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Carnivore Modification to Rudabánya Bones

Abstract
Evidence of carnivore activity as indicated by the presence of gnawed and digested bones are rather poorly represented in middle to late Miocene European localities. In this study we identified skeletal elements modified by carnivores form the late Miocene locality at Rudabánya and discuss their significance with reference to the ecomorphological attributes of extant predators to infer patterns of prey selection and feeding behaviour.

Kurzfassung
Carnivoren-Fraß an Knochen aus Rudabánya (Ungarn)
Nachweise für Carnivoren-Aktivitäten durch bekaute oder angedaute Knochen sind spärlich überliefert in Lokalitäten des mittleren und oberen Miozän Europas. In dieser Studie bestimmen wir Skelettelemente aus der obermiozänen Lokalität bei Rudabánya, die durch Carnivoren verändert wurden und diskutieren deren Signifikanz unter Bezug auf ökomorphologische Attribute rezenter Beutegreifer, um auf Muster der Beuteauswahl und Freßverhalten schließen zu können.

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Introduction

Carnivores are well represented in European Miocene localities (WERDELIN 1996a), and functional analyses of their dentitions and postcranial remains have recognised several ecomorphs relating to carnivoran hunting and feeding behaviours (CRUSAFONT-PAIRO & TRUYOLS-SANTONJA 1956, WERDELIN 1996b, WERDELIN & SOULONIAS 1996, VIRANTA 1996). Critical to these classifications is the proportion of meat to bone in the diet and the ability to break and consume bone. Specialised adaptations for bone eating and extraction of nutrients within bone occurred several times during the Cenozoic, (WERDELIN 1989) and would have conferred an adaptive advantage to carnivores (EWER 1967, TURNER 1992), as indicated by convergence of several carnivoran families into this niche

through the Tertiary (WERDELIN 1989, VAN VALKENBURGH 1991).
The categorization of carnivores into an ecomorphological classification is significant for both palaeobiological and taphonomic analyses of fossilized vertebrate remains. Gnawed and digested bones provide one of the few tangible records of past carnivore behaviour and theoretically ecomorphological designations should be reflected in predator accumulated assemblages. Variation in the composition of carnivore paleoguilds during the Mesozoic and Cenozoic has been inferred by the extent of carcass modification, (i.e. degree and frequency of tooth marks), leading to the conclusion that during certain time intervals "empty niches" for bone eaters might have existed, given the inability of the existing predator guild to fully utilize carcasses (HUNT 1987, FIORILLO 1991, PRATT & HULBERT 1995, VIRANTA 1996).
Direct evidence of predation and scavenging as evidenced by gnawed and digested bones is comparatively rare from Central European sites dating to the later Miocene. In part this reflects biases created by the collection of complete and taxonomically significant specimens at the expense of fragmentary or damaged bones, which are generally more informative of carnivore activity. Further loss of evidence occurs as bones are subjected to weathering, successive cycles of deposition and fossilization which all tend to result in a loss of surface detail (HAYNES 1980a, BROMAGE 1984, BEHRENSMEYER et al. 1989, ANDREWS & ERSOY 1990, CRUZ-URIBE 1991), rendering it difficult to attribute individual marks on bone surfaces to specific causal agents without some degree of ambiguity.
Ecomorphological studies of carnivore remains recovered from Central European middle and late Miocene localities dating between MN 6-9 (ca. 15-9.5 Ma) suggests that omnivorous and generalised, dog-like, meat and bone eaters prevailed (WERDELIN & SOULONIAS 1996), but between MN 10-13 (9.5-5.3 Ma) the balance of ecomorph types shifted to faunas containing more specialised meat and bone eaters (usually larger bodied, some more cursorial), and the medium to large bodied machairodontine cats. *Adcrocuta eximia*, the first truly bone cracking hyaena, first appeared in MN 10 and its success has been linked to its ability to exploit niches created by more

open habitats with greater scavenging opportunities (WERDELIN 1996a).

Rudabánya (MN 9, ca. 10 Ma; BERNOR et al. 1993) samples one of the youngest localities preceding this turnover event and evidence of carnivoran activity at this site provides insights upon the predatory behaviour and patterns of bone modification at this time. A wide range of carnivore taxa have been identified from the R2 locality, (WERDELIN & HEIZMANN forthcoming), and five taxa may be implicated as potential modifiers of bone according to the morphology of their dentitions. Three taxa, two primitive ursids (*Ursavus brevirhinus, U. primaveus*), and a large bodied amphicyonid, are classified as mesocarnivores (VIRANTA 1996), and have dentitions that are adapted to an omnivorous lifestyle, including molars with an enlarged occlusal surface for grinding and crushing. *Thalassictis montadai* is a medium sized hyaenid adapted to meat/bone eating (WERDELIN & SOULONIAS 1996). *Simocyon diaphorus* is also represented at Rudabánya and although its taxonomic and ecomorphological attributions are uncertain, (WERDELIN 1996b), it likely incorporated some bone in its diet.

Materials and Background to Analysis

A total of 1127 ungulate bones excavated from the R2 locality between 1973-1994 were examined for evidence of tooth marks and digestion. Forty-six elements were considered to show evidence of carnivore modification, namely, tooth marks, (38 specimens, including two specimens that were also digested), and digestion (10 specimens). A number of specimens bore marks that could not be referred to any particular agent with certainty and these are not quantified further in this analysis. There was no compelling evidence from tooth mark morphology to implicate which taxa may have been responsible for creating the marks observed, and it seems likely that more than one predator or scavenger was involved in creating the modifications observed. This study focuses upon assessing the ability of the identified carnivoran taxa to modify bone in relation to their ecomorphic type as evidenced by the remains of food items.

Studies have shown how the proportions of meat and bone consumed by extant hypercarnivorous taxa vary considerably; felids are largely specialized flesh eaters, whilst hyaenids and the larger sized canids (*Canis lupus, Lycaon pictus* and *Cuon alpinus*) incorporate larger proportions of bone and bone marrow in their diet (VAN VALKENBURGH, 1991,1996). Hyaenas (*Crocuta crocuta, Hyaena brunnea*) and gray wolves (*Canis lupus*) are both classified as meat/bone eaters, but whilst hyaenas have enlarged, conical shaped premolars adapted for breaking bones apart under point-to-point pressure, the wolf accomplishes the same task

by bone crushing (EWER 1967, WERDELIN 1989). The omnivorous ursid taxa, (*Ursus americanus, U. arctos*) have molars with enlarged occlusal areas (particularly in the length dimension), which are readily capable of breaking and consuming bones by crushing and grinding (HAYNES 1983a, HUNT 1999).

Bone breakage by carnivorans is most extreme in *Crocuta crocuta*, (ecomorph type 6 of WERDELIN & SOULONIAS 1996), which routinely crack open the long bones of mammals up to 300 kg (BRAIN 1981, HILL 1989), exerting a pressure of approximately 363 kg with its premolar teeth, (SAVAGE & LONG 1986: 80). The bone breaking capacity of the gray wolf approximates to that of ecomorph type 5 of WERDELIN's & SOULONIAS' classification, although their categories were devised solely for hyaenas and cannot be extrapolated to other groups (WERDELIN pers. comm.). Wolves readily fracture the limb bones of white-tailed deer and subadult moose with their carnassial teeth, but long bones of adult feral horses, moose and bison, are rarely broken (HAYNES 1982, 1983b).

Attributes of bone assemblages modified by spotted hyaenas and gray wolves have been well documented in a series of field and experimental studies (HAYNES 1980b, 1982, 1983a, BINFORD 1981, BRAIN 1981, BLUMENSCHINE 1986, 1988, CAPALDO 1996). Features of bone breakage and consumption by these taxa include considerations of bone completeness, degree of fragmentation, and tooth mark frequencies by bone portion.

Bone completeness

The long bones from carcasses consumed by carnivores with weak dentitions may remain largely intact (BRAIN 1981), whilst more committed bone eaters consume epiphyses and break open long bone shafts for the marrow contained within the medullary cavity. Limb bones of smaller prey may be broken by biting through the diaphyses (BONNICHSEN 1973, MAREAN & SPENCER 1991), but the constraints of bite force and/or gape size prevent carnivores from breaking open long bones of larger taxa by this means (BRAIN 1981). However, both wolves and hyaenas may gain egress to the marrow contents of long bones derived from large bodied taxa by removing epiphyses with their incisors and canines (BRAIN 1981). This process initially entails the production of bone cylinders (i.e. bone diaphysis), which may be subsequently broken apart to extract the marrow contents (BINFORD 1981, BRAIN 1981, HAYNES 1982, POTTS 1988). Assemblages containing bones with minimal carnivoran damage and bone cylinders may be considered indicative of incompletely utilized carcasses and helps establish an upper threshold of bone damage for the predator concerned (FIORILLO 1991).
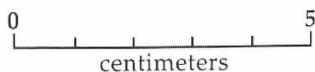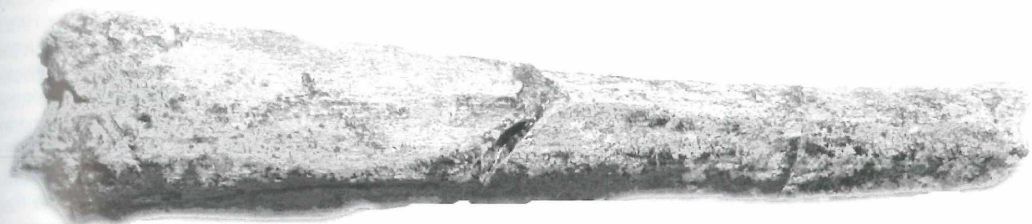
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centimeters

Figure 1. a) *Hippotherium* tibia (MAFI1993/150) showing carnivore damage; b) Detail of carnivore damage along margin of shaft (proximal end)

In the Rudabánya sample there are only seven complete ungulate long bones (four radii and three metacarpals), and three complete or nearly complete long bone shaft portions (two tibia and one metatarsal) that exhibit extensive breakage. Only one of these specimens bears tooth marks, a nearly complete left tibia diaphysis, MAFI993/150, referred to *Hippotherium* sp. (Figure 1a &b). Based on the thickness of the cortical bone which is 9 mm at the insertion point of the nutri-

ent foramen, this individual was either a subadult or mature individual at its time of death. Although broken at the time of excavation, the *Hippotherium* tibia fragments could be refitted to form most of the shaft, which would have been complete at the time of deposition. Both epiphyses are missing, and gnawing damage is visible along the surviving margins of the proximal and distal shaft portions. The margin of the proximal portion of the shaft is ragged, with several inden-

tations or punctures which have an elongate rather than circular appearance. A group of small, shallow, superimposed pits occur approximately one centimeter from the proximal margin of the shaft and these are bounded on either side by two scores or furrows, with a "U" shaped profile, orientated diagonally to the long axis of the bone. This pattern of tooth marking is consistent with the placement of the bone transversely to the cheek teeth row with the purpose of detaching and/or consuming the epiphyses and obtaining access to the marrow contents (BINFORD 1981). A similar pattern of damage is seen on bison and moose tibiae gnawed by wolf, depicted by HAYNES (HAYNES 1982, Fig 2, and HAYNES 1983a, Fig 7). The midshaft area of the bone is devoid of tooth marks indicating that the focus of attention was upon detachment of epiphyses and extraction of marrow contents.

Bone Fragmentation

High frequencies of fragmented long bones are a feature of faunal assemblages modified by carnivores whilst breaking bones to obtain marrow. Fragmentation of long bones by Recent hyaenas and wolves derived from animals with a body mass ranging between 20 and 300 kg creates assemblages where the proportion of bone fragments longer than 5 cm exceeds 50%, excepting in den sites (BRAIN 1981, HAYNES 1983b, BLUMENSCHINE 1988). Similar distributions of bone fragment length have been found in fossil assemblages interpreted as hyaena accumulations (BRAIN 1981, STINER 1994).

The Rudabánya assemblage is highly fragmented with limb bone shaft portions and undiagnostic fragments accounting for 14% and 23% of the assemblage respectively, and over 90% of these specimens were less than 5 cm in length. The degree of breakage as measured by bone fragment length far exceeds that reported for extant carnivores which suggests that multiple factors may have contributed to the pattern of breakage observed.

We do not know of any study that describes fragment length of long bones that have been initially broken by carnivores and subsequently subjected to further breakage by weathering and trampling. In the absence of these data sets, we refer to the sequence of bone fragmentation from modern human occupation sites. These sites are not strictly analogous to carnivore modified assemblages because the mean length of bones broken for marrow by humans are generally shorter than those produced by carnivores, being less than 5 cm in overall length (GIFFORD 1978, BRAIN 1981, YELLEN 1986).

Studies of faunal assemblages created by hunter-gatherer groups have documented how rapidly bones in the subaerial context may be reduced in size after discard, largely due to the effects of trampling (GIFFORD 1978; GIFFORD & BEHRENSMEYER 1977, YELLEN 1986). These effects are twofold. Firstly, bones are broken into smaller pieces. Secondly, smaller bones enter the burial substrate more rapidly than larger bones thus enhancing their potential for long term preservation (GIFFORD 1978, BEHRENSMEYER & DENCHANT BOAZ 1980). Similar studies conducted by YELLEN (1986), upon recently buried faunal assemblages have shown that bone fragments may also be reduced in size by in situ breakage, although overall loss of material is minimal.

It seems probable that the Rudabánya assemblage was subjected to subaerial and post depositional processes leading to considerable breakage of bones and bone fragments. Some evidence for post depositional breakage of bones at Rudabánya is afforded by the presence of bones that were complete or near complete at the time of deposition but in a fragmentary state at the time of excavation (eg. *Miotragocerus pannoniae* radius, MAFI1993/399; *Hippotherium* tibia, MAFI1993/150). Because the bone sample from Rudabánya is comminuted, it is not possible to identify most long bone shaft fragments to bone part following the scheme proposed by BUNN & KROLL (1986). BLUMENSCHINE (1988) has shown how the frequency of tooth marking upon long bone portion (i.e. shaft and epiphyses), may be used to identify scavenging activity, but it is not possible to draw inferences of this nature from the Rudabánya assemblage as this kind of information has been largely obscured by subaerial and post depositional processes.

Tooth Mark Location and Frequency

Tooth marks attributed to carnivore activity were most evident upon distal extremities of limb bones (25 specimens). The remaining marks were distributed upon proximal limb bone elements (7 specimens), a mandible, two limb bone shaft fragments and two unidentified bone fragments (see Table 1).

Two types of tooth marks were recorded: punctures and scores. The diameter of puncture marks ranged between 3.8-6 mm and occurred singly or at low frequencies on individual elements, especially phalanges (14 specimens). Other modified podial elements included tuber calcis of calcanei (6 specimens), astragali, (2 specimens) and the proximal end of metacarpals (3 specimens). More extensive gnawing damage (punctures and scores) were found upon long bone epiphyses, namely, proximal humerus (1 specimen), distal humeri (2 specimens), distal radius (1 specimen), proximal tibia (1 specimen), distal tibia (1 specimen). Two shaft fragments bore tooth marks in addition to the *Hippotherium* tibia shaft described above.

Analyses of bones modified by spotted hyaena and wolves indicate that tooth mark frequency is correlated with

Table 1a. Carnivore Gnawed Bones from Rudabánya

Element	Part	Sm/Med	Medium	Suid sp. 1	*Miotragocerus*	Suid. sp. 2	*Hippotherium*	Total
Cranial								
Mandible							1	1
Long bone								
Humerus	P	1						1
	D		1			1		2
Radius	D						1	1
MCIII	P						1	1
MC acces.	P						2	2
Tibia	P	1						1
	PS						1	1
	DS						1	1
	D						1	1
Unident.	S	1	1					2
Unident.		2						2
Phalanges								
Prox. main	M		1	1		1	1	4
Mid. main	P						1	1
	M			1	1	1		3
	D			1			1	2
Dist. main	P					1		1
Prox. acc.	P					1	1	2
	M						1	1
Mid. acc.	P					1		1
Podial								
Calcaneus	P			1	1		4	6
Astragalus			1				1	2
Total		5	4	4	2	6	18	39

Table 1b. Carnivore Digested Bones from Rudabánya

Element	Micromeryx	Sm/Med	Suid sp. 1	*Miotragocerus*	Suid sp. 2	*Hippotherium*	Total
Cranial							
Petrous		1					1
Phalanges							
Prox. main	1	1	1				3
Mid. main		1		1	1		3
Dist. main				1			1
Prox. acc.						1	1
Mid. acc.						1	1
	1	3	1	2	1	2	10

Explanations to Table 1a & b

Suid 1	*Parachleustoerus* n.sp.	Acc.	Accessory in *Hippotherium* is phalanges II, IV; in artiodactyls is phalanges II and V
Suid 2 =	*Propotamochoerus palaeochoerus*		
SM	Small-Medium Body 20-75 kg	Main	in perissodactyls is phalanx III, in artiodactyls is phalanges III and IV
M	Medium 75-200 kg		
		Prox.	proximal
Part		Mid.	Middle, 2nd phalanx, III in perissodactyls, III and IV in artiodactyls
P	Proximal		
PS	Proximal Shaft	Dist.	Distal, 3rd phalanx, III in perissodactyls, III and IV in artiodactyls
MS	Midshaft		
DS	Distal Shaft		
S	Shaft		
D	Distal		

the degree of carcass utilization. Spotted hyaenas and wolves are social hunters and tooth mark frequencies upon long bones at fresh kill sites are low because during the early stages of carcass utilization the primary focus of attention is upon the rapid consumption of flesh (HAYNES 1982, 1988, BLUMENSCHINE 1986). Consumption of bone and marrow is a more solitary and lengthy process usually undertaken by removing long bones to secluded locations to avoid competitive interactions (i.e. feeding patches), or to lairs and dens (KRUUK 1972: 126, HAYNES 1982, BEHRENSMEYER 1983).

Tooth marking frequency of complete bones by wolves at kill sites may be minimal although the percentage of tooth marked shaft fragments, if present, may be high, especially if the kill site is revisited by the predator or subjected to secondary scavenging (HAYNES 1982). HAYNES (1983b) has reported a frequency of 11 out of 15 tooth marked shaft fragments at a bison kill site, but seldom found toothmarks upon shaft fragments of subadult moose. BLUMENSCHINE (1988) has reported higher frequencies of tooth marking (89%) upon wildebeest long bones scavenged by spotted hyaenas, and the incidence of tooth marking at wolf den sites is also high (BINFORD 1981, HAYNES 1982). Bones and bone fragments from fully exploited carcasses acquire greater numbers of tooth marks as the sequence of killing, defleshing, dismemberment, bone transport, and bone breakage proceeds (HAYNES 1983a, BLUMENSCHINE 1988).

Tooth mark frequencies in the Rudabánya sample are low (3%), even given our conservative level of identification. However, frequencies of carnivore modified material within fossil and recent faunal assemblages shows considerable variation at local and regional scales and are not necessarily indicative of the intensity of carnivore activity. Successive kills of prey in favoured ambush sites may result in bone accumulations bearing few tooth marks (HAYNES, 1982), whilst the repeated transport of body parts to feeding patches for bone eating and marrow extraction can create assemblages bearing significantly higher tooth mark frequencies (BEHRENSMEYER 1983, 1987, BADGLEY 1986). Areas attracting high densities of herbivores, such as floodplains and waterholes, have been described as predation arenas (BEHRENSMEYER 1987), but evidence of carnivore activity may be obscured by high numbers of seasonal deaths (drought, mass drownings), creating a surplus of carcasses that may be ignored or only minimally modified by local predators and scavengers.

In attritional assemblages where the frequency of tooth marked elements cannot be precisely calculated because an unknown number of bones may have been derived from deaths due to factors other than predation, the incidence of tooth marking upon associated sets of elements showing some evidence of carnivore modification are of value. Five elements from four sets

of articulated units (5/23 elements) bore tooth marks, giving a tooth mark frequency of almost 25%. However, as they are all derived from distal extremities, they do not record tooth mark frequencies for the proximal limb bones. Seven articulated forelimb elements (distal humeri and proximal radii), are also present in the sample, but none of these bore tooth marks. The presence of articulated units suggests incomplete dismemberment of carcasses, whilst higher than average tooth mark frequencies upon phalanges (10%), could indicate scavenging (HAYNES 1983a). Most carnivores ingest foot bones acquired either through hunting or scavenging as evidenced by scat contents (HAYNES 1982).

The frequency of tooth marked bones by taxa is itemised in Table 1. Highest tooth mark frequency occurs upon *Hippotherium* bones (46% of all tooth marks identified), which is in accord with the findings of BLUMENSCHINE (1988), that tooth mark frequency is higher upon larger bodied taxa (250-750 lbs). The Rudabánya *Hippotherium* we refer to had a body mass approximately in the middle of this range (BERNOR et al., in review). No tooth marks were observed upon the bones of the small bodied *Micromeryx* or rare taxa, such as *Dorcatherium* and *Tapirus*. The remaining tooth marks were fairly evenly distributed across taxa with a mature body mass ranging between 30-110 kg.

Coprolites and Bone Eating as Evidenced by Digested Material

Six coprolites probably derived from a small bodied carnivore (<20 kg), were recovered from the R2 locality. No bone was visible in these remains, but one coprolite, (MAFI1989/13), contained a mollusc fragment.

Nine digested phalanges ranging in size from the small bodied *Micromeryx* (first phalange) to *Hippotherium* (second, lateral phalange) were identified. In all cases the proximal epiphyses of the phalanges were fused indicating that the animals were semi -mature at death, although not necessarily adult as the epiphyses of phalanges are amongst the earliest fusing elements. The associated and digested second and third phalanges (MAFI1977/11 and MAFI1977/14), most likely derived from *Miotragocerus*, are of interest in that they indicate the ingestion of a sizeable food portion, that would have been approximately 7 cms in length. Specimen MAFI1990/200 is a petrous bone derived from a small to medium sized ungulate which appears digested.

Evidence for Prey Utilization by Rudabánya Carnivores

The degree of carnivore damage to bone at R2 locality seems comparable to the level of modification observed at wolf kill sites. Evidence of bone eating is supplied by partially consumed articular ends and digested remains, whilst incomplete utilization of carcasses is suggested by articulated units and the likely inability to break open long bones of large bodied mammals. This would be consistent with an ecomorph type 5 meat and bone eater of WERDELIN & SOULONIAS (1996), but without the extreme adaptation for bone breakage which would reduce the nutrient value of larger carcasses obtained either through hunting or scavenging.

Two of the carnivores identified from Rudabánya have a predicted body mass of 80 and 90 kg (*Ursavus* sp.), but the amphicyonid would have been considerably larger, approximately the same size of *Amphicyon major*, which has a predicted body mass of 183 kg (WERDELIN pers. comm.). The procyonid, *Simocyon diaphorus*, was previously predicted to have a body mass of approximately 50 kg, but this figure is now considered to be an over estimate (WERDELIN pers. comm .). These taxa are all presumed to have been solitary stalk and pounce or ambush hunters (VIRANTA 1996). The R2 locality lies within a narrow valley, and the local topography would have provided a very suitable habitat for ambush Hunters. Under such conditions prey is disavantaged both by surprise and the difficulty of rapid flight up steep sided slopes (SCHALLER 1967).

Studies of solitary predators in extant biotopes have shown that average prey size does not usually exceed that of the predator (LEWIS 1997), although large cats and social hunters ambush and kill prey far in excess of their own body mass (TURNER 1992). The body mass of taxa bearing evidence of carnivore modification from the R2 locality ranges between 5 kg for *Micromeryx* (KÖHLER, 1993), to 200+ kg for mature *Hippotherium* (BERNOR et. al., in press). The range of prey size is rather greater than that reported for medium sized felids (KARANTH & SUNQUIST 1995), but prey diversity (6 species), is low probably because small mammals and birds were not included in the study sample.

Many carnivorans hunt disportionately high numbers of young animals and greater than predicted frequencies of juvenile remains in fossil assemblages are often considered to be indirect evidence for predation (KLEIN 1982, BADGLEY 1986, PALMQUIST et al. 1996). Over 50% (MNI of dentitions = 32), of the pecoran and suoid dentitions from Rudabánya were derived from immature individuals, but the numbers of juvenile post cranial material identified to these taxa (60 elements), was far less (ANDREWS et. al., forthcoming). Poor representation of immature elements within fossil assemblages may reflect their inherent weakness or more complete consumption by carnivores, and interpreti-

ons based upon dentitions alone are thus somewhat equivocal.

More direct evidence of predation upon juveniles at Rudabánya comprises four tooth marked postcranial elements (unfused proximal epiphyses of a humerus and tibia, and associated calcaneum and astragalus), accounting for 4% of immature bones. The high frequency of immature dentitions, and the presence of tooth marked juvenile elements in the assemblage, is indicative that young animals were regular prey items, and estimates of the average body mass of prey consumed should be correspondingly adjusted. The body mass of the majority of prey items was likely less than 50 kg at the time of death (*Micromeryx, Euprox, Parachleuastochoerus,* juvenile *Miotragocerus* and *Propotamochoerus*). The bones of these animals could have been consumed by most predators/scavengers, including those with dentitions poorly adapted for bone eating. The limb bones of juvenile animals have a low marrow fat content but are a source of calcium and other nutrients, which have been shown to be important for supplying the metabolic needs of carnivorans, such as subadult cheetahs (PHILLIPS 1993).

Evidence that mature *Hippotherium* individuals were predated upon or scavenged is provided by seven elements, which either by their size or state of epiphysial fusion would have derived from animals that had attained maximum body mass. The MNI of gnawed mature *Hippotherium* elements in the study sample is 3 (calcanei), almost 50% of the total MNI for this taxon as calculated from dentitions and this suggests the presence of an efficient predator at the site.

Postcranial remains of the larger bodied ungulates (rhinos, chalicotheres and proboscideans), are rather poorly represented at the R2 site. They exhibit two modes of preservation, some well preserved remains, including two sets of articulated units, (left tarsus, MAFI1990/35-40, partial rib cage, MAFI1990/172-179), and material that was too fragmentary for identification except for designation to body size category. None of the well preserved large bodied mammals from the R2 locality show any indication of carnivore damage, but in a survey of the earlier collections (pre- 1973 excavations), one podial bone (MAFIV11824) from a large unidentified mammal bears a tooth mark. These data suggest that the upper limit of the body mass of live prey or scavenged items did not usually greatly exceed 200 kg.

As tooth mark frequency appears fairly constant across taxa and by body mass any inferences concerning predator identity and niche partitioning within the carnivore paleoguild can only be speculative. Between MN 6-9, amphicyonids were large bodied, formidable stalk and pounce predators with a powerful bite and bone crushing abilities (VIRANTA 1996). These animals would have possessed the strength and weight necessary to successfully subdue mature *Hippotherium*, and

seem to be a likely candidate for hunting large bodied prey.

The greater majority of mammals presumed to have died by predation are derived from mammals with a body mass between 5-50 kg. Predation by *Ursavus* sp.on mammals within this size category would be consistent with the observations of ROSENZWEIG (1968) who found that large bodied carnivores with omnivorous habits tend to kill smaller sized prey compared to hypercarnivores of similar body mass. *Thalassictis montadi* was a fairly small bodied hyaenid (31 kg), which seems unlikely to have captured prey as large as mature *Hippotherium*, but probably scavenged from carcasses abandoned by larger predators.

Conclusions

Ecomorphological studies of carnivore feeding behaviours based upon functional analyses of dentitions and post cranial remains have sought to show how the balance of feeding types (i.e. hypercarnivory, mesocarnivory and bone eating) may alter in predator paleoguilds in response to community evolution, immigration events and climatic change (WERDELIN 1996a, VAN VALKENBURGH 1988, 1991, VIRANTA 1996). However, whilst the representation of carnivore ecomorphological types is critical for interpretations of community structure and ecological shifts over long time scales, uncertainties concerning specific predator/prey relationships remain. Bones modified by carnivore activity are thus a useful source of information for ecomorphological analyses of prey utilization, and in well sampled assemblages may give some indication of prey abundance and preferred prey type (BEHRENSMEYER 1987). Comparative studies of fossil assemblages modified by carnivores over time scales which sample regional turnover events may provide means of recognising shifts in carnivore feeding ecology and supply evidence by which hypotheses concerning the composition and competitive interactions of past carnivore paleoguilds may be further corroborated and tested.

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