently (Frazzetta 1988). Although these crowns are optimal for cutting soft material, the ziphodont crowns of *V. komodoensis* are poorly built for bone crushing. The direct downward force necessary for bone crushing on a laterally compressed, curved crown would not allow for axial loading, resulting in potential tooth breakage (Rieppel 1979). The lack of gnathic and dental morphologies in *V. komodoensis* suitable for bone breakage and oral extraction of within-bone nutrients is reflected in a feeding style that avoids extensive contact with bone surfaces. Finite element modeling data as well as direct measurements indicate 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 claim they would all swallow carcasses whole if possible. Our observations showed that defleshing behaviors result in subsequent size reduction and disarticulation. Defleshing proceeds until the

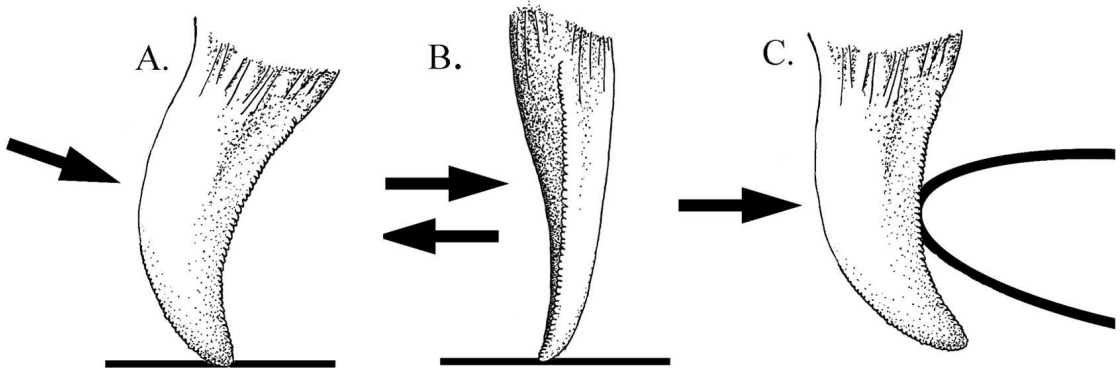


FIGURE 10. A diagrammatical representation of tooth mark production in *Varanus komodoensis*. The crown depicted is the seventh maxillary crown, thick lines represent the surface of cortical bone, and the arrows indicate the direction of crown movement. For A and C the distal carina is facing right, 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 crown 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.

individual determines the size of the carcass is sufficiently reduced to swallow. Elevating the carcass and pressing it against a fixed substrate are two ways of achieving the same end: moving a carcass or large carcass portion down the gullet without lingual assistance. This method explains how *V. komodoensis* can obtain bone and within-bone nutrients while lacking 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 crowns of *V. komodoensis* modify bone surfaces frequently. Although most marks are inconspicuous because they are small and shallow, our methodology shows unambiguously that they are present. 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 crowns through the substrate facilitated by the medial-caudal arc. These behaviors are reflected in the dominance of tooth scores, as well as their distinct morphology. Because the defleshing strokes draw the tooth crowns distally into the fleshy substrate, the apices are the first to make contact and are dragged along the bone surface, resulting in a score (Fig. 10). The width of a score is limited by the width of the apex, which is narrow for all teeth in the arcade. Scores constitute the majority of marks and they are found on all marked element types, thus suggesting that the shape of a particular element does not affect score production. The apex can 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 elements types, coupled with the fact that their average width and interquartile width ranges are so similar to those of scores (Fig. 8), lends support to this. Pits result from similar apical contact without subsequent dragging across the bone surface. As with scores, the apex also limits the pit's width, so widths are similar for both types of scores. Pits are much rarer than scores because the primary feeding method of *V.*

komodoensis involves the drawing of crowns. If a crown punctures flesh enough to contact bone but is not drawn distally, the cutting function of ziphodont crowns is not achieved. Pits are therefore infrequent because the behavior that produces them does not result in flesh removal. Unlike marks in assemblages accumulated by mammals, pits are not the result of gross 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 crown positions the mesial carina in such a way that the denticles are allowed unobstructed access to bone surface (Fig. 1). Except for edge mark production (below), it is difficult to envision the denticles of the distal carina contacting and dragging across bone surfaces, owing to the concave form of the distal carina and the linear arrangement of teeth in the arcade. In order for the dragging of denticles to create striations, the carina needs to be reoriented so movement of the crown through the substrate is lateral (in the labial/lingual direction) (Fig. 10B) as opposed to the typical distal direction. This moves the crown perpendicular to the denticulated carinae. This would be possible during the beginning of a defleshing stroke when rostral movement is more medial (Fig. 3), because this motion would be perpendicular to the carinae of most crowns. 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 due to the elongate mesial carina contacting more bone surface area than the apex typically does. The direction of crown 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 a subsequent manuscript (D'Amore and Blumenshine unpublished data).

Similar to scores, edge marks reflect distal crown movement. Alternatively, they are formed not by the crown apex, but rather by the distal carina (Fig. 10C). This makes them unique to ziphodont consumers. During a defleshing stroke, the distal drawing of a

crown 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 crown, but they are the result of the distal carina. This limited lateral motion may occur when the crown slides across the bone surface after it makes initial contact, or when the animal tries to dislodge a wedged crown. 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 production of edge marks. 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 wide, rounded rostrum, in combination with the arcing medial-caudal defleshing strokes seen. The arcing motion of defleshing strokes moves the crowns along an arcing track that corresponds to 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.

We propose two hypotheses for the production of clusters of parallel marks, both involving deviations in crown position at the point of bone-tooth contact when defleshing. The first is that several crowns 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 crowns into the fleshy substrate in sequence, each tooth should theoretically enter in the same place during a single stroke (Auffenberg 1981), thus pro-

ducing overlapping marks. In practice, though, slight differences in the positions of the crowns when they enter 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 marks being adjacent to one another. Because the motions of consecutive strokes are so similar, crowns would move in the same direction, resulting in marks of a similar orientation.

We were not able to use feeding footage to test these hypotheses. There is no evidence to indicate whether these two methods would result in different mark morphologies 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 in parallel clusters produce the marks are 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 crowns to move out of position enough to produce marks this distance apart. For parallel marks to form from 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 a carcass, the rostrum was positioned at the distal femur. The individual then displayed repetitive defleshing strokes, perhaps to try to 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 bites does not appear to be random or "mindless" in *V. komodoensis* (as stated by Hunt et al. 1994: p. 230). The

selection of elements directly reflects a 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. These marks were produced simply because these elements were in areas that the individual could properly position in its mouth when moving/swallowing the entire carcass. With the exception of edge marks, element shape does not appear to affect the frequency or type of mark production. Unlike in mammals, bone modification by *V. komodoensis* is not based on the amount of nutrients within particular bones (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 crowns 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 ziphodonts do not gnaw or crush bones. 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 loosely socketed teeth may dislodge. The behavior of *V. komodoensis* indicates that this is unlikely. Varanid dentition is pleurodont and lacks socketing altogether, yet frequent bone-tooth contact resulted in bone modification with no tooth loss.

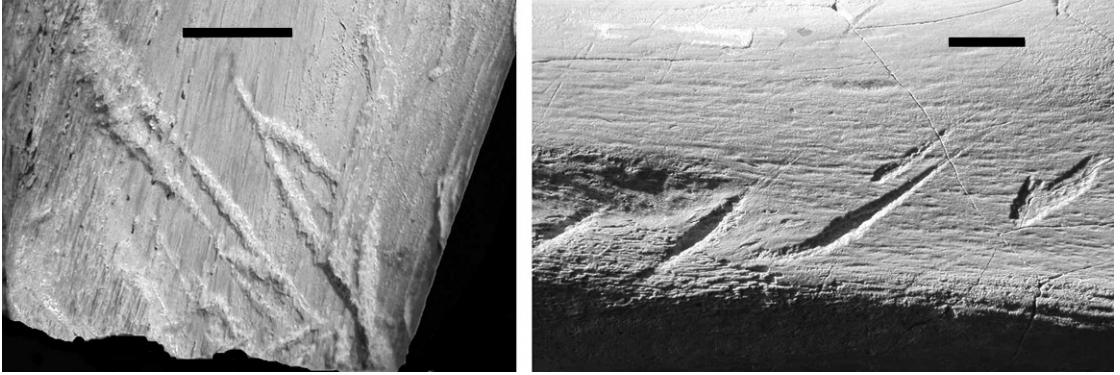


FIGURE 11. Two sets of traces on a hadrosaur ischium (RTMP 79.14.733, Royal Tyrrell Museum, Drumheller, Canada) believed to be linear, parallel theropod tooth scores. Note the similarities between these and the scores in Figure 5. Photographs were taken by A. R. Jacobsen. (Scale, 10 mm.)

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) or the carcass type fed upon. Because of the small number of individuals sampled, it is not possible to decouple these effects.

Applications of Ziphodont Controlled Assemblages to Fossil Systems.—Our results can be applied to fossil assemblages accumulated by ziphodont taxa for the purposes of deducing crown use. We use theropods as our example system; they are the majority of known ziphodont taxa as well as the alleged producers of most ziphodont fossil tooth marks (Table 1). Because of the goals of this study, we emphasize functional/behavioral inferences. In addition, inferences are drawn concerning taphonomic processes and research methodology. Our inferences are provisional because the tooth marks on fossil bones were not measured using the same methods we used to for our control assemblages.

Many morphological similarities are apparent between tooth marks produced by *V. komodoensis* and those reportedly produced by Mesozoic archosaurs (Table 1). Jacobsen (1995) has conducted the most thorough analysis of Mesozoic tooth marks, in which the majority are described as linear parallel scores (Fig. 11), many of which are striated, with punctures being less common. Other published accounts describe similar tooth marks (assuming that “grooves” are equiva-

lent 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, most marks in Mesozoic assemblages primarily indicate defleshing behavior, with little evidence of bone chewing or crushing. Elongate scoring indicates that theropods may also have drawn their apices distally across bone surfaces when defleshing. This model supports Jacobson’s (1995: p. 66) assertion that theropods drew their teeth “backwards” across a bone surface more frequently than they made “vertical” contact. Other authors have proposed defleshing models for Theropoda involving distal crown movement as well, either the “puncture and pull” of tyrannosaurids (Molnar and Farlow 1990; Erickson and Olson 1996; Rayfield 2004) or the “slashing” of *Allosaurus* and *Ceratops* (Rayfield et al. 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 with 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*'s medial-caudal defleshing technique as well as the curvature of traces. He asserts that this stroke would be ineffective in congenetics 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, clusters of parallel, or subparallel, tooth scores are frequent in Mesozoic assemblages (Table 1), and it has been suggested that several teeth scored the bone surface in one bite. If this was true, the spacing between parallel marks may indicate the spacing between tooth crowns of the alleged consumer (Colbert 1961; Jacobsen 1995). However, because we lack behavioral evidence to support this as well as our alternative hypothesis of repeated strokes, we suggest caution be taken in correlating the spacing of parallel tooth scores with the spacing of tooth crowns. If crown movement were primarily caudal as suggested here, tooth mark spacing would underestimate crown spacing in the majority of cases.

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

The high frequency of striated Mesozoic marks indicates that theropods moved their crowns in a lateral direction frequently. Jacobsen (1995, 2001) found striated marks on 40 of 79 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 crowns across a bone at an oblique angle, which could be facilitated by lateral crown 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 crown movement necessary for striation production. Currie et al. (1990: p. 123) proposed another explanation for striation production, whereby *Saurornithoides* intentionally positioned its carinae parallel to the bone surface for the purpose of "slicing flesh off of bones." We 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 consumer. 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 2–14% and Fiorillo (1991a) found only 0–4% of bones were marked in the respective Cretaceous assemblages they sampled. Conversely, our *V. komodoensis* controlled assemblage yielded marks on approximately one-third of all elements. Erickson and Olson (1996) mentioned that diagenesis could result in the underrepresentation of tyrannosaurid tooth marks. The majority of marks found in *V. komodoensis* controlled assemblages are small, shallow pits and scores. These mark types may be more susceptible to elimination by diagenetic processes than 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 can be very inconspicuous and are detectable only by 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 1).

Alternatively, differences in mark type may simply be the result of structural or 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 our *V. komodoensis* controlled assemblages is that the sample of fossil bones examined by researchers was simply not fed upon. There is no evidence that all, or even a substantial portion, of the Mesozoic bones investigated by previous researchers were available to consumers before preservation. 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. But bone beds repre-

sent potentially catastrophic situations that usually result in quick burial; with scavenging thus discouraged or prevented, there would be little opportunity for feeding traces to be left. These situations therefore would not represent a "typical" death assemblage. It would be helpful to examine fossil specimens "known" to have been scavenged in order to determine the frequency and positioning of taphonomic traces, so that the results could be directly compared with controlled assemblages.

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 by using theropods 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 carcasses used in feeding trials are not representative of the possible size range and anatomical variation of wild *V. komodoensis* prey. Third, the artificial sectioned carcasses used here are unlikely to be representative of carcasses consumed by *V. komodoensis*. Last, that carcasses 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.

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 inter-specifically (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 to investigate mark position. Although we were able to give a qualitative estimation of the amount of flesh adjacent to a particular element, 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 regarding the location of marks on a particular element might be informative.

The controlled setting we used provides an alternative explanation for the dissimilarity in mark frequency between our controlled assemblage and Mesozoic assemblages. Fiorillo (1991a) proposed that 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 theropods 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 on theropods is necessary 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 crowns 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 crown 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 affect the function of a crown, the behavior of its owner, or the types of traces produced. Although we have not identified any more appropriate extant ziphodont analogues, or any whose features show similar 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: p. 867). Both Theropoda and Varanidae have significant degrees of morphometric variation along the tooth row (D'Amore personal observation).

Other areas of theropod anatomy should also be studied in detail to narrow down behavioral and taphonomic predictions. As stated above, the rounding of the rostrum is crucial for the success of medial-caudal defleshing as well as for the production of curved tooth marks. Although many theropod rostra are considered narrow, most likely there is significant variation. It is reasonable to predict that a wider rostrum would be linked with a higher degree of lateral motion, 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 the ability of a certain taxon to damage bone surfaces. Last, studies on neck morphology, such as that of Snively and Russell (2007), also will shed light on the most likely direction of head movement during 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) used the standard terminology outlined by Binford (1981) and adopted here, and few provided 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 have stated that furrowing is common (Table 1), but Jacobsen (1995, 1998), who also utilized Binford's nomenclature, stated 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 areas of ziphodont tooth marks and general *V. komodoensis* feeding behavior. Studies of *V. komodoensis* feeding and mark production in a more natural setting are necessary, as are more in-depth morphometric and functional studies of both extinct and extant ziphodont dentition in order to understand the relationship between the degree of ziphodonty and the nature of bone modification. *V. komodoensis* tooth marks could also be compared with fossil traces to identify the consumer, as is often attempted with 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 with *V. komodoensis* traces in order to determine the diagnostic characters unique to a ziphodont mark. One could then determine whether a mark was produced by a ziphodont crown, some other type of crown, or a different agent altogether.

This type of research has great potential for reconstructing both extinct behaviors and paleoecology. A body of actualistic studies with all types of modern dental analogues can be assembled with similar techniques, cataloging a variety of dental morphotypes, behaviors, and traces. Similar experiments could also determine whether prey size, predator size, group feeding, etc. affect tooth mark morphology and frequency. Morphological and functional studies can be used to determine what behaviors were possible for the extinct taxa of interest, and therefore, what marks they would have been capable of making. Fossil assemblages can be cross-referenced with this body of data to greatly narrow down the behavior and morphology that produced them. Ultimately, tooth marks along would provide the means to identify the consumer and the environmental and

ecological circumstances under which the animal died.

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