THE RELEVANCE OF CROCODILES TO OLDOWAN HOMININ PALEOECOLOGY AT OLDUVAI GORGE, TANZANIA

by

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ABSTRACT OF THE DISSERTATION

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The Plio-Pleistocene lake-margins at Olduvai contain a stunningly rich and well-preserved paleoanthropological record, but the spatial and temporal resolution of the record is too coarse to understand the ecological contexts of Oldowan hominin trace fossils at the level of the landscape facet, as developed by the Olduvai Landscape Paleoanthropology Project. Theoretically, hominin activities and trace fossils were largely determined by the distribution of resources and hazards across the landscape.

The goal of my thesis is to understand the paleo-wetland landscapes using a taphonomic approach. This thesis develops methods and criteria for identifying ecological contexts of the archaeological record through two neotaphonomic studies: (1) controlled observations of captive Nile crocodiles feeding on large mammal carcasses; and (2) field observations of Nile crocodiles feeding, and documentation of skeletal remains in modern wetland environments with the aim of understanding the interactions between crocodilians and mammalian carnivores for animal food.

My observations demonstrate that crocodiles produce definitive tooth marks and modification that are distinctive from those produced by mammalian carnivores. Both shed teeth and uningested bones modified by crocodiles are usually deposited in or near water where crocodiles live. Findings from this actualistic-oriented research provide a referential framework for the analysis of Olduvai samples from lakeshore deposits.

Results suggest that some of the Oldowan assemblages previously inferred as hominin “living sites”, may have been formed near crocodile habitats. This evidence is amplified by a lack of butchered crocodile bones and presence of large-bodied crocodiles in the fossil assemblages. Previously, crocodile remains were viewed as hominin food-refuse.

This study considers the extinct and large brevirostrine *Crocodylus* (*“Rimasuchus”*) *lloidi* as a major predator in paleo-wetlands, and their predation hazard is reflected in the toolkit by the preponderance of large stone pieces and manuports, herein inferred as ‘defense-tools’. The degree of long bone completeness and intensity of butchery in fossil assemblages are other archaeological proxies indicative of the proximity of hominin activities to water and their exposure to crocodile predation. This study introduces the importance of crocodilians for understanding early hominin land use behavior from taphonomic perspectives.

As the living representative of the large meat-eating archosaurians, crocodile feeding traces also present a unique opportunity for modeling bone modification and feeding behavior of carnivorous dinosaurs.

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CHAPTER 1. INTRODUCTION

1. Research problem

The Oldowan paleoanthropological record at Olduvai is one of the richest bodies of evidence about early stone-tool-using hominins. However, the currently low spatial and temporal resolution of the environments from which the trace fossils derive hinders our understanding of the landscape contexts in which the Oldowan hominin activities were conducted. Stone artifacts in association with well-preserved fossil bone assemblages, including hominin body fossils, have been recovered from Bed I and lowermost Bed II exposures, first by Louis and Mary Leakey beginning in the 1930s (Leakey *et al*., 1933; Leakey, 1951, 1965, 1971; and references therein), then by the Institute of Human Origins (IHO) in mid 1980s (Johanson *et al*., 1987), and since 1989 by the ongoing Olduvai Landscape Paleoanthropology Project (OLAPP) (Blumenschine & Masao, 1991; Blumenschine *et al*., 2003).

The richest stone artifact and fossil bone occurrences at Olduvai accumulated in relatively undisturbed, wetland settings adjacent to a shallow saline alkaline lake that occupied the central basin during Bed I and lowermost Bed II times, approximately 1.9–1.7 million years ago (Hay, 1976). In order to understand the adaptations of Oldowan hominins in these archaeologically-rich lake margin environments, we need to understand the landscape contexts of the body fossils and trace fossils of hominin activities.

To the extent that the Oldowan archaeological record is informative mainly about stone tool butchery of larger mammal carcasses in landscape contexts (Blumenschine & Peters, 1998), it is particularly important to understand the nature of hominin and carnivore interactions over animal foods in these landscapes. This thesis attempts to improve our understanding of the landscape contexts of hominin activities by focusing on taphonomic processes affecting larger mammal fossil assemblages in wetland settings similar to those reconstructed to have existed at Olduvai, with particular emphasis on the impact of crocodiles, the dominant predators in these aquatic habitats.

i) The nature of the Oldowan paleoanthropological record

The extensive work of Louis and Mary Leakey in the Bed I and lower Bed II has produced a large quantity of stone artifacts, vertebrate and invertebrate remains, plant fossils, and dozens of early hominin body fossils, mainly from the eastern part of the lake margin zone (e.g., Leakey, 1951, 1959, 1960, 1961a, 1961b, 1965, 1971, Leakey & Leakey, 1963, 1964; Leakey *et al*., 1964, 1973). Leakey's site-based excavations exposed large areas of paleo-land surfaces of up to 10 m by 10 m, with some containing dense concentrations of artifacts and broken-up bones of large mammals. Some of the fossil bones bear butchery marks, traces of animal gnawing, or both. Occurrences of dense stone-bone accumulations, especially in thin layers of sediments, were interpreted as "living sites" or "living floors" of early hominin occupation (Leakey, 1959, 1971), or as "home bases" (Isaac, 1971, 1978).

Living sites were viewed to represent campsites on ancient landscapes, to which groups of hominins returned after foraging excursions to process and share the food in a manner similar to that observed in modern hunter-gatherers (Isaac, 1978, 1981). The main force behind this concept, which was formalized by Isaac (1976), is that the main force behind hominin evolution was a complex interaction of social and biological adaptations involving meat-eating, tool use and an increasing dependence on cooperation between and within sexes, resulting in the advent of organized hunting or scavenging, the family unit (Isaac, 1986), and the division of labor, with all social and subsistence activities being centered spatially around a home base.

Even before the exposures were systematically excavated in early 1960s by Mary Leakey, dense concentrations of stone tools and bashed bones on the outcrops were interpreted by Louis Leakey (1951, 1959) as occupation floors of Oldowan culture where hominins manufactured stone tools and processed animal kills. Basing on this idea, Mary Leakey (1971) opened large excavations, which were targeted at points along the outcrops bearing the densest, most conspicuous surface concentrations of artifacts and/or bones, including hominin skeletal remains. Her goal was to expose “living floors” or “occupational sites” similar to those she and Louis Leakey had previously excavated at Olorgesailie, which were later expanded by Glynn Isaac (1967, 1977), and currently by Rick Potts (1989, Potts *et al*., 1999).

Numerous layers in Bed I and Bed II deposits were considered as living sites, but those from DK (levels 1 and 2), FLK NN (level 3), FLK (level 22), FLK N (levels 1-2), HWK E (levels 1-2), BK and MNK (Table 1.1) have received more attention (e.g., Bunn, 1982, 1983a; Potts, 1982, 1988; Bunn & Kroll, 1986; Oliver, 1994; Stewart, 1994; Blumenschine, 1995; West, 1995; Monahan, 1996; Capaldo, 1997; Dominguez-Rodrigo, 1997; Selvaggio, 1994a).

Since the publications of Leakey (1971) and Isaac (1971, 1978), much research has gone into questioning the notion of living sites. Binford (1981) criticized this hypothesis and strongly argued that the stone-bone concentrations at FLK level 22 (*Zinjanthropus*-level) represent palimpsests of both early hominin and carnivore activities. He contended that the site was marginally modified by hominins, whose activities were limited to scavenging carcass parts from carnivores that were too minimal to sustain food sharing. Also, Potts (1984, 1988) argued that the purported living sites at Olduvai were simply “stone-caches”, or places with pre-positioned concentrations of stones where hominins brought carcass parts for quick processing. The results of these inquiries have led to various alternative hypotheses about the socioeconomic functions of early hominin sites, such as routed foraging (Binford, 1981, 1984), stone caching (Potts, 1982, 1984, 1988), central-place foraging (Isaac, 1983), dry season-riparian woodland scavenging (Blumenschine, 1986a, 1986b, 1987, 1991), and resource-defense locales (Rose & Marshall, 1996). These competing explanations of site function and associated land use patterns, however, remain unresolved because the spatial resolution of the landscape contexts is too coarse to understand the ecological settings of hominin activities.

Following Mary Leakey’s retirement from Olduvai Gorge in 1984, the IHO team continued with exploration of Olduvai mainly focusing on expansion of the hominin body fossil record. Their most notable discovery was OH 62, postcranial skeletal remains of *Homo habilis* (Johanson *et al*., 1987).

The OLAPP research at Olduvai, which was initiated in 1989 by Blumenschine and Masao (1991), expands on Leakey’s work by taking a landscape approach. This method permits synchronic horizons to be sampled over a broad area in an effort to understand the ecological basis for variation in the trace fossil record for hominin land use. OLAPP’s sampling program has yielded a wealth of paleoanthropological material including over 10,000 stone artifacts, over 10,000 identified vertebrate specimens, and dozens of macroplant fossil specimens (Blumenschine *et al*., 2003, 2005a, 2006; Bamford, 2005; Bamford *et al.*, 2006; Blumenschine *et al*., in press; Peters *et al*., in prep). Also, a number of hominin specimens, including isolated teeth belonging to *Paranthropus* (*Australopithecus*) *boisei* and *H. habilis* have been recovered by OLAPP, expanding the number of hominin individuals to seventy (R. Clarke, pers. comm.). A complete list of hominin specimens (OH 1–OH 61) recovered from 1911 to 1982 is provided by Day (1986). Among the hominins recovered by OLAPP (OH 64–OH 70), only OH 65, a complete maxilla/lower face with complete dentition of *H. habilis*, has been published (Blumenschine *et al*., 2003). This larger-brained early *Homo* is the first Plio-Pleistocene hominin recovered from the western lake margin.

The long-term goal of OLAPP is to reconstruct traces of hominin land use patterns within the context of an evolving paleolandscape during lowermost Bed II times (ca. 1.79–1.71 mya). The OLAPP program is committed to increase our knowledge about specific landscape contexts in which hominins prepared tool kits, processed carcass parts and plant food, and breed, bearing in mind the ecological variables such as resource availability, competition, and predation hazard that existed on the paleolandscapes.

ii) Paleoenvironmental reconstructions of Bed I and Lower Bed II

Many studies have attempted to reconstruct environments of these archaeological assemblages. These include the broad scale paleogeographic reconstruction by Hay (1976) and climatic reconstruction through oxygen isotope analysis of paleosol carbonates by Cerling and Hay (1986). Other works have attempted to reconstruct vegetation patterns of the sites through pollen (e.g., Bonnefille, 1984), fauna (e.g., Butler

& Greenwood, 1976; Kappelman, 1984), and stable carbon and oxygen isotope (Sikes, 1994) analyses. However, the environmental resolution provided by these studies is generally too coarse to place traces of hominin activities into specific landscape settings.

More recently OLAPP has attempted refining temporal and spatial resolution of landscape setting through broad scale sampling of paleoenvironmental indicators such as phytoliths, stable carbon isotopes, and fossil wood (Albert *et al.*, 2006; Bamford *et al*., 2006; Blumenschine *et al*., in press).

On the basis of predictive model of the trace fossils of hominin land use of lowermost Bed II basin, Blumenschine and Peters (1998) concluded that the Olduvai archaeological record is largely informative about stone tool-assisted butchery of large mammal carcasses. The butchery evidence includes cut marks and hammerstone percussion marks. The bones also bear tooth marks in addition to butchery marks, all of which have been assumed to have been inflicted by mammalian carnivores, raising the possibility that this trace fossil records direct or indirect interactions of mammalian carnivores and hominins. Establishing landscape variability in nature and intensity of these interactions provides one of the few instances where hominin paleoecology can be investigated.

The richest stone artifact and fossil bone occurrences are situated in the flood zone surrounding the paleolake, referred to by Hay (1976) as lake margins. Peters and Blumenschine (1995, 1996) have modeled these lake margins to be comprised of complex mosaic of landscapes distinctive from one another in hydrology, substrate, and vegetation, as well as resources and hazard potentially encountered by hominins. The model specified that the degree of exposure to predation risk had a major influence on the intensity and nature of activities hominins conducted in different landscape settings.

OLAPP’s new geological and archaeological evidences suggest that these lake-margin assemblages were formed in a mosaic of wetlands supplied by braided streams (Blumenschine *et al*., 2000). According to this new observations, it appeared that these paleo-wetlands, which were formed repeatedly between major eruptive phases of Mt. Olmoti during Bed I and lowermost Bed II times, featured a complex variety of sub-environments that were altered repeatedly by climate-driven lake-level fluctuations, volcanism, and faulting.

It is therefore important to reconstruct this wetland landscape mosaic at a high spatial and temporal resolution so that the variability in the hominin-landscape interactions can be understood. This is the major goal of the ongoing OLAPP project at Olduvai.

Taphonomic analysis of large vertebrate bone assemblages in these wetland contexts provides one avenue for producing these landscape reconstructions by determining the specific nature of the wetland setting, and whether they were potential hominin habitats in terms of resources availability or predation risk.

iii) Aspects of vertebrate taphonomy in reconstructing ancient wetlands

Among the taphonomic approaches used to reconstruct paleoenvironments, animal community structure, as well as hominin subsistence and adaptation, is the study of large vertebrate skeletal remains on recent land surfaces (e.g., Brain, 1967a; Behrensmeyer *et al*., 1979; Vrba, 1980; Blumenschine, 1989; Selvaggio, 1994a, 1994b;

Sept, 1994a; Tappen, 1995; Dominguez-Rodrigo, 1999). Only a few taphonomic studies have been conducted in wetland settings, mainly focusing on mass drowning from flooded rivers (Dechant-Boaz, 1982) and lake crossing (Capaldo & Peters, 1995; Njau, 2000), and mortality profiles of herbivores in swamp and lakebed habitats (e.g., Behrensmeyer & Dechant-Boaz, 1980; Behrensmeyer, 1981).

However, more studies need to be done because most of the prior taphonomic work has been aimed at ascertaining the effect of terrestrial carnivores on bones of larger mammals (e.g., Brain, 1967a, Sutclife, 1970; Binford & Bertram, 1977; Binford, 1981; Haynes, 1980, Richardson, 1980; Blumenschine, 1987, 1989; Hill, 1989). Other workers have focused on the attrition of land surface bones (e.g., Hill, 1979; Behrensmeyer, 1981, 1983a, 1991; Hill & Behrensmeyer, 1984) due to weathering (Behrensmeyer, 1978), trampling (e.g., Behrensmeyer & Boaz-Dechant, 1980; Gifford-Gonzalez *et al*., 1985), fluvial processes (Voorhies, 1969; Behrensmeyer, 1975, 1981, 1988), or drought (Shipman, 1975).

One potentially important wetland taphonomic agent that has been largely overlooked is the crocodile. Only a few taphonomic studies have considered the significance of this species to hominin paleoecology, but only as a potential animal food resource to early hominins (e.g., West, 1995; Gifford-Gonzalez, *et al*., 1999). Gifford's (1978; Gifford & Behrensmeyer, 1977) and West's (1995) observations of Dassanetch fishermen camps on the east side of Lake Turkana provide methods for characterizing bone assemblages dominated by fish, turtle and crocodiles, and describing the potential of fish and reptiles to early hominin diet (Stewart, 1989, 1991, 1994; Rybczynski *et al*., 1996; Gifford-Gonzalez, *et al*., 1999). Although West's (1995) study recognizes some of the Olduvai Bed I and Bed II sites as crocodile habitats due to abundance of crocodile body fossils, she does not consider the potential predation risk this carnivorous reptile may have posed to a small-bodied hominin.

Adult crocodiles are top predators in wetland settings such as lakeshores, rivers, streams, marshes or ponds, and are successful predators of large land mammals including humans (e.g., Selous, 1908; Pitman, 1941; Schmidt, 1944; Attwell, 1959; Cott, 1961; Guggisberg, 1972; Graham & Beard, 1973). The morphology of *Crocodylus lloidi* (reviewed in Chapter Three), the only crocodile that existed in the paleo-Olduvai basin during the Plio-Pleistocene, indicates a feeding adaptation on large land mammals (Tchernov, 1986). Equipped with a robust and massive skull, this extremely brevirostrine crocodile would have preyed on hominins who came near crocodile-inhabited wetlands, on routine searches for food, tools, water, or to bathe. Therefore, predation risk from crocodiles may have influenced hominin land use and the distribution of hominin trace fossils.

In this thesis I attempt to reconstruct landscape contexts of hominin trace fossils by developing taphonomic methods for identifying signatures of crocodile feeding behavior on bone, and the composition of bone assemblages in wetland settings. There are three factors that make crocodiles important taphonomic agents. First, they are habitat-specific species, preferably living in pools formed along stream mouths, streambeds, or adjacent to lakes (e.g., Cott, 1961; Modha, 1967; Neill, 1971; Watson *et al.*, 1971; Gereta & Wolanski, 1998; Wolanski & Gereta, 2001). Usually, these settings offer concealment or vegetated shallows, which facilitate ambush and capture of prey. Second, crocodiles feed on their kills near capture site. Thus, the uningested bones are deposited in water or at water’s edge. Third, crocodiles usually shed their teeth in water, mainly during feeding (e.g., Pooley, 1989). Shed teeth are therefore a good signature of habitats in which crocodile lives.

2. Goals of the thesis

In order to develop criteria for understanding characteristics of wetland bone assemblages, I conducted neotaphonomic (experimental and actualistic) research with the aim of addressing the following issues: First, to identify feeding traces of modern crocodiles through controlled observations of crocodiles feeding. Second, to investigate if crocodilian feeding traces can be identified in bone assemblages in recent wetlands settings utilized by both crocodile and mammalian carnivores. Third, to document the composition of bone assemblages and patterns of bone modification in recent wetlands presenting activities of both crocodiles and mammalian carnivores, and those containing only mammalian carnivores. Fourth, to investigate crocodilian feeding traces in the Oldowan bone assemblages.

In order to identify signature criteria of bone modification by crocodilians, I conducted systematic observations of captive Nile crocodiles feeding on larger mammal carcasses. My primary goal was to determine distinctive traces of crocodile feeding by comparing them with mammalian carnivore bone modification. The diagnosis of crocodile bone modification follows a well established procedure for describing mammalian carnivore bone modification (e.g., Haynes, 1980, 1983a; Maguire *et al*., 1980; Richardson, 1980; Binford, 1981). Complete descriptions are provided for the following features of bone modification by crocodiles:

i) Frequency of tooth marking
ii) Tooth mark morphology
iii) Pattern of tooth marking
iv) Pattern of bone gnawing
v) Pattern of carcass dismemberment and disarticulation
vi) Pattern of bone fragmentation and destruction

The second goal of the study was to conduct naturalistic observations of bone accumulation, distribution, and modification in semiarid tropical wetland settings utilized by crocodiles and mammalian carnivores. Since crocodiles are the major predators in these inland waters, diagnosis of their feeding traces and occurrences of their shed teeth in bone assemblages provide ecological and taphonomic information about wetland environments. Systematic inventories of large vertebrate bones were carried out in wetland settings of protected wildlife ecosystems with the aim of documenting the following information:

i) Density of bone occurrences
ii) Species and skeletal composition of bone assemblages
iii) Degree of bone completeness
iv) Diagnosis of crocodilians feeding traces (following variables specified in the first goal above)
v) Comparison between crocodiles and mammalian carnivores in bone modification

The third goal was to analyze the Oldowan fossil assemblages using the results from neotaphonomic studies above as referential framework for investigating landscape contexts of hominin trace fossils. The aim here is to investigate the composition of fossil bone assemblages and patterns of fossil bone modification with the goal of identifying the agent(s) of bone modification (i.e., crocodiles, mammalian carnivores and/or hominins). Only fossil samples from lake-margin wetlands at Olduvai were investigated for the following attributes:

i) Skeletal part and taxonomic composition

ii) Bone surface modification

iii) Agents of bone modification

Table 1.1. Principal Bed I and lower Bed II "living sites" reported by Mary Leakey in the central eastern basin. The sites are listed by stratigraphic level. LF= Living floor, BS= Butchering site, OS= Occupation site, OH= Olduvai hominid (Leakey, 1971: 234, 258, 282). FLK N basal clay with root casts (lower Bed II) corresponds stratigraphically to HWKE level 2 (Leakey, 1971). The *Deinotherium* cf. *bozasi* remains associated with stone artifacts in this layer at FLKN are inferred as a butchering site (BS). FLK *Zinj* level is equivalent stratigraphically to FLK NN level 1 (Leakey, 1971). New dates from Blumenschine *et al* (2003).

		Age Ma	FLK	FLK N	FLK NN	HWKE	DK
Lower Bed II	IIA	1.70-1.75[†]					
				Basal clay BS		L2 OS L1 LF	
Upper Bed I	IF	1.785					
				L1 OS L2 OS L3 OS L4 OS L5 OS *OH10* L6 BS			
Middle Bed I	ID	-					
			–	–	–	–	–
	IC	1.839	*Eroded*		*Eroded*		
			L7,10-21 OS L22 (*Zinj*) LF *OH5, OH6, OH35*		L1 L2 OS L3 LF *OH7, OH8*		
Lower Bed I	IB	1.845					
					L4 *(Many crocs & aves)*		L1 OS L2 OS L3 LF *OH24, 52*
	IA	2.0[‡]					

[†] Hay (1976)
[‡] Walter et al. (1992)

3. Conceptual framework

i) Hay's paleogeographic model

Hay's (1976) geological work at Olduvai established a stratigraphic sequence across the gorge, laying the foundation for all further interpretations of biological, cultural and paleoenvironmental change over time. He divided the sequence into Beds I through IV, Masek, Ndutu, and the Naisiusiu Beds. Hay's paleogeographical reconstruction of the local environments at Olduvai showed that the center of the basin was occupied by a small, shallow, saline and alkaline lake. The perennial portion of the lake measured approximately 10 km long and 5 km wide (Figure 1.1). This paleolake intermittently flooded across the low terrain surrounding it in response to rainfall input. During the maximum lake stand, an area of approximately 16 by 25 km was covered by water (Figure 1.1). The episodic flooding caused interfingering of lake deposits with tuffs and the alluvial fan deposits that formed on the eastern margin of the basin, and with lavas from the eastern highland volcanoes. Interfingering of lake deposits with lake margin deposits was also documented on the west side of the lake.

The lake sediments on the eastern shore had the lowest salinity and alkalinity, indicating generally fresher water conditions, while highly saline, alkaline water persisted in the central and western parts of the lake (Hay, 1963, 1976). During times of high lake stands the lake was freshest, particularly on the eastern side and near the mouths of the streams that drained the eastern and southeastern volcanic highlands. This condition is supported by the presence of *Typha* (cattail) or reed marshes as evidenced by apparent root casts, *Typha* pollen, and fossil rhizomes of papyrus found in the sediments (Hay, 1976, 1990; Bonnefille, 1984). Occurrences of murid rodents in some of Bed I assemblages also suggests the presence of marshlands along lakeshores (Jaeger, 1976).

Since only a few archaeological sites were located (but not excavated) by the Leakeys in the western lake margin zone, Hay (1976) suggested that population densities of game in this side of the lake were possibly low, or the vegetation pattern was different from that in the east, making the west side less attractive to hominins.

ii) Fossil indicators of plants and animal communities

Numerous paleoecological analyses of Olduvai faunal and geological samples have been carried out to determine the vegetation patterns of the paleobasin, with the aim of understanding early hominin adaptations to local environments. The analyses are based on pollen, geochemistry, fossil wood, and vertebrate paleontology. Results from these studies have produced broad-scale reconstructions of Olduvai ranging from forest to open grasslands (e.g., Andrews *et al*., 1979; Andrews, 1983; Bonnefille, 1984; Kappelman, 1984; Shipman & Harris, 1988; Plummer & Bishop, 1994; Sikes, 1994; Fernandez-Jalvo *et al*., 1998). The lake margin environments are considered to have supported mosaic of grassland, bushland, wooded grassland, woodland, and marshland.

Pollen analysis

Pollen analysis has been employed in many African fossil sites (e.g., Bonnefille, 1984), but has failed to resolve spatial differences in plant cover at fine landscape scales because of the potential for long-distance transport (Prentice, 1988). Although useful in broad scale paleoenvironmental interpretations, pollen data alone are inadequate for understanding the mosaic of habitats at Olduvai Basin. The poor pollen preservation in many Plio-Pleistocene deposits at Olduvai hinders fine scale reconstruction of paleo habitats in the basin.

Fossil plants

Macro-plant remains such as fossilized sedges, grasses, twigs, and wood have been recovered from Plio-Pleistocene Olduvai sediments (Bamford, 2005; Bamford *et al*., 2006). OLAPP's lowermost Bed II trenches sampled by Marion Bamford include a fossil wood species identified as *Guibourtia coleosperma* (Caesalpiniaceae), a relatively uncommon tree today. This fossil evidence indicates that large trees, up to 19 m high, and a more or less evergreen vegetation may have existed in the eastern part paleo-lake margin during the lowermost Bed II times (Bamford, 2005). However, macro-plant fossils are usually rare in archaeological sediments, and therefore cannot alone give information about how vegetation varied across ancient landscapes.

Isotope geochemistry

Relatively recently, OLAPP has utilized a paleosol carbon isotope method to refine paleoenvironmental reconstructions on the eastern portion of the lake margin in lowermost Bed II. Initial stable isotope values of pedogenic carbonates collected in 1989 by Hay were interpreted by Sikes (1994) to indicate the presence of grassy woodlands to riparian forest within a 1 km^2 area at the eastern lake margin (FLK and HWK area). However, due to uncertainty of time of carbonate formation, the results must be interpreted with caution. This is because climatic changes occurring over a periods of decades such as *El Nino* can transform the vegetation pattern in the lake margins from woodlands to grassland. For example, the *Acacia xanthophloea* trees on the western shore of Lake Manyara and *Suaeda monoica* (semi-woody bushes) on the north beaches of Lake Masek, died during the 1998 *El Nino* following floods by lake water, and the trees have not recovered yet. Nevertheless, stable carbon isotopes of paleosol carbonates techniques can be improved provided they are supported by actualistic information sought from integrated geological, vegetation and ecological analog studies from relevant modern settings (e.g., Sikes, 1995; Copeland, 2004; Peters *et al*., in prep.).

Vertebrate faunal

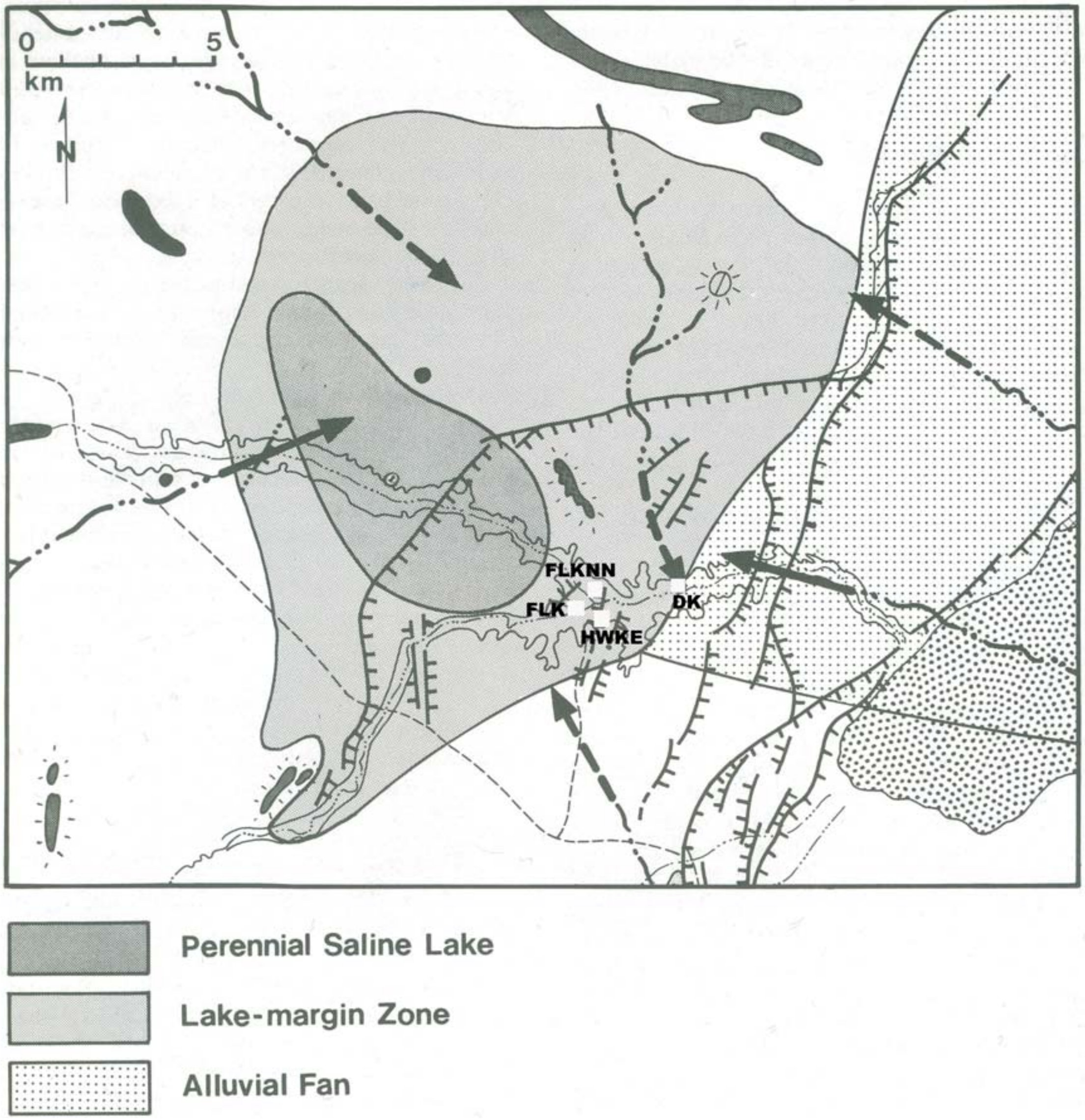
Vertebrate fossil remains are generally useful paleoenvironmental indicators. Modern animal species have been used to infer similar habitat preferences for the related animal species in ancient times (e.g., Van Couvering & Van Couvering, 1976; Marean & Ehrhardt, 1995). Bovids are commonly used for this purpose because of their abundance and variety both in present and past times (e.g., Gentry, 1966; Vrba, 1980; Kappelman, 1984, 1988; Shipman & Harris, 1988; Dodd & Stanton, 1990; Plummer & Bishop, 1994; Kappelman *et al*., 1997; Spencer, 1997; Reed, 1997).

Remains of crocodiles, hippopotami, fish (i.e., *Clarias* or catfish and cichlids or tilapia), turtles (Greenwood & Todd, 1970; Auffenberg, 1981; Stewart, 1994, 1996; West, 1995), and certain terrestrial water-dependent taxa such as *Kobus* (Gentry & Gentry, 1978a, 1978b), and murid and gerbil rodents (Butler & Greenwood, 1976; Jaeger, 1976; Fernandez-Jalvo *et al*., 1998) have been used to indicate moist climates, vegetation structure of proximity of fossil records to freshwater.

With the exception of aquatic and semi-aquatic species such as fish and crocodiles, information based on vertebrate fauna cannot predict with adequate resolution the distribution of specific habitats. They can only indicate the proximity of environmental factors such as water, pastureland, or woodland forest in the case of arboreal species. This is because the distribution of terrestrial animals varies across landscapes due to their movements, and due to various taphonomic factors acting during and after their deaths. Crocodiles (i.e., Nile crocodile) are relatively good indicators of freshwater systems because they cannot tolerate excessive salinity or alkaline conditions (e.g., Cott, 1961; Grenard, 1991).

In sum, vertebrate fossil indicators of paleoenvironments are useful in providing general and often complementary information on ancient environments, but the spatial resolution is too low to delineate landscape facet, the level at which tremendous variation in hominin landscape activities have been predicted. Therefore a more detail and finer spatial resolution is needed, in particular from observations of contemporary environments and various processes operating therein.

Figure 1.1. Hay’s (1976: Figure 18) paleogeography of the Olduvai Basin for the interval between basal Tuff IB and the top of Bed I, superimposed on the outline of present-day Olduvai Gorge. The inner ring represents the perennial paleolake and the outer ring shows the Lake-Margin zone. During dry times, the lake retreated to the perennial part, and during wetter periods, the lake flooded the broad Lake Margin zone. The Alluvial Fan originates from streams draining the Crater Highlands on the east. The extent of the Lake-Margin zone and the Alluvial Fan are based on the paleogeography of Tuff IF. Solid arrows indicate flow direction of streams from Crater Highlands. Dashed arrows show flow direction inferred from clast composition and regional paleogeography. White square = localities sampled in this study for bone assemblages. FLKNN lie about 180 m northwest of FLK.



iii) Ecologically-based models by Peters and Blumenschine

Peters and Blumenschine developed models of paleolandscape ecology (Peters and Blumenschine, 1995, 1996), and of hominin land use that predicted the stone artifact and butchered bone traces for various hypothetical landscape facets in the lowermost Bed II basin (Blumenschine & Peters, 1998). Landscape facets were hypothesized mainly on the basis of Hay’s paleogeographic model and other published paleoenvironmental reconstructions reviewed in the previous section.

The model outlines the ecological distinctiveness of localized environments and their hypothetical effects on hominin land use. The Lake Margin was classified into distinctive ecological zones, each offering different resources and hazards to the stone tool-using hominins. Theoretically, the distribution and nature of stone artifacts and modified bones were considered to strongly reflect variability in landscape ecostructure (Blumenschine & Peters, 1998). For example, it became apparent in their model that the ecostructure and affordances of wetland systems (e.g., riparian woodlands and marshes) are different from non-wetland and open settings (i.e., barren flats, interfluves etc.). These contrasting landscapes were expected to yield different types of resources and hazards, which are key features in influencing the distribution of hominin activities across landscapes, and ultimately the traces of their activities. Based on these ecological oriented models, trace fossils of hominin were then specified across landscapes (Blumenschine & Peters, 1998).

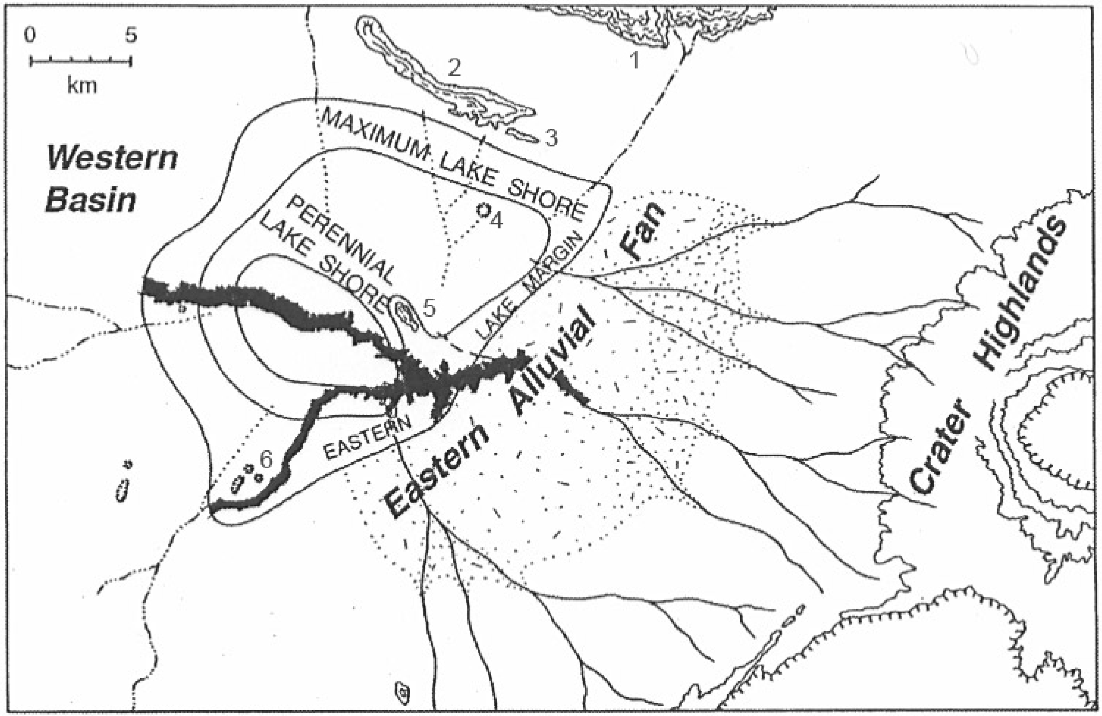
a. Landscape classification system

In order to develop hominin land use models with landscape perspectives, Peters and Blumenschine (1995, 1996) divided the Olduvai paleobasin into a number hypothetical landscapes (Figure 1.2). The land classification system adopted by Peters and Blumenschine, following Christian (1958), Mabbutt and Stewart (1963), Webster and Beckett (1970) and Gerresheim (1974), is based on a combination of geomorphic and ecological principles of the landscapes. According to their classification scheme, a *landscape region* is the broadest land unit defining the entire paleobasin. This closed lake basin was bounded on the east and south by Ngorongoro/Sadima/Lemagrut highlands, bounded on the north by the Gol mountains, and extended to the west onto the vast Serengeti plains. The *landscape sub-regions*, which are comprised of Eastern Serengeti Plains, Gol Mountains, Lake Olduvai, and West Crater Highlands are sub-units of the landscape regions. The sub-regions were divided into *landscape associations*, which are the group of closely related adjacent land systems (e.g., Serengeti Peneplains, Lower to Upper Lacustrine Plains, Piedmont Plains, Major Rock Outcrops (inselbergs), and Mountainsides. The next lower rank in the hierarchical landscape classification is the *landscape locale*, a localized land system that tends to be of the order of 25 km^2 to 250 km^2 in area, and has a unique place and name (e.g., Naibor Soit Hill). The *landscape facet* is the smallest basic working unit of the terrain classified for the paleobasin. Various landscape facets were hypothesized for different landscape associations. These include, stream channels, floodplains, deltas, springs, lacustrine plains, alluvial fans, peneplains etc.

Peters and Blumenschine (1995: 334) defined landscape facet as “a relatively homogenous part of the local landscape with a distinct morphology on a common parent material mappable at a scale of 1:10,000 to 1:50,000, roughly corresponding to the *habitats* of neontological ecology”. This land unit can be subdivided into *sub-facets*, which are land units intermediate in scale to *land elements* and landscape facet (Peters, per. comm.). For example, a river system (landscape facet) can be composed of channel bed, riverbank, and or over-bank, or floodplain sub-facets. The land elements are the finest-scale features of the landscape classification, such as game wallows, termite mounds or an isolated large tree (Peters & Blumenschine, 1995: 334).

The ability of paleoanthropologists to document paleoenvironmental features at or below the landscape facet scale is a major challenge in the field, but one that has great potential for the reconstructing the contexts of hominin activities and trace fossils (Peters & Blumenschine, 1995, 1996). Conceptually, the landscape facet is the coarsest scale for reconstructing details of hominin land use, and in this thesis I expand on sub-facet as unit of land analysis.

Figure 1.2. Map of the lowermost Bed II Olduvai Lake Basin superimposed on the outline of present-day Olduvai Gorge (from Peters and Blumenschine,1995, 1996). Peters and Blumenschine's paleogeography model is based originally on Hay's (1976). The map shows the perennial (inner ring) and maximum (outer ring) paleolake shorelines, between which lies the lake margin zone that was exposed during periods of relatively low lake level. The Eastern Alluvial Fan originates from streams draining the Crater Highlands on the east and southeast margins of the basin. The western part of the paleobasin extends into Serengeti Plains, north to Gol Mountains, and east and south to Crater Highlands. The numbers identify the following: (1) the Gol Mountains; (2) Olongoyo Ridge; (3) Engitati Hill; (4) Engelosin Hill; (5) Naibor Soit; and (6) Kelogi Hill (from Blumenschine *et al.*, 2005: Figure 1).



b. Landscape ecology model

The landscapes hypothesized by Peters and Blumenschine for lowermost Bed II were conceptualized through observations of modern landscape analogs of the hydrology, terrain, vegetation physiognomy, and distribution of potential resources and hazards hypothesized for early hominins at the level of landscape facets. The resources and hazards that may be offered to an animal by the environment are termed *affordances* by Peters and Blumenschine (1995, 1996; following Gibson, 1977, 1986). Therefore the distribution and abundance of positive affordances (e.g., potable water, plant foods, scavengeable carcasses, safe sleeping sites, refuge breeding sites, and sources for tool material) and negative affordances (e.g., predation hazard) were key determinants of hominin land use.

According to their landscape model, the perennial lake was surrounded by an intermittently flooded zone on the western side, following Hay (1976). The upper part of the lacustrine plain was intermittently dry. The sparsely wooded ephemeral streams were predicted to traverse the southeastern Serengeti Peneplains before entering the low-gradient Lake Margin zone on the west side of the lake (Figure 1.2).

The east lakeside was surrounded by open lacustrine plains that were subdivided into the lower-zone or mudflats, and the mid- and upper-zone, or sedge/grassland plains. The lower lacustrine plains were intermittently flooded, while the upper parts were rarely flooded (Figure 1.2). Freshwater springs and stream-fed marshes on river mouths occurred on the lower and upper lacustrine plains, depending on the extreme climates and seasonality. The wetlands were hypothesized to support a variety of vegetation such as sedges and reeds on the marshes and riparian woodlands on the drainages.

The Upper Lacustrine Plain is bordered by the Alluvial Fans on the east (Figure 1.2). The fan extends to the footslopes of Olmoti and Ngorongoro-Sadiman-Lemagrut mountains. A series of ephemeral and probably perennial streams draining the western mountainsides were modeled to traverse the Eastern Alluvial Fan and probably the northern landscapes before entering the lacustrine plains. The streams were modeled to support riverine woodlands with sparsely treed interfluves. The Mountainsides were modeled to support relatively numerous ephemeral to perennial streams and springs, while the Major Rock Outcrops (e.g., Kelogi, Naibor Soit and Engelosin Hills) were minimally vegetated by bushes, and lacked drainages.

The landscape model suggests that the Olduvai paleobasin was environmentally complex spatially and temporally, representing a mosaic of landscape facets. Based on this model, I provide a brief summary of the distribution of affordances hypothesized for the lowermost Bed II landscapes by Peters and Blumenschine. The affordance matrices allow us to predict the nature and intensity of hominin land use in prehistoric landscapes. The affordance matrices were constructed on the basis of two extreme climatic regimes, the dry seasons of dry years, and wet seasons of wet years.

c. Landscape affordance matrices

Wet climate regime

Relatively low quantities of potable water, plant food, carcasses and tool material were modeled to be available only during the dry seasons in the sparsely wooded streams draining the Serengeti Peneplains in the West Lake Olduvai area. The population density of terrestrial carnivores and crocodiles were modeled to be moderate. Carnivores were predicted to concentrate in drainages and interfluves, while crocodiles were restricted to the wetlands of the upper lacustrine plains (Peters & Blumenschine, 1996; Table 3A). The western lacustrine plain was submerged during the wet seasons, and game was more dispersed towards Serengeti plains.

The lacustrine plains in the east side of the lake were flooded during the wet seasons, therefore a high quantity of resources was restricted in the streams of the Eastern Alluvial Fan and Mountainsides. These landscape systems provided unlimited potable water, plant (tree and bush fruits) and animal foods, and arboreal refuge trees during wet seasons. The channels were modeled to support woodland corridors that connected the resource-rich footslopes and the lakeshore, and also provided stone tool materials. The interfluves adjacent to the streams were less vegetated by trees but offered bushes with fruit and probably minimal animal food (e.g., ostrich eggs).

When the lake receded during the dry seasons, marshlands developed on the exposed parts of the Upper Lacustrine Plain, particularly on river-mouths and seeps on the lake edge. The wetlands were predicted to provide carcasses for scavenging hominins. The *Typha* marshes were predicted to support good quantities of rootstock. The *Acacia xanthophloea* woodland belt modeled to have occupied the uppermost margin of the Lacustrine Plain, and the *Acacia tortilis* woodland modeled for the uppermost Lacustrine Terrace, would have acted as corridors for hominins exploiting resources on the lakeshore. Crocodiles were restricted to the streams in the uppermost lacustrine plains and Alluvial Fan, and mammalian carnivores to the Mountainsides (Peters & Blumenschine, 1996; Table 3A).

With the exception of Olongoyo Ridge, the Major Rock Outcrops, which were the source of raw material for stone tools, were islands during extreme wet climates, therefore most stone material derived from the channels in the Mountainsides and Eastern Alluvial Fan.

Dry climate regimes

According to this model, the Western Lake Basin was "non-productive" during the dry seasons. Only few mammal carcasses and probably fish and birds were available in the pastures at the lake edge. Also few mammalian carcasses were predicted in the sparse trees on the drainage lines during the wet seasons.

When the Eastern Lake Margin zone was fully exposed due to drought, many freshwater sources disappeared, and the few resources (e.g., rootstocks and scavengeable carcasses) available were restricted to the Large Springs, *Typha* marshes and drainages. The wetlands that existed in the lacustrine plains during the wet seasons may have dried out, or tremendously reduced during the dry seasons. Although these landscapes were modeled to be hazardous due to exposure and high concentration of crocodiles and terrestrial carnivores, the riparian corridors and hypothesized *A. tortilis* and *A. xanthophloea* woodlands would have provided arboreal refuge. Terrestrial carnivore activities were related to commuting, while crocodiles were restricted in the freshest parts of the lake edge, probably in the stream-mouths entering the lake.

The major source of potable water during the wet and dry seasons was the headwater springs in the mountainsides. The riverine woodlands supported by ephemeral streams, provided a substantial quantity of fruit and arboreal refuge trees in the upper parts of the Alluvial Fan and on the footslopes of Mountainsides. The channels in these land-systems would provide potential source of stone tool material. Prime scavenging opportunities was provided in the headwater springs of the Mountainsides, as well as in the upper most margin of Alluvial Fan, through carcasses abandoned by large felids and those stored in trees by leopard. The adjacent interfluves in the Alluvial Fan, which mainly consisted of shrublands during wet climates, were modeled to be open grasslands during the dry season of dry climates.

The Major Rock Outcrops such as Naibor Soit, Kelogi and Engolosin Hills were fully exposed and provided sources of stone materials. Only a few bushes and scattered trees that provided some fruit and refuge trees were modeled in these areas. Minimal predation risk was expected from denning carnivores (e.g., hyenas, large canids).

d. Hominin land use model

Peters and Blumenschine modeled the land use patterns of Oldowan hominins across the paleobasin, based on the affordance matrices they hypothesized for the lowermost Bed II basin. Hominin activities were preferably located in places that would lend them potential survival requirements and minimal predation risk and competition from carnivores. Hominin movements across landscape were influenced by availability of resources, which were conditioned by the wet and dry climates and seasonalities (Peters & Blumenschine, 1995, 1996: Figures 6A-6B).

During the wet seasons of a wet climate regime the Lake-Margin zone was flooded and hominin activities were restricted in the Eastern Alluvial Fan and the uplands in the Mountainsides. Hominins ventured between the interfluves in the Alluvial Fan in search for carcasses abandoned by large felids in the riverine corridors, and fruit provided by the bushes in the interfluves. When the lake withdrew during the dry season of the wet climate, hominins extended their foraging activities to the Uppermost Lacustrine Plain.

During the wet season of the dry climate regime, when the Lake Margin was exposed, hominins extended their search for carcasses from the Eastern Alluvial Fan to the middle/lower lacustrine plains. They also occasionally visited the Lower Lacustrine Plain in the Western Basin for animal foods and exploitation of stone materials at Naibor Soit, Engolosin and Kelogi Hills. Exploitation of plant foods was restricted in the upper part of the Alluvial Fan. Hominins were modeled to retreat to the springs on the heads of drainage lines located on the Mountainsides during the dry season of the dry climates due to lack of potable water and predictable food resources in the basin. Also the decreasing of refuge trees and the increasing of exposure and predator densities in the basin may have forced hominins to abandon the basin in favor of the adjacent basins such as Lakes Eyasi and Manyara.

According to this model, the riparian corridors in the Eastern Alluvial Fan and Mountainsides provided the most stable positive affordances during extreme weather conditions. The Western Lake Basin was considered “non-habitat” for hominins, especially during dry climates, due to exposure, high predator density, and lack of predictable water sources, plant food, scavengeable carcasses, arboreal refuge trees and tool materials.

Also the Eastern Lake Lacustrine Plain was predicted to be less attractive to hominins due to exposure, high predator densities, and poor water condition. The wetland sites located in the intermittently dry zone on the uppermost Lacustrine Plain are the only places hominins were likely to visit periodically. Scavenging trips to the Lower Lacustrine Plains were possible only during the wet seasons of the dry years. However, the increasing harsh wind-blown trona dust and predator densities in the lacustrine plains during the dry seasons of dry years would prevent hominins from scavenging in the Lower Lacustrine Plains.

In the reminder of the thesis I expand on Peters and Blumenschine’s landscape model in the following way:

1) To examine a variety of modern wetlands, with the aim of modeling paleolandscape settings in which hominins interacted with mammalian carnivores and crocodiles for resources.
2) To develop affordance matrices for large carnivores, including primarily crocodiles, hyenids and felids in these wetland settings.
3) To develop criteria for distinguishing crocodilian feeding traces from those of mammalian carnivores.
4) To use the results of the combined studies above as a taphonomic basis for interpreting the landscape contexts and distribution of hominin and carnivore trace fossils at Olduvai during Bed I and lowermost Bed II times.

4. Outline of the reminder of the thesis

In Chapter Two I will discuss taphonomy in general, the approach I take to interpreting hominin-carnivore interactions. I discuss the role of neotaphonomy and zooarchaeological approaches to paleoanthropology, and apply this approach to interpret vertebrate assemblages from wetland environments. This chapter also provides a brief background on controlled observations of living crocodiles and mammalian carnivore feeding. In Chapter Three I review the natural history of crocodiles, with the aim of linking feeding morphology to the feeding behavior and pattern of bone modification by this species. In Chapter Four I describe the methods and sample characteristics of the study I conducted on crocodile feeding. The results of the study are reported in Chapter Five.

Chapter Six provides descriptions, sample characteristics, and results of the field observations of modern wetland bone assemblages. Chapter Seven describes the fossil samples and analytical procedures, and reports on the results of the analysis. Chapter Eight discusses the relevancy of controlled and naturalistic studies in reconstructing paleo-wetland settings, using the Olduvai sample as a case study. Results from the fossil samples are compared against results from modern samples to make inferences on the landscape setting of fossil assemblages, and the nature of hominin land use. The effect of crocodile predation on hominin adaptation and trace fossils is also discussed. Chapter Nine summarizes some of the important findings of the naturalistic observations of crocodile feeding and taphonomy, and their significance in understanding the landscape contexts of Oldowan hominin trace fossils at Olduvai.

CHAPTER 2. JUSTIFICATION

1. Neotaphonomy in paleoanthropology

i) Introduction

Neotaphonomy provides a methodology for inferring the nature of prehistoric processes and events surrounding animal deaths, through relevant experimentation or observation of the conditions of modern faunal remains (e.g., Rudwick, 1976; Hill, 1978; Lyman, 1994). This approach is necessary in paleontology and paleoanthropology due to uncertainty in the nature of ancient processes (e.g., ecological, physical, behavioral) that formed the fossil record. In recognition of the inferential complexity involved in reconstructing past behaviors and contexts in which faunal remains exist (e.g., Gifford, 1991), conceptual frameworks such as Middle Range Research (Binford, 1981) were put forth to approach this problem.

Since the inception of this method, observations of relevant taphonomic processes, including naturalistic and controlled observations, have played a central role in taphonomic research. For example, a wide range of modern taphonomic studies have been conducted by paleobiologists and archaeologists with the goal of ascertaining the effect of mammalian carnivore consumption and damage to bones in paleontological assemblages (e.g., Brain, 1967a, Binford & Bertram, 1977; Haynes, 1980, Richardson, 1980; for early examples). Similar studies have been conducted to examine the effect of human butchery practices on bones (e.g., Binford, 1978; 1981; Bunn, 1983b; Crader, 1983). These include replicative experiments aimed at evaluating purported prehistoric bone tools (e.g., Dart, 1957; Bonnichsen, 1973; Shipman, 1981b; Shipman & Rose, 1988; Smith, 2003), and the damage their use may inflict on bones.

Other studies have examined the attrition of bones on land surface bones (e.g., Behrensmeyer, 1981, 1983a, 1991; Hill & Behrensmeyer, 1984) and buried bones (e.g., Gifford & Behrensmeyer, 1977; Njau, 2000) in modern settings arising from physical processes (e.g., Shipman, 1975; Behrensmeyer, 1978; Haynes, 1988a, 1988b; Weigelt, 1989), and carnivore consumption (e.g., Hill, 1979, 1989; Blumenschine, 1989).

ii) The history of taphonomy

Investigations on the processes of bone preservation fossil record using taphonomic procedures were formalized in early 1920s when paleontologists began to systematically study processes operating in recent systems in order to model past phenomenon. Pioneering studies by Ussher (1906), Abel (1914), Barrell (1916), Case (1919), Buckland (1923), and Weigelt (1927) set forth the idea that basic observations of modern phenomenon provide information on fossilization processes of vertebrate fauna. This neotaphonomic approach in paleontology, which was dominated by the German School, established referential framework for understanding and interpreting taphonomic pathways of vertebrate fossilization from pre-mortem to fossil record (Figure 2.1). This was a departure from descriptive paleontology to a more problem-oriented approach resulting in the formation of a sub-field in paleontology, which was named “taphonomy” by Efremov (1940). Efremov defined taphonomy as the “systematic study of the transition of animal remains from the biosphere into the lithosphere”.

Following Efremov’s descriptions, taphonomy has been divided into biostratinomy and diagenetic phases (Figure 2.1). Biostratinomy has been described as the study of effects of the environment on organic remains in the interval between death of an animal and the burial of its bones (Weigelt, 1927). According to Lawrence (1971), biostratinomy explores the effects that surroundings have upon organic remains during the interval between death and final burial. Diagenetics deals with post-burial chemical as well as physical processes affecting organic remains (e.g., Lawrence, 1971; Noe-Nygaard, 1977; Olson, 1980).

The conceptual development of the field and the shift in methods for interpreting the fossil record became a prominent key to paleoecological research. The use of “laws of uniformitarianism” and “principles of ecology” became customary in the field and revolutionized paleoecological research. These ideas, which were borrowed from geology and ecology, helped paleontologists to understand how modern environmental factors and behavioral biology of living communities may affect the processes of bone deposition and eventually fossilization.

Early taphonomic works, which appeared after Efremov’s (1940), still used traditional methods (e.g., Shotwell, 1955, 1958). Most paleontological studies obtained data from the fossil assemblages of interest and from associated sediments, and by themselves these data were inductively used to provide inferences concerning the deposits with utilization of only the most general sort of biological and physical uniformitarian principles (Olson, 1966; Johnson, 1972).

However, not until in the late 1950s did taphonomy became formally established in the vertebrate paleontological community largely through the efforts of Olson (1962), Brain (1967a, 1969a), Voorhies (1969), Dodson (1971), and Behrensmeyer (1975).

Figure 2.1. Taphonomic pathway for formation and transformation of fossil faunal assemblage (adopted from Clark & Kietzke, 1967; Lawrence, 1968; Medlock, 1975; Blumenschine, 1986a; Capaldo,1997).

Taphonomic Stage	Sub-stage	[1]Actors/ effector	Trace	Depositional Context
Live community	Life assemblage		Group size, structure, species diversity, habitat preference, biomass	_
DEATH	Death assemblage	Predation, disease, injury, accident	Mortality profiles	Subaerial/ subaqueous
1. Biostratinomic	Nutritive	Carnivores	Tooth marks, “green-bone fracture”, fragmentation, digestive etching, low density bones underrepresented	Subaerial/ subaqueous
	Post-nutritive	Ungulates	Trample marks, bone fragmentation & dispersal	
		Rodents	Rodent gnaw marks	
		Fluvial transport	Abrasion, rounding, sorting	
		Weathering	Cracking, explosive cracking, bone fragmentation, underrepresentation of low density elements & portions	
2. Diagenetic	Burial			
	- Early burial	Plants	Root etching, root staining	Burial/ partial burial
		Soil moisture	Explosive cracking & flaking, bone fragmentation	
	- Post-burial	Compaction	Crushing, deformation, perpendicular fractures	
		Burrowing	Burrows, biotubation	
	Fossilization	Soil chemistry	Corrosion, deletion of low density elements and portions, mineralization, encrustation	
	Fossil assemblage	Exposure, transport, trampling	Fragmentation, recent breaks, exfoliation, trample marks	Burial/ exposure
	Collection	Excavators	Recent breakage and surface marks	Subaerial/ subaqueous

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[1] Actor or effector is the agent or cause of trace. For example, carnivore is an actor, while the tooth of the carnivore that produce a physical mark on bone surface is an effector. Therefore, tooth marks or trample marks are the traces of carnivore feeding or ungulate trampling (Gifford-Gonzalez, 1991).

iii) Neotaphonomy

Actualistic observations of modern abiotic and biotic factors, and how these factors affect processes of bone accumulation is known as neotaphonomy. This field puts emphasis on controlled observations that are designed to replicate natural processes, which are thought to contribute to bone loss, dispersal, and concentration, as well as modification and alteration of the contents of bone assemblages prior to deposition and subsequent formation of archaeological deposits. Typically, the results of observations and experiments are compared with the original community to see whether the bone samples represent modern processes before they are tested against archaeological data. This method provides reliable interpretations of fossil data, and helps to evaluate the extent to which paleontological and archaeological assemblages can represent actual fossil ecosystems and behaviors.

Most archaeologists, especially those who are interested in Early Stone Age of the Old World, have employed various neotaphonomic approaches in their research because they have been challenged by three main questions related to the concentration and preservation of modified and non-modified bones in association with stone artifacts in archaeological sites: 1) Who, or what processes, accumulated bones on the land surfaces? 2) Why are they accumulated at certain points (sites) on the landscape? 3) How were they accumulated? Methods of observations of modern bone loss and accumulation with an awareness of the implications for fossil occurrences were necessary to serve this purpose.

iv) Application of neotaphonomy to paleoanthropology

The field of paleoanthropology revolutionized vertebrate neotaphonomic research by conducting systematic studies of modern processes relevant to fossil record. Much work was prompted by Raymond Dart, who studied the animal remains from the early hominin site of Makapansgat in South Africa (Dart, 1925). Following his observations of bone assemblages from Member 3, which is now estimated to be between 3 and 2.5 million years old, he discounted the possibility that the bones had been accumulated by hyenas. He found that some skeletal parts and portions such as thoracic and caudal vertebrae, and proximal humeri were grossly underrepresented, while cervical vertebrae, distal humeri, and mandibles among other parts predominate the fauna fossil sample.

Dart viewed the disproportion of proximal and distal humeri ends as a result of australopithecine predatory activities. Among other tools, he postulated that distal humeri had been used as daggers, while bovid mandibles served as saws. Based on this analysis, Dart proposed that the Australopithecines' "osteodontokeratic" industry was the oldest material culture in the human antiquity (Dart, 1953, 1956, 1957). Dart noted another remarkable feature of the Makapansgat assemblage: he found that bovid parts were well represented in the sample, while primates and carnivores were underrepresented. However, the occurrence of the latter animal group were almost invariably cranial, suggesting to Dart that the hominids that brought them back to the cave had been "head-hunters", professional decapitators.

C. K. Brain suspected another cause for the disproportional representation of skeletal elements at Makapansgat. His work was particularly instrumental in demonstrating the value of the neotaphonomic approach to paleoanthropology (Brain, 1967a, 1967b, 1968, 1969a, 1969b, 1980, 1981, 1995). Brain conducted systematic studies on site formation processes of the South African Plio-Pleistocene cave deposits. His Namib Desert neotaphonomic study and Swartkran fossil faunal analyses were the foundation of neotaphonomic studies in paleoanthropological research, and his work led to the production of a series of seminal publication in the field of vertebrate taphonomy (e.g., Brain, 1967a, 1976, 1981).

Brain undertook a series of feeding observations using leopards and cheetah in an attempt to understand differential survivorship of vertebrate skeletons. His analysis of goat bones from human food remains that had already suffered human breakage for marrow extraction, chewing by people, and gnawing by dogs, but which had not been used to manufacture tools, showed remarkable skeletal disproportions, which closely resembled those seen in the Makapansgat fossil sample. He found that the disproportions were simply the result of differential robusticity (structural density) between different parts and portions, and predicted survivorship of skeletal parts under various destructive regimes such as human and dog feedings and weathering. (Brain, 1967a, 1969a). Based on his modern observations he concluded that the disproportions in the Makapansgat assemblage was more likely to result from the feeding carnivores such as hyenas (Brain, 1981).

Anna K. Behrensmeyer is another pioneering figure who demonstrated the value of the neotaphonomic approach. Over three decades of work in Amboseli, she emphasized the taphonomy of community structure and ungulate habitat preferences (e.g., Behrensmeyer *et al*., 1979; Behrensmeyer & Dechant-Boaz, 1980; Behrensmeyer, 1981; 1993).

Following earlier studies by Voorhies (1969), Behrensmeyer carried out a series of investigations on bone fluvial transport in modern environments (e.g., Behrensmeyer, 1975). She noted that skeletal parts can be grouped according to their degree of susceptibility of fluvial transportation: Group I skeletal elements have the highest tendency to be transported by flotation, followed by Group II skeletal elements, which are usually transported by traction (Table 2.1). Group III skeletal elements resist transport and usually lag far, behind other groups.

Behrensmeyer's actualistic/neotaphonomic perspective grew relatively quickly between the 1970s and the 1980s to include time averaging of fluvially reworked fossil assemblages (e.g., Behrensmeyer, 1982a, 1988). However, during this period the discipline was considered simply the study of information loss and bias (e.g., Behrensmeyer & Kidwell, 1985), and most studies emphasized the paleoenvironmental contexts of sites only.

Table 2.1. Voorhies (1969) skeletal elements dispersal groups flume-experiment based on sheep and coyote.

GROUP I	GROUP II	GROUP III
Ribs	Femur	Skull
Vertebra	Tibia	Mandible
Sacrum	Humerus	*ramus
Sternum	Metapodial	
*scapula	Pelvis	
*phalanx	Radius	
*ulna	*scapula	
	*ramus	
	*phalanx	
	*ulna	

*Occurrence in more than one group.

Even with the development of neotaphonomic methodologies, analysis of archaeological faunal materials were, until more recently, often in the hands of paleontologists specializing in specific taxa (e.g., Gentry, 1970; Coryndon & Cooke, 1973; Van Couvering & Van Couvering, 1976). As a result, little discussion was given to taphonomic and ecologically-oriented factors, such as differential survivorship among elements, bone modification, or even analytical considerations such as quantification methods (see Lyman, 1994).

Unlike in the past, most workers today emphasize the use of animal biology and community ecology as a means of contextualizing the history of bone deposition on modern and fossil landscapes, and not simply the study of loss and biases in bone accumulation. For example, faunal analyses aimed at elucidating hominin paleoecology require investigations into the taphonomic histories of faunal assemblages, including analogically based models of the survivability and modification of faunal materials under varying accumulation contexts, such as seasonality and how it relates to carcass availability, carcass fat content, and the foraging activities of vertebrate carnivores and hominins.

The period between the 1980s and 1990s witnessed a virtual explosion of neotaphonomic research under the name of “actualistic studies”, with the application of results to the reconstruction of early hominin archaeological sites. The approach was accompanied by a voluminous growth of literature, from studies of modern landscape ecology as analogues for the past, to the interpretation of archaeological sites and reconstruction of prehistoric dietary ecology, behaviors and paleoenvironments. This method formed a cornerstone in paleoanthropology. Desmond Clark (1990:189) labeled the period “the modern behavioral and actualistic period of research”.

2. Naturalistic and controlled observations of feeding in mammalian carnivores

The interaction between predators and prey is a paleoecological concern that can be addressed taphonomically. For example, the damage to skeletal remains (bone modification) produced by feeding carnivores may reflect their degree of bone utilization, which may provide information on other ecological parameters such as competition, community structure and the environmental setting in which the predation took place. In order to understand these ancient behaviors and ecology we need information from contemporary processes, including observation of carnivorous feeding in relevant modern settings. These kinds of naturalistic and controlled observations, or neotaphonomy, allows generation of testable expectations regarding the composition and characteristics of bone assemblages. This approach has proven to produce reliable information regarding the characteristics of fossil assemblages created under analogous conditions.

Bone modification analysis is a powerful method in taphonomy because it provides the most direct measure of carnivore and hominin exploitation of animal resources. It also measures the degree of predator-bone interaction in a variety of recent and prehistoric environments, and provides information regarding behavior of large carnivorous taxa in carcass consumption and bone destruction (e.g., Sutcliffe, 1970; Hill, 1980; Richardson, 1980; Haynes, 1982a, 1982b; Hill & Behrensmeyer, 1984; Blumenschine, 1986a, 1986b, 1987).

Numerous studies have established criteria for recognizing different classes of surface modifications with the aim of linking the agent of bone modification to the physical traces (marks) produced on the bone surface (e.g., Haynes, 1980; Maguire *et al*., 1980; Binford, 1981; Brain, 1981; Bunn, 1981; Horton & Wright, 1981; Shipman, 1981a, 1981b, 1989; Potts & Shipman, 1981; Shipman & Rose, 1983; Behrensmeyer, *et al*., 1986; Blumenschine & Selvaggio, 1988, 1991; Noe-Nygaard, 1989). The major motivation behind these studies came from the need to develop new approaches for reconstructing adaptive strategies in early *Homo* evolution, including dietary practices and acquisition of animal food resources.

Hominin diets can be investigated using a number of techniques ranging from tooth microwear (e.g., Walker, 1981; Walker *et al*., 1978), stable isotope analysis (e.g., Van der Merwe & Vogel, 1978, 1983; Sponheimer & Lee-Thorpe, 2002; Sponheimer *et al*., 2005a, 2005b), to analysis of physical traces left on the surface of bone residues as a result of hominin and carnivore feeding activities. They include replicative butchery observations and ethnographic observations of modern human butchery practices (e.g., Bonnichsen, 1973; Binford, 1978, 1981; Bunn, *et al*., 1980; Bunn, 1983b; Crader, 1983; Johnson, 1985; Blumenschine & Selvaggio, 1988; Capaldo, 1995; Nilssen, 2000), as well as observation of mammalian carnivore carcass feeding (e.g., Brain, 1967a; Miller, 1969, 1975; Bonnichsen, 1973; Binford & Bertram, 1977; Mills & Mills, 1977; Shipman & Phillips-Conroy, 1977; Binford *et al*., 1988; Blumenschine, 1988; Marean & Spencer, 1991).

While butchery studies have established reliable methods for identifying cut-marks and hammerstone impacts in recent and fossil assemblages (Bunn, 1981; Potts &

Shipman, 1981; Shipman, 1981a, 1981b, 1983, 1986a, 1986b; Blumenschine & Selvaggio, 1988, 1991; White, 1992), recognition of specific carnivore species based upon tooth mark data is not well developed (see Pobiner & Blumenschine, 2003).

i) Surface bone modification by mammalian carnivores

A wide range of neotaphonomic research has examined damage to prey skeletons by various large carnivore taxa. Hyenas are the most studied large mammalian carnivores due to their capability for destroying bones of large animals procured through hunting or scavenging. Bone modifying behaviors have been extensively documented for three extant species; the brown hyena (*Hyaena brunnea*), the striped hyena (*Hyaena hyaena*), and the spotted hyena (*Crocuta crocuta*) (e.g., Sutcliffe, 1970; Hill, 1979, 1989; Skinner *et al*., 1980; Brain, 1981; Haynes, 1983a; Richardson *et al*., 1986; Horwitz & Smith, 1988; Skinner & van Aarde, 1991; Kerbis -Peterhans & Horwitz, 1992; Lam, 1992; and references therein). The spotted hyena has received more study in recognition that it is the most effective bone-crusher and assemblage ravager of all three extant species (e.g., Blumenschine, 1986b, 1988; Binford *et al*., 1988; Marean & Spencer, 1991; Capaldo, 1995).

Other studies have documented bone modifying behaviors of North American canids such as wolves (*Canis lepus*), coyotes (*Canis latrans*), and domestic dogs (*Canis familiaris*) (e.g., Haynes, 1980, 1982b; 1983a; Binford, 1981; Kent, 1981; Klippel *et al*., 1987). Few studies, however, have been done for the felids (e.g., Brain, 1981; Haynes, 1983a; Cavallo & Blumenschine, 1989; Dominguez-Rodrigo, 1999; Pobiner & Blumenschine, 2003; Pobiner, n.d.). Also, studies on bone modification by non-human primates such as great apes (e.g., Pickering & Wallis, 1997; Plummer & Stanford, 2000; Tappen & Wrangham, 2000), and baboons (e.g., Dominguez-Rodrigo *et al*., 1998) are beginning, though they are still rare.

ii) Significance of tooth marks data in paleoecological analysis

Tooth mark profiles and patterns of bone disarticulation and fragmentation provide important ecological information on landscape bone assemblages such as degree of competition among predators for meat resources (e.g., Blumenschine, 1989; Blumenschine & Marean, 1993). Tooth mark analysis is the most effective method in assessing these ecological parameters in bone assemblages. This is because the morphology of tooth marks can be identified more accurately than signatures associated with bone fracturing or disarticulation by carnivores, which can be mistaken for abiotic or other biotic processes.

The analysis of tooth marks has been widely applied in vertebrate paleontological research as a tool for interpreting predatory behaviors in fossil assemblages. For example, most researchers studying Mesozoic assemblages use tooth mark data as direct evidence to infer mode of predation deployed by carnivorous dinosaurs to acquire meat resources (e.g., Cruickshank, 1986; Hunt *et al*., 1994; Currie & Jacobsen, 1995; Chure *et al*., 1998; Hungerbuhler, 1998). By contrast, vertebrate taphonomists working in Late Neogene times use “middle range research” to guide inferences about predation strategies and paleoecological circumstances surrounding the formation of assemblages. This concept, which was formalized in archaeology by Binford (1981), relies on information obtained from observations of known processes acting in controlled conditions. Taphonomic models deduced from these control samples are used to guide analysis of bone modification, whereby a more informative interpretation of bone assemblages can be provided.

With the exception of spotted hyenas, which are capable of breaking bones of animals as large as size 4 (< 900 kg), the distinction of various taxa based upon tooth mark data is still problematic due to the lack of rigorous middle range research, and standardized analytical procedures. This is because all major extant families of carnivores are represented by several species with more or less similar tooth cusp morphologies.

Several methods have attempted to remedy this problem by developing various protocols for identifying carnivore taxa in bone assemblages, at least at the taxonomic level of the family (e.g., Haynes, 1982b, 1983a; Selvaggio & Wilder, 2001; Dominguez & Piqueras, 2003; Pobiner & Blumenschine, 2003). These studies have addressed some of the key issues pertaining to carnivore feeding strategies, yet they do not produce a taphonomic link between a particular tooth such as incisor, canine or postcanine (effector) of a certain taxon (actor/ consumer) to the morphology of the trace produced by that effector. This approach may be complicated because the dentition of mammalian carnivores is divided into four types of teeth comprised of incisors, canine, premolars and molars, each type specialized for a different function. Therefore, the variation in tooth pits, punctures, scores and furrows produced on bone surfaces may be the result of differences in the basic tooth or cusp morphology (e.g., Shipman, 1981b; Shipman & Rose, 1983).

Generally, the anterior teeth of large mammalian carnivores are used primarily for defleshing. These may generate pits and scores. The robust postcanine teeth are used primarily for slicing meat and for gnawing. Gnawing may produce punctures on cancellous bone as well as pits and scores. The carnassial blades, which are committed to slicing and shearing flesh, may produce punctures on cancellous margins of bones. In addition, different species have different morphology in each type of tooth, which further complicates the analysis. For example, hyena premolars are robust with blunt cones, specialized for bone cracking, whereas those of hypercarnivorous species such as cheetah are more delicate and possess elongated carnassial blades designed for slicing.

By contrast, crocodilians possess “thecodont” dentition consisting of an array of uniform bicarinated teeth that are continuously replaced throughout life. Unlike mammalian carnivores whose different types of teeth on tooth rows allow different masticating tasks (i.e., shearing, gnawing, crushing), crocodiles are expected to produce types of tooth marks that are more uniform due to lack of a heterodont dentition in their tooth rows (Njau & Blumenschine, 2006).

iii) Bone modification by crocodilians

Although crocodilian species routinely prey on large animals (e.g., Selous, 1908; Pitman, 1941; Barker, 1953; Attwell, 1959; Cott, 1961; Guggisberg, 1972), investigation of crocodile bone utilization and modification is rare and anecdotally mentioned in paleontological literature. Fisher (1981a) provides the only actualistic investigation of crocodile digestion of small vertebrates with the aim of contextualizing the occurrences of microvertebrate concentrations in the paleontological record. Davidson and Solomon’s (1990) report of a human killed by a saltwater crocodile (*Crocodylus porosus*) provides initial indications on patterns of bone modification produced by these carnivorous reptiles on uningested bones. However, they did not provide detailed information on tooth mark morphology, size, incidence, and location on skeletal elements.

Information on prehistoric bones tooth marked by fossil crocodilians is rare, and is usually inferred anecdotally. Pickford (1996) ascribed tooth marks on large mammalian fauna from Miocene deposits in Namibia as produced by crocodiles. He inferred that serial punctures on a small proportion of mammalian limb bones were *Crocodylus lloidi* feeding traces. Other reports come from Buffetaut (1983), Evans (1983) and Avilla *et al*. (2004), who described bite injuries on Mesozoic crocodylomorph skeletons probably inflicted during combat over food or other social interactions (e.g., territoriality, mating). Schwimmer (2002) provides some examples of tooth marks on the dorsal shells of Mesozoic turtles inferred to have been generated by the giant teeth of *Deinosuchus*. Also Dubois (1927) reported what he thought were crocodile tooth marks on the original Pithecanthropus femur and Sangiran mandible.

Large crocodiles are major predators in wetland environments and their feeding apparatus differs significantly from mammalian carnivores despite both groups relying heavily upon mammalian food (e.g., Schwenk, 2000). Differences in feeding habits exhibited by the two groups are a function of their dental and gnathic morphology, and are useful for identifying signatures of their feeding in bone assemblages (Njau & Blumenschine, 2006). The heterodont dentition of mammalian carnivore is effective for masticating and crushing bones, hence generating diverse patterns of bone modification, while crocodilians’ primitive form of dentition cannot perform extensive oral processing of food. Instead, food items are externally reduced prior to swallowing whole.

Crocodilian feeding morphology is therefore expected to produce patterns of bone modification different from that of mammalian carnivores.

3. Zooarchaeological Goals and Method

Methods of reconstructing prehistoric hominin subsistence pattern behaviors, and the environments in which they were active rely on zooarchaeological methods of analyzing fauna material. Zooarchaeology is defined as the study of faunal remains from archaeological contexts (e.g., Lyman, 1994 and references therein). Depending on the theoretical paradigm of individual researchers, whether oriented toward behavioral reconstructions of hominins, or toward environmental reconstructions, zooarchaeology is applied to key paleoanthropological problems. Its primary goal is to describe human subsistence behavior in evolutionary terms with respect to issues such as the origins of animal resource utilization, the origins and evolution of hunting, and the potential significance of scavenging in the hominin quest for animal tissues. It is believed that important anatomical and behavioral hallmarks of early hominins such as bipedalism, encephalization, tool making and use, butchering of large mammal carcasses, and food sharing, relate to the shift of hominins from the ancestral hominoid forested environments into the more open, varied mosaic grasslands that appeared during the later Miocene.

As such, zooarchaeology has to rely on neotaphonomic methodologies as a means of stripping away the taphonomic overprint from the fossil record (Gifford, 1981, 1991) and understanding the complex formational histories of early archaeological sites (e.g., Isaac 1983; Schiffer, 1987). The goals of zooarchaeology include quantifying skeletal and species representations, animal size and age, density of bone occurrences, weathering profiles, and bone surface modification, which includes tooth marks, butchery marks, digestion and root etching, and insect traces. These analytical variables have proven to be significant measures of various ecological and taphonomic processes in ecosystem (e.g., Klein & Cruz-Uribe, 1984; Bettinger, 1991; Blumenschine *et al*., 1994).

i) Taxonomic abundance

Although taphonomic processes may alter the original association between paleoenvironments and faunal communities (e.g., Behrensmeyer *et al*., 1979; Badgley, 1986; Cutler *et al*., 1999), identification and quantification of species abundance and diversity has been discussed in numerous zooarchaeological studies (e.g., Grayson, 1973, 1984; Watson, 1979; Klein, 1980; Gilbert & Singer, 1982; Lyman, 1982; Turner, 1983). Species abundance data have also served as an important quantitative tool for reconstructing paleoenvironments (e.g., Vrba, 1975, 1980; Grayson, 1979, 1981; Behrensmeyer & Hill, 1980; Shipman & Harris, 1988).

Based on the ecology and behaviors of savanna land mammals (e.g., Field & Laws, 1970; Sheppe & Osborne, 1971; Kingdon, 1979, 1982; Estes, 1991) and semi-aquatic vertebrates (e.g., Cott, 1961; Parker & Watson, 1970; Coryndon, 1978a, 1978b; O’Connor & Campbell, 1986; Eltringham, 1999), the skeletal assemblages from fossil wetlands are expected to contain a good representation of crocodiles and hippos, and to preserve a record of both migrant and resident mammalian herbivores that prefer habitats associated with wooded grassland near water and flood plains. However, grazing species, in particular obligate drinkers, are expected to predominate the total assemblages due to their large biomass in the live community and mortality patterns in savanna ecosystems (e.g., Western, 1975; Behrensmeyer *et al.*, 1979; Sinclair & Norton-Griffiths, 1979; Sinclair & Arcese, 1995). Taxonomic profiles, however, may vary depending on the type of wetland setting.

ii) Animal size classes

Animal size is another parameter of zooarchaeological analysis useful for categorizing bone specimens into groups of animals with similar size, when their specific taxon cannot be determined (Brain, 1981; Bunn, 1982; Capaldo, 1995). The size of a bone can be correlated to the size of an individual.

iii) Skeletal part profiles

Skeletal part profiles provide explanations for differences and similarities between observed fossil skeletal part frequencies and the frequencies of skeletal parts in a set of complete skeletons (Lyman, 1994). Also, inferences about local ecological conditions can be made by examining the skeletal part frequencies, and the extent of damage to particular elements. Generally, in the context of mammalian carnivores, durable and denser carcass bones (e.g., Klein, 1975, 1976; Klein & Cruz-Uribe, 1984; Blumenschine, 1989; Marean & Spencer, 1991; Kreutzer, 1992; Blumenschine *et al.*, 1994; Lam *et al.*, 1998) are more likely to survive consumption and to be well represented in the archaeological record. Provided that high competition conditions prevail, trunk skeletons, long bone ends, and the premaxilla and nasal portion of the face are often missing in the record.

Over the past four decades, archaeologists have tried to perfect methods to explain variation in the skeletal representation of animal carcasses in zooarchaeological assemblages by employing various interpretive assumptions to complement their explanations. For example, White (1952, 1953) suggested that people might have transported carcass parts differentially based on the economic value of the parts, while Perkins and Daly (1968) proposed the concept of the “schlepp effect” to account for variations in skeletal part abundances. The authors suggested that the distance carcass portions had to be transported may have influenced which carcass parts would be transported. Their economic and differential transport assumptions gained empirical support in the ethnoarchaeological record through the studies of Binford (1978) and O’Connell *et al*. (1988, 1990). However, taphonomic biasing processes operating during the resource life and post-resource life of bones may lead to differential survivorship of bones in an assemblage.

Different skeletal elements are preserved in different depositional contexts depending on their bulk density (Lyman, 1984). Therefore, denser elements and portions of skeletal elements, which enhance survivorship, are likely to dominate the total sample (see Klein, 1975, 1976, Klein & Cruz-Uribe, 1984; Blumenschine, 1989; Marean & Spencer, 1991; Kreutzer, 1992; Lam *et al*., 1998). Compact bones and phalanges are pushed into soil easily by trampling and survive better in subsurface context, and therefore are expected to be well represented in burial contexts compared to the surface context (e.g., Behrensmeyer & Dechant-Boaz, 1980; Njau, 2000). Complete crania, mandibles, teeth, axial elements, girdles and ribs will be destroyed by subaerial processes unless they face rapid burial. The longer bone items stay on the surface, the more they will be damaged by both biotic and abiotic forces.

Depending on the research question, some experts in vertebrate taphonomy have used skeletal representation from the landsurface to reconstruct minimum numbers of individuals of different species in order to be compared with the living community (e.g., Behrensmeyer *et al*., 1979; Behrensmeyer, 1981; Dechant-Boaz, 1982). Others were only interested in understanding vertical displacement of small bones (e.g., Gifford & Behrensmeyer, 1977). For example, Gifford-Gonzalez *et al*. (1985) relate the effects of trampling to vertical displacement, and Gifford (1977) argued that trampled objects may sort by size and surface area, with small objects becoming more deeply buried than large objects or objects with large surface area. Olsen and Shipman (1988) discussed the influence of sediment compaction to vertical movement of bones, while Yellen (1991) suggested that buried bones are less susceptible to horizontal movement from kicking.

iv) Bone surface modification

Various biotic and abiotic factors are known to introduce physical damage such as pits, scratches, grooves, burrows, incised marks, stain, and deep fractures to bone surfaces. The major agents of this modification includes carnivore masticatory action on bones, insect burrowing, root staining and etching, trampling, subaerial weathering and tool-associated butchery. Since this study focuses on the effect of carnivore feeding to bones, physical, vegetation, insect and tool damage to bones, which are very distinctive (e.g., Behrensmeyer, 1978; Andrews, 1990; Lyman, 1994; Blumenschine *et al*., 1996), are not described here.

Consumption of bone by mammals is a common phenomenon on modern terrestrial landscapes. Gross gnawing of bones by mammalian carnivores indicates the extent of nutrient extraction from prey carcasses. Nutrients such as calcium and phosphorous, and other contents such as grease and fat are usually contained in abundance in the epiphyseal portions of long bones. Quite often these parts of bones suffer gross damage or destruction by mammalian carnivores (e.g.,). Naturalistic observations suggest that a medium-sized mammals preyed upon by hyena would retain a high proportions of tooth-marked long bone shafts, and depending on the ecological context and degree of competition, the epiphyses would be heavily gnawed and the middle shafts broken open (e.g., Binford *et al*., 1988; Blumenschine, 1988; Marean *et al*., 1992; Capaldo, 1995).

v) Carnivore tooth marks

Tooth mark data enable zooarchaeologists to quantify carnivore modification of skeletal elements in both pre-buried and buried assemblages. Tooth mark profiles become more useful and reliable when used in conjunction with proportions of long bone shaft to end ratios to characterize the degree of carnivore ravaging (Blumenschine & Marean, 1993). Mammalian carnivores (e.g., Maguire *et al*., 1980; Richardson, 1980; Binford, 1981; Haynes, 1982a, 1982b, 1983;), carnivorous dinosaurs (e.g., Fiorillo, 1991; Chure *et al*., 1998; Jacobsen, 1998; Erickson, 1999), and crocodiles (Njau & Blumenschine, 2006) produce a variety of tooth marks and bone modification that can be distinctive to their taxa.

vi) Bone fragmentation

The major causes of bone fragmentation include feeding carnivores (e.g., Binford, 1981) and hominin activities such as butchery and tool making (Lyman, 1978; Noe-Nygaard, 1997). Bone fragments are qualitatively described based upon their fracture patterns such as parallel, spiral, perpendicular and irregular (e.g., Shipman *et al*., 1981; Johnson, 1985; Marshall, 1989; Gifford-Gonzalez, 1989; Villa & Mahieu, 1991). Fracture patterns of long bones complement other criteria used to infer agents of bone modification. For example, a high incidence of spirally-fractured limbs would suggest carnivore modification, while transverse fractures would suggest physical processes such as trampling (e.g., Haynes, 1991; Villa & Mahieu, 1991). With the exception of notches (Blumenschine & Selvaggio, 1991; Capaldo & Blumenschine, 1994), rarely will a particular type of break identify the agent of breakage unambiguously (Shipman *et al*., 1981). Nonetheless, identifying the general class of taphonomic agent responsible for the fractured bones in an assemblage can tell us much about the formational history of a bone assemblage.

Other causes of bone fragmentation include trampling (e.g., Haynes, 1991), subaerial weathering (e.g., Behrensmeyer, 1978) and post-burial factors such as compression forces induced by overburden weight (e.g., Villa & Mahieu, 1991). Since bones become structurally weaker as they become progressively more weathered, Lyman and Fox (1989) suggest that the time a bone is broken relative to its weathering stage may be important taphonomic information for revealing the exposure duration and the accumulation history of a bone (fresh bones are more likely to be accumulated by biological agents such as predators and scavengers than weathered bones). A fresh-break of a long bone is characterized by spiral or oblique fracture.

vii) Weathering

Although the value of weathering data for interpretation of paleontological assemblages has been debated (Lyman & Fox, 1989), descriptions of the freshness of skeletal materials have been included in taphonomic analyses of modern landsurface and early archaeological bone assemblages (e.g., Gifford, 1978; Potts, 1988). Pioneered by Behrensmeyer (1978) subaerial weathering profiles provide information about the accumulation history of skeletal remains (e.g., Bower *et al*., 1985; Potts, 1988). Based on this assumption, an assemblage with relatively similar patterns of weathering suggests that the bone specimens were formed under similar circumstances or conditions (e.g., attrition, catastrophic), or deposited during the same time period. In addition, weathering data may also contain information about taxonomic composition (e.g., Bower *et al*., 1985), skeletal element representation, vegetation cover, and depositional microenvironment (Behrensmeyer, 1978).

CHAPTER 3. CROCODILE EVOLUTION, FEEDING BIOLOGY AND ADAPTATION

1. Evolution of the crocodilians

An understanding of crocodilian feeding biology, including the evolution of the feeding apparatus, is necessary for understanding their behavior in carcass consumption and bone modification. Crocodilians are the last surviving reptilian representatives of the subclass Archosauria, or the ruling reptiles. Among living vertebrates, crocodilians are more closely related to birds than to lizards, with the former representing the only other surviving archosaurian clade. The Archosauria, which dominated animal communities on the continents during the Mesozoic, include crocodilians, dinosaurs, pterosaurs, and thecodontians (e.g., Langston, 1965; Bellairs, 1968, 1987; Neill, 1971; Benton, 1982, 2004). Thecodontians include a variety of primitive archosaurs, some of which may have been the precursors of later groups such as crocodilians.

All crocodilians belong to an order Crocodylia and are traditionally classified into three suborders: Protosuchians, Mesosuchians, and Eusuchians (e.g., Densmore, 1983; Grenard, 1991; Brochu, 1997, 2000, 2003). Protosuchians are the earliest forms, which flourished in the Late Triassic. These primitive crocodilians were short (ca. 1 m long) and had a rather lizard-like appearance with a short snout. Judging from their long and slender limbs, the earliest crocodilians were probably terrestrial predators capable of fast running. Mesosuchians underwent considerable evolutionary radiation and became dominant in the Jurassic and early Cretaceous. Eusuchians radiated and became dominant in the Late Cretaceous and Cenozoic. This group includes all modern crocodilians and their immediate fossil ancestors such as *Deinosuchus*, *Sarcosuchus*, and early Tomistomas (e.g., Erickson & Brochu, 1999; Schwimmer, 2002; Brochu, 2003).

Modern crocodilians (Eusuchians) are normally divided into three subfamilies: Alligatorinae (alligators and caimans), Crocodylinae ("true" crocodiles and the African dwarf crocodile), and Gavialinae (gharials and "false" gharials or Tomistoma) (e.g., Norell, 1989; Grenard, 1991; cf. Brochu, 2003). There are about 22 surviving crocodilian species living in various parts of the world. Seven species belong to Alligatorinae, thirteen to Crocodylinae, and two to Gavialinae.

The twelve extant species belonging to the genus *Crocodylus* ("true" crocodiles) live in various tropical parts of the world. They include the Nile crocodile (*C. niloticus*), the African slender-snouted crocodile (*C. cataphractus*), the American crocodile (*C. acutus*), the Cuban crocodile (*C. rhombifer*), Morelet's crocodile (*C. moreletii*), the Orinoco crocodile (*C. intermedius*), the Saltwater or Estuarine crocodile (*C. porosus*), Johnston's crocodile (*C. johnsoni*), the Mugger (*C. palustris*), the Siamese crocodile (*C. siamensis*), the Philippine crocodile (*C. mindorensis*), and the New Guinea crocodile (*C. novaeguineae*).

The term 'crocodile' is used in this work to refer to members of the genus *Crocodylus*, in particular the Nile crocodile, while the term 'crocodilian' may refer to any member of the order Crocodylia or family Crocodylidae, which includes alligators, caimans, gharials, "false" gharials (Tomistoma), true crocodiles and African dwarf crocodiles.

The earliest record of *Crocodylus* comes from the basal Oligocene deposits of Fayum, Egypt, represented by two species: *Crocodylus megarhinus* and *Crocodylus* *articeps*. Although both species disappeared from the record by the end of Oligocene, *C. articeps* is considered to have given rise to the early stocks of *C. lloidi*, which by the early Miocene was already a predominant crocodilian species in North Africa (Tchernov, 1986). All African and Asian crocodiles are considered to be derivatives of this early stock. The earliest record of *C. lloidi*, the presumed direct ancestor of Nile crocodiles, comes from the lower Miocene deposits of Gebel Moghara, Egypt (Tchernov, 1986). However, the first record of this species in East Africa comes from the upper Miocene deposits of Baringo Basin (Bishop, 1972).

C. lloidi was an extremely brevirostrine (short- and broad-snouted) and generalized species before it speciated gradually into more longirostrine forms such as *C. checchiai* (an extinct North African crocodile), *C. cataphractus* and *C. niloticus* (Tchernov, 1986; *contra* Brochu, 1997, 2003, Storrs, 2003). Once this short-snouted crocodile entered East Africa, it predominated all water bodies during the Late Neogene and Pleistocene before going extinct in the mid-Quaternary. By the Pliocene this species was sympatric with the Nile crocodiles, *C. cataphractus*, and *Euthecodon brumpti* in some parts of the Turkana Basin. However, *E. brumpti*, an extremely longirostrine form, faced extinction during the mid-Quaternary (Tchernov, 1976, 1986), while *C. niloticus* and *C. cataphractus* survived to modern times. The demise of brevirostrine predecessors led to a progressive spread of Nile crocodiles throughout Africa, where they predominate inland waters, while their counterparts *C. cataphractus* retreated to Lake Tanganyika, the only place they are found today.

A number of factors complicate taxonomic classification in the crocodilian fossil record, including incomplete fossil material, morphological conservatism, and ontogenetic variability among individuals (e.g., Kalin, 1933; Iordansky, 1973; Steel, 1973; Dodson, 1975). These issues have led Arambourg (1947) to lump *C. lloidi* and *C. niloticus* in the Omo material, while Brochu (1997) has separated *C. lloidi* and *C. niloticus* into distinct genera based on synapomorphic analysis. More recently fossil material from Turkana Basin (Koobi Fora, Kanapoi and Lothagam), which were originally described by Tchernov (1976, 1986) as *C. lloidi*, have been reassigned to a new genus, *Rimasuchus llyoidi* (Storrs, 2003). However, since Tchernov (1986) and Storrs (2003) were looking at the same material, their differing classification of this taxon may largely reflect different methods of analysis (see Storrs, 2003). Although the material from Olduvai, which is located south of the Turkana Basin, can just as well belong to this new genus, I refer the crocodilians from Olduvai as *C. lloidi* until further analysis is done on the material.

Although the Nile crocodile is a less robust species than its ancestor (*C. lloidi*), the two species possess similar postcranial morphology and dental structure. Tchernov's (1986) descriptions of Plio-Pleistocene crocodilian materials from Lake Turkana, Omo, and Olduvai demonstrate that the difference between *C. lloidi* and *C. niloticus* is restricted to the physical configuration of the rostrum (Figure 3.1). The latter possesses a slightly more delicate and elongated snout, and generally smaller body size compared to its predecessors. The maximum body length of the Nile crocodile provided by various workers is estimated to range from 5–9 m (e.g., Schmidt, 1944; Guggisberg, 1972; Graham & Beard, 1973), but the most reliable average length provided by Cott (1961) is 6.2 m. The body size estimated for *C. lloidi*, based on the most complete cranial specimens from Koobi Fora and Lothagam, is 7 m or more in length (Storrs, 2003).

Given the large size and robustness of *C. lloidi* skull, the body size of this extinct reptile is inferred to be larger than their descendants.

i) Rostrum modification and evolution of dietary adaptation

The speciation from *C. lloidi* is accompanied primarily by elongation of the rostral region. The postcranial skeleton and entire posterior region of the skull (cranial table, the rear area of the palate and occipitalia) remains unchanged (e.g., Tchernov, 1986; Densmore & Owen, 1989; Schwimmer, 2002; Storrs, 2003). Typically, the broad and short snout of the ancestral forms evolves toward long, slender-snouted species, and once a long rostrum is attained by a new species, this trend appears to have become irreversible. Such morphological conservatism has been explained as an adaptive response to diet (e.g., Iordansky, 1973; Langston, 1973).

Generally, the evolutionary trend in crocodilians reflects the adaptive shift from feeding on large land animals (practiced by brevirostrine forms) towards the more piscivorous diet, practiced by longirostrine forms. It has been argued that differences in rostral shape and length among different species correlate with diet and adaptation to different feeding niches (e.g., Meyer, 1984). For example, *C. lloidi* have been inferred to rely on large mammal prey (Tchernov, 1986; Storrs, 2003), while the intermediate-form, *C. niloticus*, are known to feed on fish and large mammals (Cott, 1954, 1961). Exclusive piscivory characterizes the most longirostrine species, such as gharials (*Gavialis gangeticus*), *C. cataphractus*, and *E. brumpti*. The morphological statis and evolutionary conservation of the post-rostral skeleton in crocodilians has been documented in upper

Mesozoic and early Cenozoic materials, leading to some workers to label these reptiles as "living fossils" (e.g., Simpson, 1944; Schopf, 1984).

ii) Evolution of crocodilians in the paleo-Olduvai Lake Basin

During the Plio-Pleistocene, four crocodilian species lived in East Africa. They include *C. lloidi, C. niloticus, C. cataphractus,* and *E. brumpti*. All four species were sympatric in the Turkana Basin, sharing the different adaptive zones according to the shape of their snouts. Only *C. lloidi* is known in the paleo-Olduvai Basin during the Plio-Pleistocene times. Olduvai is the southernmost region where *C. lloidi* was originally recorded (Tchernov, 1976, 1986) but Pickford (1996) extended their geographic range to southern Africa with the discovery of specimens from the Namibian Miocene deposits that are closest in overall morphology to *C. lloidi*.

According to Tchernov (1986) *C. lloidi* disappeared from Olduvai record by Bed IV time, and *C. niloticus* did not venture into Olduvai waters prior to upper Bed II times. The Olduvai materials were originally attributed to two sympatric species, the "normal-snouted" crocodile (i.e., *C. niloticus*) and "short-snouted" or brevirostrine crocodile (*Crocodylus* sp. nov.) (Leakey, 1971, Tchernov, 1976). Further taxonomic analysis by Tchernov (1986) revealed no significant traits displayed by Olduvai specimens to warrant the existence of *C. niloticus* during the Oldowan times. Earlier analyses by Arambourg (1947) failed to distinguish between *C. niloticus* and *C. lloidi,* which led to initial problems in assigning Olduvai crocodiles into specific groups.

iii) Ecological implications of crocodile evolution

In places where *C. lloidi* and *C. niloticus* occurred sympatrically, competitive exclusion may have resulted in the more piscivorous adaptive niche of the latter (e.g., Meyer, 1984). The absence of *C. niloticus* at Olduvai during Oldowan times may indicate lack of habitats that supported a piscivorous niche (cf. Stewart, 1994, 1996). In this case, *C. lloidi* depended largely on land mammal prey captured near water edges.

According to Tchernov (1986), Nile crocodiles appeared at Olduvai after Lemuta Member (ca. 1.7 Ma). Some of the crocodile specimens came from the flood zone of the lake, in the fluvial-lacustrine facies at MNK Skull site. OH 13 (*Homo habilis* mandible and partial cranium), OH 14 and OH 15 (molars and canine) were also found in the assemblage (Leakey, 1971). The presence of trona crystals in the perennial lake zone indicates that the lake was highly saline at the time (Hay, 1976).

Other *C. niloticus* fossil materials came from upper Bed II at BK in stream channel deposits. This site is known for the *Australopithecus* teeth (OH 3), its high number of *Pelorovis* (giant bovine) remains (MNI=24) and its rich representation of stone tools. By this time the ancient lake had shrunk and broken into isolated wetlands (Hay, 1976). The increasingly dominant position of *C. niloticus* from mid-Quaternary to present time in the region probably reflects the currently arid condition of the East African Rift Valley that did not favor brevirostrine crocodile habitats.

2. Taphonomic implications of crocodile's feeding-morphology

i) Crocodile feeding behavior

The feeding behavior of crocodiles is largely related to their anatomy and differs from mammalian carnivores in prey bone modification capabilities. Crocodiles do not chew food. Rather, they prefer to swallow their food whole, including the bones (Njau & Blumenschine, 2006). This behavior is different from mammalian carnivores (Valkenburgh & Molnar, 2002), which process food orally through mastication. For this reason, gross gnawing or extensive ravaging of bones is expected to be lacking in assemblages produced by crocodilians (see Fisher, 1981a). Quite often mammalian carnivores utilize soft bone elements and portions such as the sternum, ventral thoracic ribs, premaxilla, and spongy long bone ends as a source of within-bone nutrients such as grease, fat and marrow, brain tissues and minerals such as calcium and phosphate. In the process, the bones are grossly gnawed, crushed to various degrees, or destroyed, with surviving long bone fragments bearing a high frequency of tooth marks (e.g., Blumenschine & Marean, 1993; Capaldo, 1995).

Historical and scientific accounts of the life history and feeding ecology of crocodiles demonstrating the great carnivorous capability of this species are numerous (e.g., Grabham, 1909; Pitman, 1941; Nelson, 1949; Neill, 1971; Guggisberg, 1972; Pooley & Gans, 1976; Minton & Minton, 1973). Adult crocodiles possess a strong, muscular neck and a massive skull with a large gape, that together are used in an unusual technique for killing and dismembering larger prey. As exothermic animals, crocodiles do not wander around searching for food and using up vital energy. Rather, they lay quietly hidden under water and wait patiently for prey to get within range of attack. The reptile will then surprise the prey animal by launching an explosive ambush and capturing its victim with its powerful jaws, before dragging it below the surface, where it is drowned. This technique allows crocodiles to overpower even large-bodied animals such as lion, buffalo, hippo, rhinocerous and giraffe (e.g., Selous, 1908; Attwell, 1959; Pienaar, 1969). Also, the massive skull and strong dentition of the crocodile can endure stress associated with prey struggle, and can produce enormous bite forces on prey skeletons during capture and consumption.

ii) Feeding morphology and implications for bone modification

A large skull and gape allows crocodiles to ingest relatively large food items without much difficulty. This feature is enhanced by possession of a primitive form of tongue also found in snakes and varanids, which allows them to gulp very large and heavy food items (e.g., Gans, 1961; Cundall, 1983; Smith, 1986) by employing "inertial feeding", in which food is transported into the esophagus by gravity rather than by the action of the tongue (Gans, 1969). According to Cleuren and De Vree (1992) the wide and flat tongue of the crocodile is too simple to perform a true lingual transport of food into the esophagus, hence necessitating the gulping of complete elements. Some of the historical accounts of crocodile feeding behavior show that before swallowing, the animal will surface from water and throw its head up and back to enable the food to pass down its throat. If the morsel is too large, the front part of the body may be partly lifted off the ground in order to assist in the swallowing process (e.g., Carpenter, 1928; Attwell, 1959).

The following morphological features are essential in determining crocodile feeding strategies and the resulting traces on bones.

1) Crocodiles retain the “thecodont” dentition shared by most reptiles, in which teeth are set in deep alveoli (e.g., Bellairs, 1968; Romer and Parsons 1978; Lubkin, 1997), and are replaced repeatedly during the lifetime through resorption of the root and shedding of the crown (e.g., Owen, 1840-1845; Mummery, 1924; Poole, 1961; Edmund, 1960, 1962, 1969). Each successional tooth grows to be larger than its predecessor, with tooth replacement slowing in older individuals (Poole, 1961; Erickson, 1996a, 1996b). Interlocking of upper and lower teeth is preserved during succession, although great variation in tooth size is evident in single individuals due to variation in eruption age of each tooth.

2) The thecodont form of primitive dentition prevents precise tooth-to-tooth occlusion. Instead, the upper and lower teeth interlock antero-posteriorly when the mouth is shut restricting the sideways movement of jaws (or mastication). The absence of occlusion, however, helps to prevent premature dislodging of an advanced resorbed tooth from the socket (e.g., Pooley, 1989).

3) Crocodile teeth have robust and pointed cylindro-conical crowns, which are slightly flattened bucco-lingually, and slightly curved inward. The crowns of the front teeth are long (about twice the maximum diameter) and markedly curved inward. Teeth that are placed from a point approximately halfway along the jaw to the hinder end gradually become shorter and possess squat crowns, which are only slightly curved and have a height equal to the maximum diameter. The crown surfaces have a number of round linear folds (ridges) running vertically from the neck to the tip of the crown. This ridge pattern is pronounced on the anterior teeth but is often weak and irregular on the hind teeth. The teeth are armored by carinae, an elevated cutting ridge formed on anterior

and posterior faces of a tooth. This feature is more pronounced in the anterior dentition. The carinae display a continuous series of very fine denticles only when newly erupted, a function of which is associated with cutting. Juvenile crocodiles have slender and sharp teeth (effective, for example, for piercing insect exoskeletons) compared to adults, whose more robust and blunt teeth are suited for puncturing and tearing large prey. In addition to their variable eruptive morphology and wear, chipping of the tip of the crown expectedly leads to diverse tooth mark morphologies, even on a single bone fed on by one crocodile.

4) The upper jaw of an adult Nile crocodile has an average of 36 erupted teeth, while the lower jaw has an average of 30 teeth (cf. Brazaitis, 1973; Iordansky, 1973). The anterior dentary teeth lie labial to the premaxillary tooth row. The premaxillary fourth tooth is distinctly enlarged, bearing pronounced carinae, well adapted to puncturing and gripping struggling prey. The enlarged upper tenth tooth and lower eleventh tooth are robust and less pointed, and are important for crushing less durable bones. A notch occurs between the eighth and ninth dentary teeth to allow room for the protruding upper tenth tooth. Similarly, a notch occurs on the upper jaw between the fifth and sixth teeth, and the twelfth and thirteenth teeth. When the jaws are closed these notches accommodate the enlarged lower fourth and eleventh teeth, respectively.

iii) Feeding sequence and implications for bone modification

The anatomy and feeding biology of crocodiles suggest that these carnivorous reptiles use techniques for procuring and processing animal food that differ from mammalian carnivores. Njau and Blumenschine (2006) modeled six feeding stages employed by crocodiles (cf. Bramble & Wake, 1985; Hiiemae & Crompton, 1985;

Cleuren & De Vree, 1992; Schwenk, 2000), with each stage (with exception of stage six) having a potential of producing tooth-damage to bones of the prey (see Table 3.1).

1) Prey acquisition: This stage is hereby specified as capturing of prey through stunning ambush, or scavenging of carrion deposited along riverbanks or lake margins (e.g. Attwell, 1959; Grenard, 1991; Guggisberg, 1972). Most often the anterior portions of the jaws are involved in apprehending the prey, although the cheek teeth may also be used (e.g. Cleuren & De Vree 2000: 348). The muzzle, skull, intermediate and lower limbs, or other convenient parts of the prey may suffer injuries inflicted by the teeth of the reptile, amplified for large crocodiles by the blunt force trauma inflicted by their massive heads.

2) Prey killing: After acquisition, the struggling prey is dragged and subdued underwater until it dies (e.g. Pooley & Gans, 1976). The seized-upon prey is positioned more aborally before a forceful bite is applied by pressing the jaws together in order to crush and compress part of the carcass into the mouth. The reptile may spend a considerable amount of time at this stage with its head pointing upwards to initiate swallowing. The enlarged premaxillary fourth teeth grip and puncture the prey, while the tenth maxillary teeth and the eleventh mandibular teeth may be involved in crushing less dense bones. These and other teeth will expectedly penetrate flat bone completely, and even the thicker cortical bone of long bone midshafts, which in the process, may be fractured obliquely or longitudinally along the shaft and will be embedded with skin and flesh.

3) Reduction: This stage includes gross dismemberment of the carcass into large pieces that can be swallowed. It is accomplished through death-rolling, vigorous shaking

or forceful battering of carcass parts against rocks. This action expectedly produces numerous tooth pits, punctures and scores at grasping sites (e.g. distal limb elements), sometimes associated with minimal snapping of long bones, axial bones and vertebrae processes. Some of the fractured bones will be embedded in flesh and are, therefore, likely to be swallowed.

4) Defleshing: The reptiles rip meat off bones with anterior and lateral teeth, before tearing and pulling in a death-roll action. Although crocodiles do not deflesh bone as cleanly as do mammalian carnivores or vultures, this behavior facilitates skeletal disarticulation. Large scraps of near-bone flesh that cannot be torn off remain on abandoned parts. Defleshing may be accomplished by nipping, and therefore may produce high densities of shallow pits and scores (mostly produced by premaxillary teeth). Also, vertebral processes, axial bones and protruding bone ends such as olecranon processes are likely to be snapped.

5) Swallowing: A reduced or whole carcass part is maneuvered into the mouth, accompanied by a rapid series of light bites, before being swallowed by inertial feeding. If a food item is still too large to swallow at once, the animal will deliver several fast-closing bites or work the food item back and forth in its mouth, biting in many locations (e.g., Carpenter, 1928; Attwell, 1959; Neill, 1971; Cleuren & De Vree, 2000). Depending on the size of the food item, a forceful bite may be delivered during this phase of carcass manipulation in order to crush bones. If jaw adduction is not complete due to the size and density of the food item, the bone is abandoned. Many shallow pits and slight fractures are likely to be produced on these bones.

6) Carcass abandonment: Large and robust skeletal elements may escape complete ingestion as they are discarded, either complete, broken or defleshed, and allowed to sink to the bottom of the pool. Also, smaller isolated bones as well as fragments produced during the reduction process are often ignored. Some of these items are dispersed from the feeding site when carcasses are vigorously shaken.

Table 3.1. Crocodilian bone modification model for large crocodile (> 3.5 m long) feeding on medium to large size mammalian prey (ca. 100–900 kg).

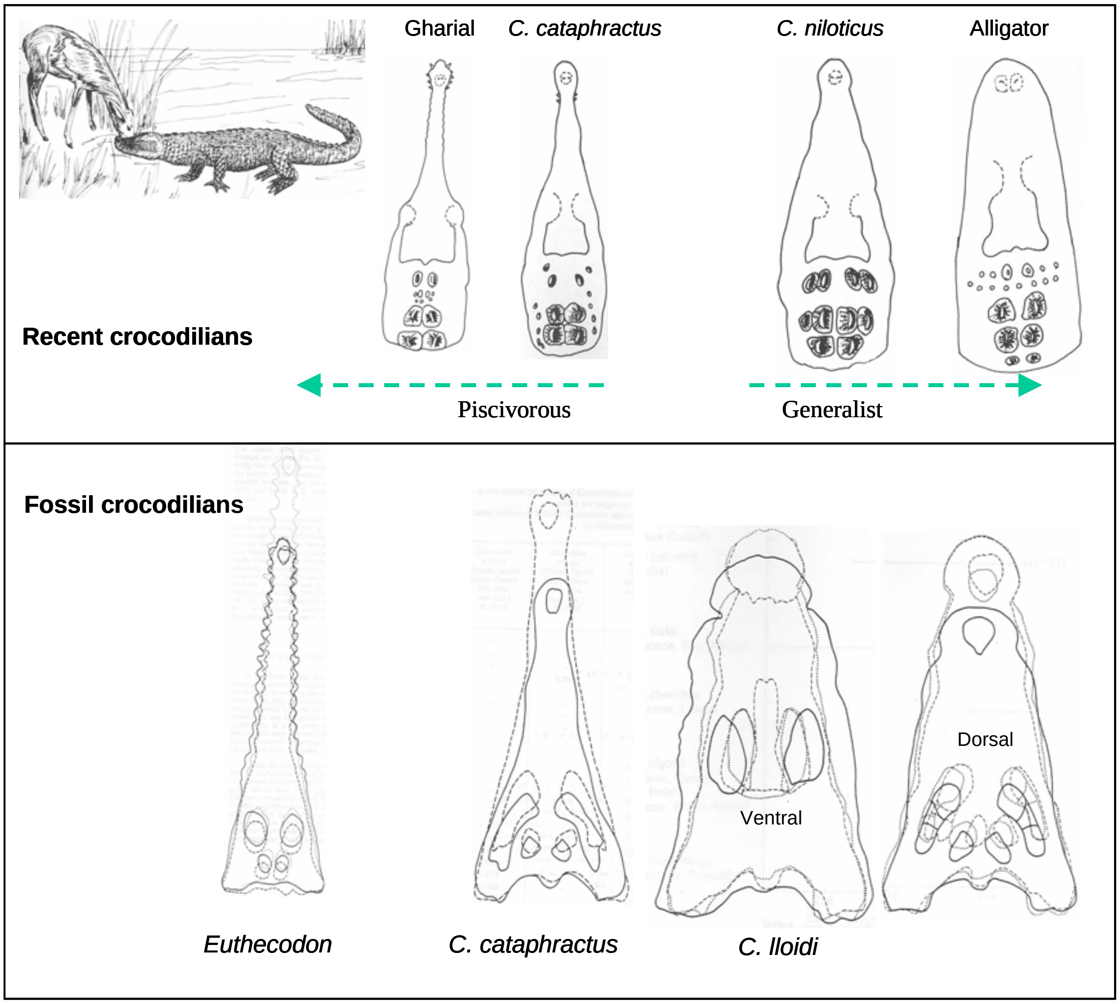
Crocodile		Prey		
Feeding Stage	Strategy/ Action	Skeletal Region Injured	Bone Modification	Notes
Prey acquisition: - Ambushing	- Massive skull force & wide gape (head hunting) - Anterior>> lateral teeth	- Muzzle & anterior cranium - Intermediate & lower limbs - Horn cores may be broken	- [1]Isolated patches of pits & serial punctures on skull - Scores>> pits, punctures on lower limbs>> upper limbs	- Trunk & girdles are wide/ broad & protected by bulk flesh - Scores from struggling prey
- Scavenging from mammalian carnivore kills	- Drag carcass into water nearby using anterior jaws	- Any grabbed part	- Shallow pitting, snapping of less dense bones & processes	
Prey killing: Subduing & squeezing	- Complete jaw adduction - Anterior & lateral teeth	- Intermediate, lower limbs & skull	- [1]Isolated patches of shallow to deep pits	Crushed bones embedded with periosteum & flesh
Carcass reduction: Gross dismemberment	- Death-rolling, vigorous shaking, beating & pulling - Anterior & lateral teeth	- Distal ends of limbs - Proximal ends of limbs (after detached from girdles) - Portions near knee & elbow joints - Skull – neck - Trunk (various) - Isolated girdles	- [2, 3]Transverse to oblique scores - Shallow to deep pits, some bisected? - Snap, step & spiral fracture on long bones & axial - Protruding bone processes snapped	- Whole limbs detached from the trunk -Concentration of marks on grasping sites -Fractured bones embedded with periosteum & flesh
Defleshing	- Anterior & lateral teeth used to grab, twist & pull, or death-rolling deployed	- Upper limbs & girdles - Trunk - Proximal portions of intermediate limbs	- Shallow pitting (some bisected) and short scores - [2, 3]Shallow & short scores (linear, curved & hook scores) - Transverse/ oblique scores - Snapping of vertebra processes & axial bones	- High density of marks all over the bone surface
Swallowing	- Anterior & lateral teeth - Numerous but gentle bites	- All reduced food items - Upper & intermediate limb	- Isolated to patches of shallow pits - Slight fractures	
Carcass abandonment	- Lost or ignored items	- Articulated limbs & axial skeleton - Isolated skull & girdles - Small & broken bones	- Damage to some complete elements & sets of articulating units - Minimal fragmentation - Lack of gross gnawing	- Minimal fragmentation - Lack of gross gnawing

[1] The interspacing of teeth in tooth rows may produce serial marks, depending on the nature of tooth-bone contact

[2] Slender and fresh (unworn) successional tooth may produce sharp, narrow and cut-like scores on cortical bone

[3] When tip of functional tooth is worn, chipped or broken during use may produce incised scores

Figure 3.1. Morphological modification of rostrum reflecting dietary specialization of modern (Top) and fossil (Bottom) crocodilians. The more longirostrine modern species, the gharials and *C. cataphractus* are more piscivorous, and this diet specialization is inferred for fossil *Euthecodon* and *C. cataphractus*. The more brevirostrine modern species, Alligators and *C. niloticus*, are generalists combining both fish and large mammals in their diet. Adult crocodiles are effective in capturing land mammals in aquatic settings (insert-upper left), and *C. lloidi* is inferred to rely on mammals for food. In the bottom picture, *C. lloidi* (solid line) is superimposed on recent *C. niloticus* (dashed lines), and fossil *C. cataphractus* (solid line) is superimposed on modern *C. cataphractus* (dashed lines) to demonstrate the evolution of these species, which is through sheer elongation of rostral region. The phylogenetic relationships among major crocodilian groups reconstructed by Tchernov is illustrated in page 288 of this thesis.
Figures adopted from Tchernov (1986) and Grenard (1991). Figures not to scale.



CHAPTER 4. CONTROLLED FEEDING OBSERVATIONS: METHOD, ANALYTICAL PROCEDURES AND SAMPLE CHARACTERISTICS

1. Study areas

The procedures used in this study were designed to document the feeding behavior of crocodiles and the patterns of bone modification they create. Feeding observations were made on captive Nile crocodiles at two animal farms in Tanzania. Primary work was carried out in a crocodile Farm located in Bagamoyo, a historic town north of Dar es Salaam. Bagamoyo is located on the coastline along the Indian Ocean (Figure 4.1). Other observations were made at Engosheraton farm located in Arusha, northern Tanzania (Figure 4.1). The farm is relatively small in comparison to Bagamoyo, and in addition to crocodiles, it keeps a variety of wildlife including spotted hyena, baboons, snakes and various species of rodents. Most of the animals in this farm are brought in by game officers who have rescued them from the hands of local villagers who threaten to kill wild animals that get near their livestock.

i) Bagamoyo crocodile farm

The farm is situated approximately 2 km inland on the upper beach of the Indian Ocean, and its rich sandy soil supports a number of cultivated and permanent plants such as cassava, pineapples, cashew trees and coconut/palm trees. The weather in the coast region is warm (ca. 95° F) during most part of the year, with the exception of June and July, which are the coolest months (ca. low 62° F). Most of the mature crocodiles were introduced to the farm in the early 1990s, while the small and young ones were hatched at the farm. Many of the large reptiles come from the Ruaha, Kilombero and Rufiji rivers in southern Tanzania, where large populations of Nile crocodiles have been documented (Barker, 1953). The Great Ruaha is one of the largest systems that drains the Udzungwa Mountains (southern highlands) before joining the Kilombero-Rufiji on the Rufiji Basin, finally draining into the Indian Ocean (Figure 4.1**)**. The number of crocodiles at the farm has increased tremendously since the early 1990s due to a successful breeding program. Hundreds of eggs are hatched annually.

The farm consists of three enclosures (termed *banda* in Swahili) of 10m x 30m in size, each housing animals according to their body size. Each *banda* is divided into two areas by a solid wall partition, which includes a small opening to allow free movement of crocodiles between the two areas. One side of the *banda* has no roof and bare sandy ground. This area is essential for the basking activities of the reptiles, and also provides a retreat for subordinate individuals. The other part of the *banda* has a thatched roof and contains a pool of 8m x 16m area. Among the large crocodiles are two females and one male, measuring 4 m, 2.8 m, and 3.1 m from nose to tip of tail, respectively. Approximately 100 animals were grouped into the medium size class (2–2.4 m), and 40 animals were classified as small (0.9–2 m) (Table 4.1).

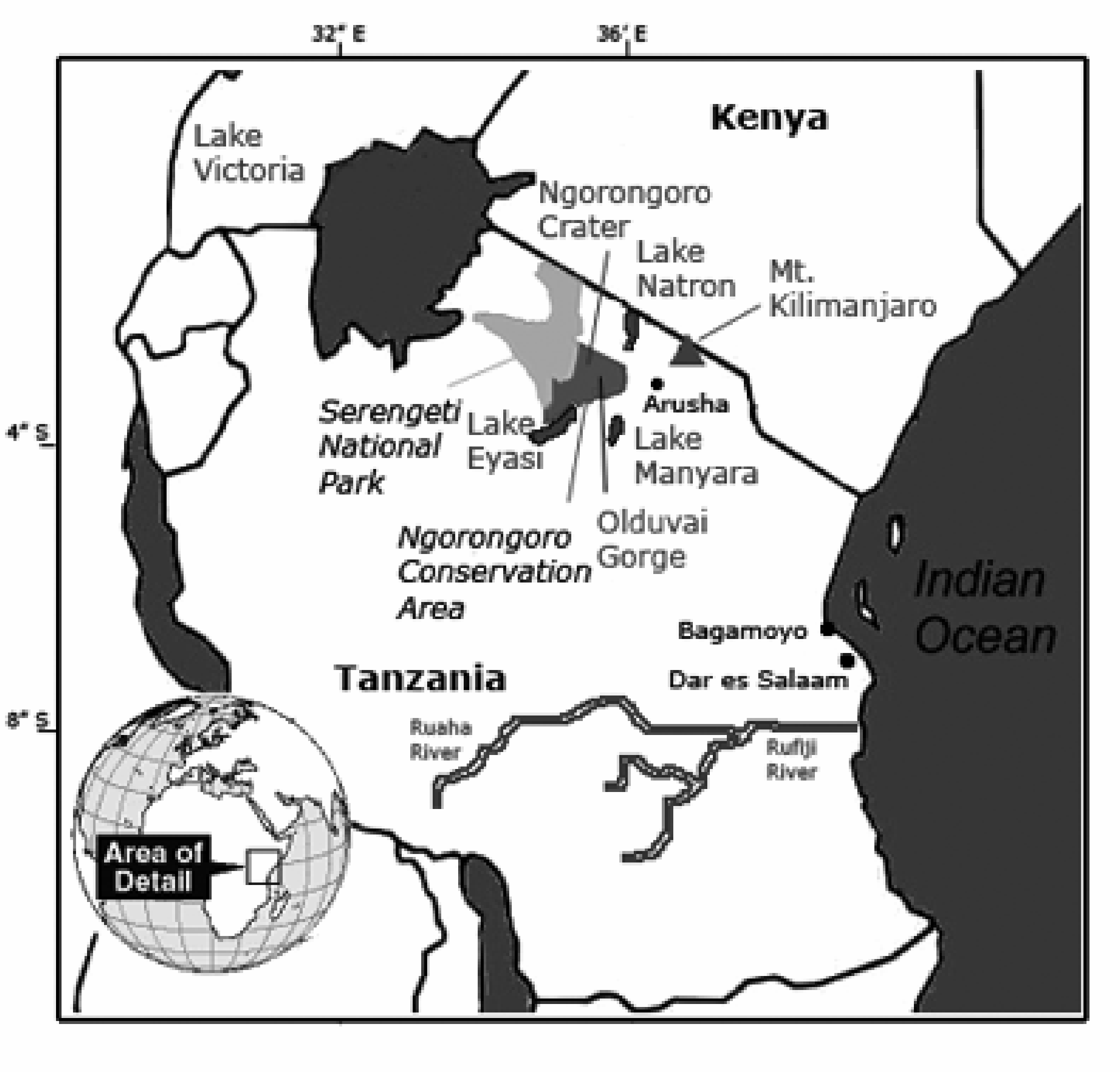
The crocodiles are raised primarily for the skin trade, which means an animal is more valuable when is not too old or when the skin is free of wounds or defects. For this reason, animals may not attain their full size before being culled. In order to reduce feeding and maintenance costs, the animals are culled when they reach about 2 – 4.3 m in length. Large crocodiles eat large quantities of meat and need more water and space than smaller crocodiles. Also the rate of growth slows down as the animal gets older. Once the animal attains a certain body size (ca. 2.2 m or 7 ft), the rate of growth decreases and becomes remarkably steady, during which the animal gains only an average of 1.4 inches (36 mm) in length per annum (Cott, 1961). This condition forces the farm owners to cull of the animals while they are sub-adults.

ii) Engosheraton crocodile farm

This farm, which is located about 5 km southwest of Arusha suburbs, has no large size crocodiles. Arusha is at a higher altitude (ca. 1600 m) on the foot hills of mount Meru, and experiences a relatively cool climate compared to Bagamoyo. There are two small-sized (1 – 1.2 m long) and three medium-sized crocodiles, one measuring about 2.3 m and two measuring ca. 1.7 m in length. All crocodiles arrived at the farm after being rescued from ponds and streams in various local villages in Arusha Region.

The farm contains several *bandas* but only one is committed to crocodiles. This *banda* has no roof, but is located under two large trees, which provide adequate shade. It contains two small pools, which are connected by a small door. The large pool is round (ca. 5 m in diameter) and the small one is elongated (approximately 6m x 2.5m). The reptiles bask on the elevated ground above the edge of the pools. All of the crocodiles are kept together in one *banda*. Due to the difference in body size between individuals, the small crocodiles are routinely threatened by the larger individuals. The larger individuals bite and chase the small ones away from food, and one of the smallest crocodiles (ca. 1.1 m long) is missing its entire premaxilla as a result of a bite probably from one of the larger individuals.

Figure 4.1. Map of Tanzania showing geographical locations of major study areas.



2. Observation protocol and procedures

Whole quartered carcasses of cow and whole carcasses of goats were provisioned to crocodiles as part of each farm's regular feeding schedule. The cow (*Bos taurus*) carcasses were supplied by local butchers, while still fresh, and the live goats (*Capra hirtus*) were bought from the nearby villages and butchered at the farm. Bulk muscles and mass flesh on the girdles, upper limbs (i.e., femur and humerus) and upper parts of intermediate limbs (i.e., tibia and radio-ulna) of cows were removed without slicing the bone surface. However, a substantial amount of meat was left on these skeletal regions in order to provide sufficient meat for the crocodiles to feed upon. As part of local butchery practices, the lower limbs (i.e., metapodial and foot) were not skinned or defleshed. Although all goat carcasses were skinned and their internal organs removed, their skeletons were not defleshed. Therefore, they were introduced to the crocodiles fully fleshed.

Prior to commencement of feeding observations, crocodiles were categorized according to body size (Table 4.1). In many cases the largest individuals among the small-sized group were observed interacting with the medium-sized animals, making it difficult to separate the groups.

i) Determining crocodile age and body size

The body size of a crocodile is a key factor in determining the type of food the reptile can take (e.g., Cott, 1954, 1961; Guggisberg, 1972; Pooley, 1989; Alderton, 1991). Length is a useful variable of characterizing crocodilian feeding ecology and behavior, and many herpetologists have developed methods of estimating crocodile age by using this variable, usually by measuring the animal’s length from nose to the tip of tail (e.g., Schmidt, 1944; Cott, 1954, 1961; Graham, 1968; Pooley, 1962; Choquenot & Webb, 1987; Moody & Ceril, 1988; Magnusson *et al*., 1989). A hatchling measures only ca. 25 cm. A fully grown animal may grow to thirty times its birth length, by far the largest increase in length of all vertebrates (Wermuth, 1953), during which its diet changes widely from insects and fish to vertebrate fauna larger than itself.

The crocodile length-groups developed in this study are based on information from Cott’s (1961) growth rate study of Nile crocodiles. The length-groups are modified to accommodate all the subjects under observation (see Table 4.1). Three length classes of crocodiles were observed in this study: 1) three large crocodiles measuring from 2.5 m to 4.8 m in length, 2) about 100 medium-sized crocodiles measuring from about 2 m to 2.4 m in length, and 3) about forty small-sized crocodiles measuring from about 0.9 to 1.8 m in length. Young individuals were not used in this study because they are not known to prey on larger mammals (**Table 4.1**), while very large crocodiles (>5 m) were not available at either farm.

ii) Carcass placements

Before an experiment began, all animals were locked in one side of the *banda* and a few (according to size) were released into the pool area to eat. Usually, once the animals smell meat they congregate near the wall ready to jump for the food. The attendants would toss the carcasses on the ground near the pool as part of the normal feeding regimen. For each feeding episode the condition of the carcass was recorded, including skeletal part, weight, adhering flesh, animal size and age. Usually the Bagamoyo animals were fed between 3–4 pm, while in Engosheraton food was provisioned between 11 am and 2 pm.

Table 4.1. Crocodile length-group and corresponding diet composition (following Cott, 1954, 1961, *contra* Moody & Coreil, 1986). The amount of mammal food intake, and the body size of prey increase with body size and maturity of the reptile. Young crocodiles take mammals of only very small size, and so are excluded from the feeding observations reported here. Very large animals were not available for observation. Larger mammal size groups are as follows: size 1, 5–25 kg; size 2, 25– 100 kg; size 3, 100 – 350 kg; size 4, 350–900 kg (following Bunn, 1982). Table adopted from Njau and Blumenschine (2006).

Length Class	Length (Foot)	(Meter)	Animal Age	Food intake
Young	< 3	< 1	Young	Insects> frogs> spiders (mainly aquatic foods)
Small	3–6	1–1.8	Juvenile	Fish>insects>mollusks>mammals (mammal size 1 only)
Medium	6.5–8	2–2.4	Sub-adult	Fish>mollusks>mammals=insects (mammal size 1 and 2)
Large	8.5–15.5	2.5–4.8	Adult	Mammals> reptiles >fish (mammal size 1- 4)
Very large	>15	> 5	Prime adult	Mammals (mammal size 1- 4)

iii) Observation of crocodile feeding

Once a carcass was tossed on the ground, the reptiles would grab the meat and immediately drag it into water to feed. Observations were conducted from the outside of the *banda* in a place that afforded a good view and minimal disturbance to the crocodiles during feeding. Only one person (author) was making the observations in order to reduce disturbances, although the reptiles seemed not be disturbed by human presence.

Occasionally the farm attendants would toss pieces of meat into the pool in order to disperse the animals fighting over the same carcass. This method helped to reduce severe bite injuries among crocodiles when fighting over the same carcass. For the same reason, the farm attendants recommended that at least two carcasses be provided for each feeding bout. Injuries from biting lead to damage of the animal's precious skin, which is the primary product obtained from crocodiles. In the wild crocodiles have been observed fighting over food, resulting in serious injuries and even deaths among the smaller combatants. This behavior sometimes leads to cannibalism of small individuals by large ones, who are immune from predation.

iv) Observation cessation

Each set of crocodiles was observed for the full duration of feeding, which ended after crocodiles lost interest in disarticulated large pieces that were difficult to ingest or reduce, or after bones were lost in the water and abandoned for more than 24 hours. Observation was not made beyond 7 p.m. so the carcasses that were abandoned in water were collected the following day (24 hrs from the time the feeding trial began). Crocodile feeding strategies were recorded in notebooks, videos and still photos. Usually, crocodiles were fed once after every two to three weeks at both farms, and my observations were planned according to this schedule. Crocodiles have relatively small gullets and stomachs that limit meal size (Grenard, 1991). Also, as ectotherms, wild crocodiles can survive without eating for several months (e.g., Cott, 1961). These characteristics provide some expectations on the amount of food that can be consumed by an individual over a period of time.

v) Retrieving carcass remains from the pool

Carcass residues, including complete and incomplete skeletal remains, were collected from the pools after cessation of each feeding episode. The pools were drained first, and the animals were released into the other room. After shutting the door behind them, the attendant would jump into the dry pool, collect the bones, and put them into a plastic bucket. Articulated and broken skeletal parts were then cleaned and degreased by cooking in simmering solution of water and non-enzymatic laundry detergent ("Foma" brand) for approximately three days (4-6 hours per day), depending on the size and age of the bone. A blunt wooden knife and fingers were used to remove adhering flesh and other soft tissue from the bones. Cleaned bones were dried in the sun for about 45 minutes and later placed in a room to air-dry for longer periods of time before being taken to the laboratory for analysis.

The bones were transported to the paleoanthropology laboratories in Arusha and Olduvai Gorge for preliminary analyses and later shipped to Rutgers University's Zooarchaeology laboratory for complete analysis.

3. Analytical procedures and laboratory methods

The analysis of skeletal remains was carried out in two phases. The first phase consisted of comparison of fresh carcass parts introduced to crocodiles to those recovered after feeding, while the second phase involved the analysis of bone modification after cleaning and preparation.

i) Analysis of skeletal parts introduced and recovered

Observations of live crocodiles feeding on fresh carcasses of cow and goat were recorded on a digital video camera. In addition photographs and written notes were taken. Each feeding episode was given a field number (i.e., 1A, 1B, 2A…) and the following attributes were directly recorded in the field;

1) number and body size of live crocodiles released to feed on a single episode (see Table 4.1),
2) skeletal region of carcass introduced to crocodiles,
3) type and age of animal from which the carcass derived,
4) sequence and process of carcass disarticulation by crocodiles,
5) sequence of ingestion of carcass parts and conspicuous fragmentation of bones,
6) time taken for a whole carcass or skeletal region (i.e., head, trunk) to be ingested whole or partially before being abandoned, and
7) condition of carcass remains recovered after feeding cessation (i.e., degree of disarticulation, breakage, adhered flesh).

While live crocodiles were classified according to length, the animal carcasses were introduced using four major skeletal regions (Table 4.2), which include:

1) head,
2) trunk (neck, ribcage, sacrum and caudal),
3) forelimb (scapula, humerus, radio-ulna, carpals, metacarpal and phalanges), and

4) hind limb (pelvis, femur, tibia, patella, tarsals, metatarsal and phalanges).

In most cases the lower limbs from cows (metapodial and foot) were disarticulated from the upper limbs by butchers as part of their standard practice. The front lower limb, which is comprised of metacarpal and phalanges, is disarticulated from the upper part at the distal carpal – metacarpal joint. The rear lower limb is usually disarticulated at the astragalus – naviculocuboid joint (Table 4.2).

ii) Analysis of bone specimens after recovery

The second phase involved the analysis of skeletal remains retrieved from the pools after being cleaned. The analyses were conducted in the vertebrate paleontology and zooarchaeology laboratories at Arusha Natural History Museum in Tanzania and Rutgers University in the USA, respectively. Each bone specimen was labeled prior to analysis. The label indicated the identification number assigned for each feeding episode. My analysis focused on the patterns of bone modification by crocodiles. The task was accomplished by conducting a thorough investigation of surface bone modification, which included tooth marks and degree of bone completeness. Since crocodiles were not observed in this study to fragment and ravage bones the way mammalian carnivores do, the analysis of tooth marking was further emphasized.

A systematic search for tooth marks was performed with the aim of identifying diagnostic features and patterns of modification produced by crocodiles. Tooth marks were counted to generate data on the incidence of crocodilian tooth marks in bone assemblages (e.g., Blumenschine, 1988; Fiorillo, 1991; Blumenschine & Marean, 1993). All bone elements, including skeletally indeterminate splinters (which were very few) were analyzed for this purpose. The analysis was guided by published criteria of bone modification by mammalian carnivores (e.g., Binford, 1981; Shipman, 1981b; Haynes, 1983a; Blumenschine *et al*., 1996), and my experience on modern bones modified by known large mammalian carnivores.

Following Blumenschine *et al*'s. (1996) procedure, each bone specimen was carefully inspected on the cortical surface under a 100 watt table light. This was first done with the naked eye, and then repeated using a low magnification 16 x hand lens, until all marks had been located and identified. Located marks were examined again individually with a hand lens, in search of micromorphological features distinguishing crocodilian from known mammalian carnivore tooth marks. Only tooth marks that showed measurable penetration of cortical surfaces, and that exhibited internal surface features (i.e., crushing, cross-section) were analyzed and recorded. Morphological features of tooth marks, even the very tiny pinprick-like pits, produced by the tip of small and slender anterior teeth of crocodiles, are clearly visible using this technique.

Inspection of bone surfaces using this low-power macroscopic method has been demonstrated to be sufficient in identifying classes of marks produced by different agents, and has proven reliable in detecting the distinguishing micromorphological characteristics of carnivore tooth marks and butchery marks (e.g., Bunn, 1981, 1883a; 1991; Bunn & Kroll, 1986; Blumenschine *et al*., 1996).

After a specimen was examined carefully, attribute states were coded using a bone coding system, modified from Blumenschine's Zooarchaeological Coding Conventions (see Appendix I), and entered in the Excel spread sheet program. Since only carcasses of cow and goat of known age and size were used in this study, and the fact that most of the skeletal remains were easily identified (because they were complete), diagnosis of crocodilian tooth marks and bone damage was emphasized. For each skeletal part at least 24 attribute were analyzed and recorded in order to generate the following data;

1) Tooth mark morphology (i.e., type, size, shape, cross-section, internal features)
2) Pattern of tooth marks (i.e., count of marks per specimen, location of marks, orientation to long axis of bone, isolated *vs.* cluster of marks),
3) Presence or absence of gross gnawing on bone epiphyses, and
4) Completeness and fragmentation of skeletal elements.

Tooth marks were categorized into four major types (*pit, puncture, score* and *furrow*) as described for mammalian carnivores by Binford (1981). Tooth mark data were stratified by skeletal portion such as proximal end, middle shaft or distal end for limbs, or glenoid end, spinous process and blade for scapula, or iliac blade, ischio-tuberosity and pubic regions for pelvis.

Dimensions of the smallest and largest mark on a bone specimen was recorded by measuring its maximum and minimum breadth for pits and punctures or its maximum length for score or furrow. These measurements were obtained directly from the bone (*cf.* Pickering *et al.*, 2004) by using digital calipers. I also recorded the occurrence of distinctive morphologies of tooth marks resulting from the cusp morphology of the crocodile tooth. Internal morphology and cross-sections of tooth marks were described in order to determine features that are diagnostic of crocodiles, not being produced by mammalian carnivores. The following methods were used to distinguish crocodilian from mammalian carnivore tooth marks:

1) Impressions of upper and lower tooth rows of spotted hyena, bear, leopard and domestic dog were made on silicone rubber (mold) to determine the cusp morphology, shape and internal features produced by incisors, canines, premolars and molars under different bite forces. Similar molds were made for crocodile teeth of varying size, and bite force.
2) I examined Blumenschine's and Capaldo's bone assemblages consumed only by known mammalian carnivores in Serengeti and Ngorongoro Crater (Blumenschine, 1988; Capaldo, 1995) in order to see if mammalian carnivores produce types of tooth marks that are diagnostic to crocodiles.

The shapes of marks (in plan form) were determined using a hand lens. For example, pits and punctures were round or oval, while scores were either linear or curved. Orientation of scores were also described as transverse, oblique or longitudinal to the long axis of the bone.

The basic quantitative unit used for this analysis is NISP, or the number of specimens identified to skeletal part. One bone specimen counts as one NISP (see Grayson, 1979; Klein & Cruz-Uribe, 1984; Lyman, 1994) and each specimen, including skeletally non-identifiable fragments, was included in the NISP tally. Since most of bone specimens in this control sample are complete, the minimum number of elements (MNE) is very high for each assemblage (feeding episode), and the whole assemblage, therefore, exhibits a low rate of fragmentation.

4. Characteristics of the control sample

Feeding trials, crocodiles and carcass profiles

The interaction between crocodiles and larger mammal carcasses was documented systematically through observation of captive Nile crocodiles feeding from carcass parts of cow and goat in a total of nineteen trials. Detailed description for each feeding trial is provided in Appendix II.

Fifteen feeding trials were conducted in Bagamoyo and four in Engosheraton (Table 4.3). Four trials, all involving goat carcasses, are excluded from further analyses because the carcasses were completely consumed by the hungry crocodiles (Trials 1B, 2B, 18 & 19; see Table 4.3). In Trial 2B, a carcass was consumed by large crocodiles without leaving any significant remains behind. In Trial 18, a carcass was introduced to about forty medium-sized crocodiles and was completely consumed. In Trial 19, the number of crocodiles was reduced to 30 medium-sized individuals, who were released to feed on another whole goat carcass. However, like Trial 18, the reptiles were observed to consume the whole carcass. Finally, in Trial 1B, during which twenty small and medium-sized crocodiles were allowed to feed on the complete hind limbs of a goat (pelvis still attached to the rest of the limbs), the pelvis was disarticulated from the limbs, and the limbs were ingested without much difficulty. The pelvis were also consumed separately.

It became obvious that crocodiles (> 2 m in length) can effectively tear apart a goat-sized carcass and consume large portions ripped off from the carcass without generating extensive breakage to bones. Based on this observation, large crocodiles were eliminated from the goat feeding trials. Also, the number of medium-sized crocodiles feeding on goat carcasses was reduced to increase survivorship of skeletal remains.

Three of the feeding trials (Trials 15-19) were initiated in August, 2000, at Bagamoyo and were comprised of complete but isolated elements of cow only (Table 4.3). The rest of the Bagamoyo trials (n=12), which were mostly composed of articulated limbs and whole animals, were conducted from April to June, 2002, and November to December, 2002. Engosheraton feeding trials were conducted in October, 2002, and February to March, 2003. All trials from Engosheraton involved articulated limbs of cow and whole goat carcasses (Table 4.3).

A total of five whole carcasses, twelve complete articulated limbs, four articulated lower limbs, and 23 isolated but complete skeletal elements were introduced to crocodiles (Table 4.3). The whole carcasses came from goat only, and were consumed by crocodiles of different body size. The number of crocodiles used in each feeding episode varied and depended on the carcass size and availability of the reptiles at the farms. The average number of medium-sized crocodiles feeding in an episode was twenty, while the average number of large-sized crocodiles was three (Table 4.3).

Large crocodiles were observed feeding in five trials, three of which involved articulated cow limbs, and one a whole goat (Tables 4.3 & 4.4). Two complete cow heads and one pelvic girdle with a large quantity of meat were introduced to this set of large crocodiles but none were eaten at all or moved from the location they were set (Trial 17). The animals were most likely still sated from the meal they had consumed fourteen days previously.

In many cases the small crocodiles, especially those nearing 1.8 m long, were kept and were fed together with the medium-sized animals. A total of fourteen trials were observed for this size group, including five goat and nine cow carcasses (Tables 4.3 & 4.4).

Skeletal specimens recovered

A total of 191 bone specimens including complete and broken pieces (>2 cm in length) were collected for taphonomic analysis. Most of the skeletal materials were articulated when collected from the pool. However, they were disarticulated during cleaning and bone preparation. Each specimen was treated as 1 NISP, including fragments > 2 cm long. More feeding trials were conducted in Bagamoyo, but fewer specimens (NISP) come from this assemblage than from Engosheraton. Carcass consumption in the former was more complete than in the latter, where carcasses were abandoned without being fully utilized. The Bagamoyo sample contains 90 specimens (MNE=83), whereas the Engosheraton sample contains 101 specimens (MNE=98).

Table 4.2. Skeletal composition of carcasses introduced to crocodiles. With exception of goat, carcasses were restricted to complete limbs only due to regulations of the crocodile farms. Skeletal element names and counts adopted from Sisson (1927), Schmid (1972), Lyman (1994), Capaldo (1995).

Skeletal region	Skeletal elements	N
Cranium (complete)	Include mandibles, tissues and tongue	1
Mandible[1]	Hemi-mandible with tissues but no tongue	2
Trunk (axial)	Cervical	7
	Thoracic	13
	Lumbar	6
	Sacrum (5 segments fused)	1
	Caudal[2]	16
	Rib	26
	Sternum (6 segment fused)	1
	Sub-total	70
Forelimb	Scapula	2
	Humerus	2
Intermediate limb[3]	Radioulna	2
	Carpal	
	scaphoid	2
	lunate	2
	pisiform	2
	cuneiform	2
	magnum	2
	unciform	2
Lower limb[4]	Metacarpal[5]	2
	Phalanx	12
	Sub-total	32
Hind limb	Pelvis	
	innominate	2
	Femur	2
Intermediate limb[3]	Tibia	2
	Patella	2
	Tarsal	
	calcaneum	2
	fibula[6]	2
	astragalus	2
Lower limb[4]	*cuneiform*	4
	naviculocuboid	2
	Metatarsal[5]	2
	Phalanx	12
	Sub-total	34
	Grand total	136

[1] Isolated mandible. *Italics*= elements incorporated.

[2] Tail ends were removed during butchery so only the first four caudal vertebrae were counted.

[3] Radio-ulna and tibia.

[4] Metapodials and phalanges. In addition, cuneiform and naviculocuboid for hind limbs.

[5] Sesamoids not counted because they are small, vestigial elements which usually fuse to the metacarpals and metatarsals in adults.

[6] Technically, the fibula is not a tarsal and were not counted.

Table 4.3. Total number of feeding trials including size and number of live crocodiles per trial, type of carcass introduced and condition of carcass recovered. S=small size crocodile; S-M=medium size (1.8 m crocodiles mixed with medium size, which are sometimes not easy to distinguish); M=medium size; L=large crocodiles. Crocodile size is estimated from body length (see Table 4.1). †Engosheraton Crocodile Farm; ¶Detailed descriptions are provided in Appendix II.

NO	Trial #	Crocodile Size				¶Carcass Parts Introduced		Age/taxa	¶Carcass Parts Collected
		S N	**S-M** N	**M** N	**L** N		N		
1	1A	-	-	20	-	Whole including head	1	Adult goat	Articulated axial skeleton
2	1B	-	20	-	-	Hindlimbs + pelvis	4	Adult goat	None
3	1C	-	10	-	-	Isolated femur	1	Immature cow	Complete bone with loose scraps
4	2A	-	-	-	3	Hindlimb with pelvis, sacrum & 1 lumbar vertebra attached	1	Immature cow	Articulated femur-tarsal bones. Isolated pelvis & vertebra bones
5	2B	-	-	-	3	Whole	1	Adult goat	None
6	3A	-	20	-	-	Forelimb with scapula	1	Adult cow	Isolated scapula Articulated humerus-lower limb
7	3B	-	-	10	-	Lower limbs (metapodial-phalanges)	4	Adult cow	Articulated metatarsal-phalanx
8	4A	-	-	-	3	Forelimb with scapula	1	Adult cow	Isolated scapula Articulated humerus-carpal bones
9	5B	-	20	-	-	Forelimb with scapula	1	Immature cow	Isolated scapula Articulated humerus-carpals
10	6C	-	-	-	3	Hindlimb, missing pelvis & lower limb	1	Adult cow	Articulated femur-tarsal bones
11†	7	-	5	-	-	Forelimb with scapula	1	Immature cow	Isolated scapula Articulated humerus-carpals
12†	11	-	5	-	-	Whole goat missing head	1	Immature goat	Articulated humerus-foot; Articulated rib cage
13†	13	-	5	-	-	Hindlimb with pelvis	1	Immature cow	Isolate pelvis Articulated femur-lower limb
14†	14	-	5	-	-	Hindlimb missing innominate	1	Adult cow	Articulated femur-lower limb
15	15	5	-	-	-	Isolated elements	19	Immature cow	19 complete elements
16	16	5	15	-	-	Same bones as above	-	Same above	9 complete elements
17	17	-	-	-	3	Whole crania with tongue & flesh Pelvis	2 1	Immature cow	Not attended Not attended
18	18	-	-	40	-	Whole missing head	1	Adult goat	None
19	19	-	-	30	-	Whole missing head	1	Adult goat	None
							44		

Table 4.4. Number of feeding trials stratified by carcass type introduced to each crocodile size group.

Carcass Type	Crocodile Length-group	
	Large	Small-Medium
Cow	4	9
Goat	1	5
Total	5	14

CHAPTER 5. FEEDING EXPERIMENTS: RESULTS OF FEEDING TRIALS

This chapter describes the results of crocodile feeding trials on large mammal carcasses. The immediate goal of this study to describe feeding traces produced by crocodiles during carcass utilization and compare them to those of mammalian carnivores. Since most scientific accounts often describe crocodilian feeding behavior from a biological or ecological point of view, this study provides the first detailed descriptions of crocodilian feeding strategies and resulting modifications to uningested bones from a taphonomic perspective.

1. Direct observations from feeding trials

i) Feeding in crocodiles

From a submerged position in the water, crocodiles will lunge at a carcass tossed in the pool, using its massive head to strike. It will grab the nearest part or any part of the carcass convenient for grasping by the anterior teeth, and pull the entire carcass into deeper water. One or more crocodiles will join and hold the carcass under water (between 5 – 30 minutes), while maneuvering for a better positions to strike or dismember the carcass by vigorous shaking, twisting, pulling, battering, and/ or “death-rolling” (e.g., Schmidt, 1944). Although crocodiles employ different ways of dismembering their victims, the death-roll is the most effective technique used, in which the crocodile spins its whole body along the longitudinal axis while anchored by the jaw to a carcass part (e.g. Schmidt, 1944; Attwell, 1959). The death-roll is often performed by one crocodile, or by multiple crocodiles working at opposite ends and spinning in opposite directions, while holding the carcass parts firmly between their jaws.

The largest and probably the most dominant individuals usually have priority of access to the carcass. If the carcass is too large for one individual to manage alone, it will allow other crocodiles to pull and rip off meat from the other end of the carcass, thus providing anchorage for rolling. Subordinate animals usually gather around the carcass once this opportunity arises, each waiting for an opportunity to move in, grab a chunk of flesh, and then retreat to eat its portion and wait for the next opportunity. This behavior facilitates carcass reduction into parts easy to break or ingest. I have observed up to fifteen captive animals surrounding one carcass, while more than forty crocodiles have been observed in the wild fiercely scrambling over large kills (see Attwell, 1959).

Observations made on the different length groups of crocodiles showed that individuals > 1.9 m in length share a common behavior in consuming carcasses. The Nile crocodile has an extremely wide range of mammals in its diet, and an individual begins to take Thomson's gazelle-sized mammals when it reaches at least 2 m in length (see Table 4.1). The small individuals (ca. 1 -1.8 m long) that participated in feeding trials were engaged more often in defleshing, with the larger individuals holding the carcass in place. Larger individuals (>1.9 m) were more actively engaged in disarticulating carcasses than defleshing them. The narrow and flattened snout of small crocodiles is better suited to tear flesh off carcasses compared to the robust and broad snouts of large individuals. The more slender the snout, the faster and more effective are the sideways snaps. Crocodiles, however, do not deflesh carcasses as effectively as mammalian carnivores do. A typical pattern of carcass disarticulation and ingestion is summarized below.

Sequence of disarticulation

1) The entire forelimb is detached from the trunk (shoulder still articulated to the limb).
2) Hind quarters (pelvis articulating to limb) are broken off at the torso between the most caudal lumbar vertebrae and the sacrum.
3) Limbs are detached from the girdles.
4) The entire cranium is detached from the neck by vigorous shaking, pulling or spinning without chewing off the premaxilla portion or extracting the tongue and other soft tissues from the cranium. Usually, the atlas and sometimes the axis and third vertebrae may remained attached to the occipital.
5) Elbow and knee joints are rarely disarticulated. Typically, goat limbs are folded at the elbow or knee joints, and if the crocodile is large enough, the limb will be ingested starting at these joints. Disarticulation is accomplished by battering the bone on the ground and vigorous shaking.
6) Carpal and tarsal joints usually resist disarticulation, with the lower limb remaining attached to the intermediate limb (i.e., radio-ulna, tibia).

Sequence of carcass ingestion

1) A goat carcass (regardless of animal age) is usually ingested whole by large and medium-sized crocodiles after minimal disarticulation, without necessarily defleshing the carcass. Small crocodiles may swallow disarticulated parts such as scapulae. Usually, the girdles are ingested first (by one individual), after being detached from the limbs. The other part of the limb may be battered on the ground, shaken or twisted until the joints (elbow or knee) are weakened and detached. If a

limb is disarticulated in this way, one end of the limb (i.e., upper or intermediate-lower) may be thrown out the pool or even outside the *banda*. If the animal fails to dismember the limb it will attempt to swallow the entire limb. There is no particular sequence of consuming the trunk, although large individuals can tear apart a carcass, and squeeze large parts into their mouths. None of the goat crania were observed to be ingested because they sink to the bottom of the pool after disarticulation. However, the skulls must have been later discovered by crocodiles and ingested whole because none of them were found at the completion of an experiment.

2) Quarters of cows of various age survived complete ingestion by crocodiles of all sizes used in the study. Usually, the girdles are pulled off the limbs during disarticulation attempts but are not swallowed. The upper, intermediate and lower limbs remain articulated despite vigorous defleshing and dismembering attempts. After initial defleshing through ripping large meat mass off bones, the limbs are abandoned after the consumers lose interest. Bone size relative to crocodile size, therefore, is a major determinant of crocodile food ingestion.

In each feeding trial, animals were observed to fight and chase one another for food, each one trying to get hold of a carcass. This behavior occurred even when more than one carcass was available in the pool area. It seems that the tendency of crocodiles to follow the individual that holds food in its mouth is important in facilitating defleshing and dismemberment (e.g., Attwell, 1959). Bones, especially those derived from large kills, pass between several crocodiles prior to ingestion or abandonment, potentially increasing the number of tooth marks on bones.

ii) Carcass utilization and expected bone damage

Crocodile feeding anatomy and techniques do not permit gnawing of epiphyseal ends, dorsal margins of girdles, premaxilla or other cancellous bone portions. However, protruding bones such as the olecranon processes, vertebral processes and the posterior part of the calcaneum can be snapped during defleshing and dismembering. Most often mammalian carnivores preferentially consume soft bone elements and portions (e.g., sternum, ventral thoracic ribs, premaxilla, spongy portions of girdles and long bones), by chewing and crushing in order to obtain within-bone nutrients such as grease, fat and marrow, brain tissue and other nutritious elements such as calcium and phosphate.

A single crocodile can hold a carcass perpendicularly across its jaw's long axis by its strong lateral teeth and vigorously shake or batter the carcass part on a hard surface with a powerful force. This technique may weaken various joints (i.e., elbow and knee) that will accelerate the dismemberment of carcass, or shattering and fracturing bone elements. As predicted in Table 3.1, long bones, ribs and vertebral processes may suffer transverse, step, or parallel breakage from this vigorous beating. The crocodile can then squeeze the carcass into its mouth, and swallow the food whole. The crushed bones that are held together by periosteum tissues and encased within the flesh are swallowed together with the meat (Table 3.1). During this process teeth may penetrate the bones and produce marks of various types and number. If a bone is battered on a sharp rock, crushed notches, spiral fractures and flakes can be produced on the long bone shafts.

Crocodile employ another method of carcass reduction involving tossing the carcass part repeatedly up into the air, catching and mouthing it each time, while delivering severe bites. The forceful biting may result in breaking less durable bones such as distal end of the ribs and vertebral processes. Alternatively, this action may result in the failure to break large long bones, therefore leaving behind complete elements that will not attract further attention from the animals.

Since crocodiles do not utilize or reduce bones through gross gnawing, skeletal parts are either swallowed whole or discarded without extensive fragmentation. Unlike bones attended by large mammalian carnivores, crocodilian food refuse is composed of complete elements that escape ingestion due to size and shape. Crushed bones are usually swallowed together with the flesh they adhere to. Also, crocodiles may avoid fragmenting bone to reduce injury by sharp or pointed fracture edges (Coulson, 1970, cited in Fisher, 1981a), although such caution is not apparent during voracious feeding.

Typically, the ingested bones are completely dissolved by the strong stomach acid of crocodiles. As a result, feces with high concentrations of calcium phosphate and carbonates are excreted (Coulson *et al*., 1950; Coulson & Hernandez, 1964). Usually, mammalian carnivore feces contain macroscopic bone fragments. Fisher (1981a, 1981b) reports that with the exception of teeth, bones of prey are demineralized completely, leaving only fragile organic matrices in the feces. Previously, Weigelt (1927, p. 92) had suggested that alligator feces are free of bone because it is regurgitated. However, Fisher's (1981a) observation show that crocodilians regurgitate hairballs devoid of bone.

2. Quantifying bone modification by crocodiles

The reptiles were observed to abandon all introduced bones after consumption of flesh in about 58% of the feeding episodes. Both large and medium-sized crocodiles were unable to ingest large articulated limb quarters of cow, but were able to deflesh major muscle masses and disarticulate girdles from the limbs (Trial 1C, 2A, 3A, 4A, 5B, 6C, 7, 13, 14, 15 and 17; Table 4.3).

Crocodiles were also observed to consume entire carcasses without leaving behind significant bone remains for study in about 21% of the feeding trials. Complete consumptions involved goat carcasses that were provisioned whole or as articulated limbs to crocodiles (Trial 1B, 2B, 18 and 19; Table 4.3). On only two occasions were the hindlimbs broken at the knee joints before each part of the limb was ingested whole by two medium-sized crocodiles (Trial 1B; see full descriptions in Appendix II).

Approximately 21% of the feeding trials contain remains of carcasses that were partially consumed by medium-size crocodiles, two of which involved goat and two of which involved cow. In one of the episodes (Trial 1A), all limbs, the head and cranial portion of the ribcage were torn from the trunk and swallowed, leaving behind the middle portion of the torso unutilized (Table 4.3). Although few ribs were snapped on the ventral ends, ribs were often attached to the articulated vertebral column when recovered from the pool.

i) Carcass part profiles and consumption

The sample included 5 whole goat carcasses, 12 articulated limbs from goat and cow, 4 articulated lower limbs from cow, and 23 isolated elements from cow. Only 24 carcasses (54.5% of the carcasses introduced) were recovered from the pools in various conditions of completeness and destruction after cessation of feeding trials (Figure 5.1; Table 5.1). Among the whole goat carcasses introduced to small-medium sized crocodiles, 50% were completely consumed, and 50% partially consumed (Figure 5.2; Table 5.1).

Articulated quarters of cow limbs endure crocodile destruction, with none of the eight limbs provisioned to crocodiles having been completely ingested (Figure 5.2). About 75% of the cow limbs were disarticulated at the scapula-humeral joint (n=5) or femoral-acetabular joint (n=1). Innominates from two of the cow hindlimbs were missing from butchery (Trial 6C and 14). The articulated limbs of goats, however, were ingested whole by small-medium-sized crocodile. Therefore, this skeletal region was not provisioned to large crocodiles (Figure 5.2). The lower limbs from cows were provisioned only to small-medium size crocodiles because large crocodiles could easily swallow these skeletal segments.

ii) Bone specimens recovered after crocodile feeding

With the exception of approximately ten pieces that were snapped by crocodiles during feeding, most of the recovered bones were complete and all cow bones were still articulated when retrieved from the pool, making the NISP/MNE values close to 1 (Table 5.1). The meatier bone elements such as girdles, femora, and humeri, and proximal portions of radio-ulna and tibia had substantial amounts of loose scraps hanging from the bones as a results of defleshing through ripping. The Bagamoyo assemblage is made up a total of 90 bone specimens (NISP value, MNE=83), whereas 101 bone specimens (MNE=98) come from Engosheraton (Table 5.1).

Table 5.1. Carcass remains collected after feeding and number of bones (after preparation). Bone specimens are reported as NISP and MNE values and NISP/MNE ratios.

Feeding Trial	Carcass taxa and part retrieved from the pool after crocodile feeding	NISP	MNE	NISP/MNE
BAGAMOYO				
1A	Adult goat: Articulated part of ribcage (2 thoracic spine fragments)	20	18	1.1
1C	Sub-adult cow: Complete femur; loose scraps	1	1	1
2A	Sub-adult cow: Isolated innominate, Articulated femur to tarsal bones, Articulated sacrum & lumbar (2 lumbar vertebra fragments)	10	8	1.2
3A	Adult cow: Isolated scapula, Articulated humerus to lower limb	16	16	1
3B	Adult cow: Articulated metatarsal-phalanx	4	4	1
4A	Adult cow: Isolated scapula, Articulated humerus to carpals (1 scapula & 2 ulna fragments)	12	9	1.3
5B	Sub-adult cow: Isolated scapula, Articulated humerus to carpals	10	10	1
6C	Adult cow: Articulated femur to tarsal bones	5	5	1
15 & 16	Sub-adult cow: Metacarpal (n=1), scapula, mandible	9	9	1
17	Sub-adult cow: Crania (not attended)	2	2	1
	Sub-adult cow: Pelvic girdle (not attended)	1	1	1
Sub total		90	83	1.08
ENGOSHERATON				
7	Sub-adult cow: Isolated scapula, Articulated humerus to carpals (1 scapula fragment)	15	14	1.07
11	Sub-adult goat: Articulated humerus to lower limb; Articulated rib cage (2 rib midshaft fragments)	57	55	1.03
13	Sub-adult cow: Isolate innominate, Articulated femur to lower limb	15	15	1
14	Adult cow: Articulated femur to lower limb	14	14	1
Sub total		101	98	1.03
Grand total		191	181	1.05

3. Surface bone modification

Comprehensive search for tooth marks was conducted on all 191 bone specimens from fourteen feeding trials. Specimens from four feeding trials are not included in this analysis (Trial 1B, 2B, 18 & 19) because the carcasses were completely consumed. The remains from Trial 16 & 17 are combined because the same skeletal parts were used in both trials (see Methods section). The quantitative and qualitative analyses of tooth marks include frequencies, size, shape, density, internal morphology and orientation. The results are compared with the published mammalian carnivore tooth mark data in order to determine differences, between the two groups of carnivores in modifying bones (see Appendix III).

i) Incidence of tooth-marked bone specimens

Unlike mammalian carnivores, crocodiles produced tooth marks on relatively few specimens in the bone assemblages. About 21% of all bone specimens attended by crocodiles bore at least one tooth mark (Table 5.2). This means that majority of uningested bone elements left no bite traces. By contrast, in assemblages of skeletally diverse parts consumed by mammalian carnivores, the majority of surviving bone specimens (42%-63.7%) are tooth marked (Capaldo, 1995).

Long bones are the most frequently tooth-marked skeletal group by both crocodiles (ca. 69%) (Table 5.3, Figure 5.3) and mammalian carnivores [ca 82% (Blumenschine, 1988)]. Humeri are the most tooth marked long bone elements by crocodiles, followed by radio-ulna, metapodials and femurs, and tibia. While girdles are moderately tooth marked by both carnivore groups, postcranial axial parts survive crocodilian destruction usually without marking. Only 3% of the axial specimens in my assemblages are tooth marked, contrary to 42% in mammalian carnivore assemblages reported by Capaldo (1995) (Table 5.2).

A high proportion of tooth-marked long bone and girdle specimens is a result of carcass reduction and defleshing as predicted in Table 3.1. Mammalian carnivores purposely gnaw and break bones in order to access marrow, grease, brain tissue and micro-nutrients, and in the process they produce tooth marks on long bones and girdles more frequently than other skeletal groups.

Compact bones, comprised of podials (carpal and tarsal) and phalanges (Capaldo, 1995), are infrequently tooth marked by crocodiles. Only ten specimens out of 74, or 13.5%, are tooth marked (Table 5.2). Among the compact bones, the calcaneum is the most tooth-marked element by crocodiles (Table 5.3, Figure 5.3). The calcaneum, which articulates postero-medially to the distal tibia are tooth marked as frequently as the distal tibia (50%). Calcaneum and distal tibia are probably damaged simultaneously during grasping of the lower limb. The cuneiform (lateral carpal bone), magnum and unciform are among the podial bones that were tooth marked, although rarely. The marks on these elements, however, occur in isolation. Among the phalanges, only the proximal and intermediate elements bore bite marks. The distal phalanges lack tooth marks because they are well protected by hooves.

Generally, the most tooth-marked groups of skeletons include upper limbs (humerus and femur, 80%), intermediate limbs (radio-ulna and tibia, 62.5%), lower limbs (metapodial, 60%), and girdles (scapula and pelvis, 46.7%) (Figure 5.4). Axial and compact bones (podials and phalanges) were infrequently tooth-marked (13.5%).

Table 5.2. Incidence of tooth-marked specimens (NISP with at least one tooth mark) Among skeletal groups for the captive Nile crocodile control sample and for mammalian carnivores. Data for mammalian carnivores are assemblage means from Capaldo's (1995, Table 6.11) "whole bone to carnivore" sample, which reflects modification mainly by spotted hyenas. Compact bones include, podials (carpals and tarsals) and phalanges.

	Crocodile NISP with Marks			Mammalian carnivore Tooth Mark Percent	
Skeletal Group	Total NISP	n	%	Mean	S.D.
Cranial	5	0	0.0	60.0	40.0
Postcranial Axial	66	2	3.0	42.0	29.4
Girdle	14	6	42.9	53.5	47.1
Long Bone	32	22	68.8	63.7	25.9
Compact Bone	74	10	13.5	-	-
Total	191	40	20.9		

Table 5.3. Incidence of tooth-marked specimens (NISP with at least one tooth mark) by skeletal part produced by crocodiles in 14 feeding episodes.

Skeletal Element	Total NISP	NISP with Marks only	
	n	n	%
Cranial	5	0	0.0
Postcranial axial (trunk)	66	2	3.0
Scapula	11	5	45.5
Humerus	5	5	100.0
Radio-ulna	12	8	66.7
Pelvis	4	2	50.0
Femur	5	3	60.0
Tibia	4	2	50.0
Metapodial	5	3	60.0
Calcaneum[*]	4	2	50.0
Podials	42	4	9.5
Phalanges	28	4	14.3
Total	191	40	20.9

[*] Calcaneum is excluded from podial bones, which include carpals and tarsals.

Figure 5.1. Number of goat and cow carcasses introduced vs. those recovered at least partially after feeding by crocodiles, stratified by completeness of carcass.

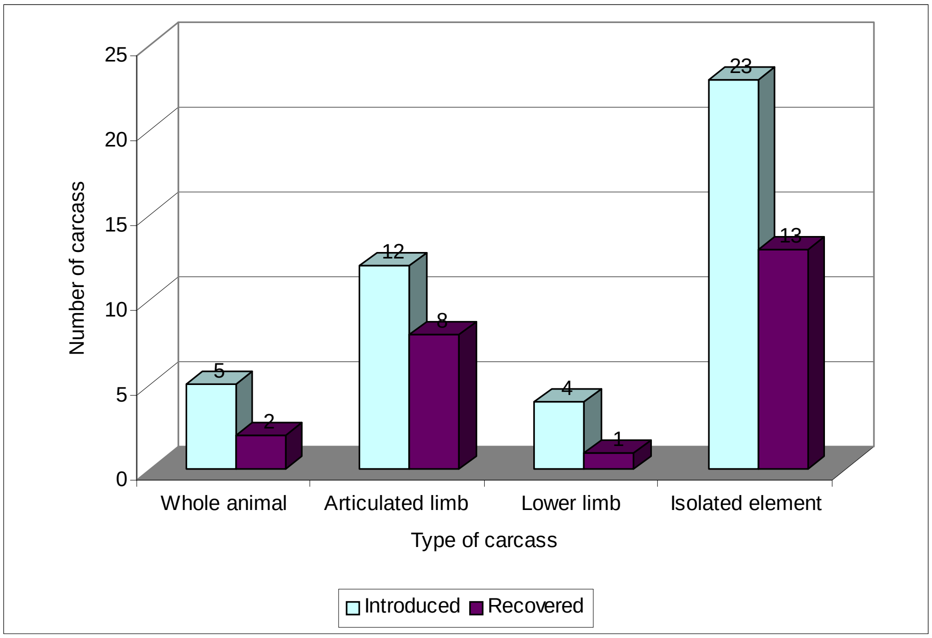


Figure 5.2. Percent of animal carcasses ingested by small-medium and large crocodiles. Goat limbs, cow lower limbs, and other isolated elements were swallowed whole by large Crocodiles. Therefore these skeletal units were not provisioned to large crocodiles. Limb quarters of cow survived complete ingestion by both groups of crocodiles.

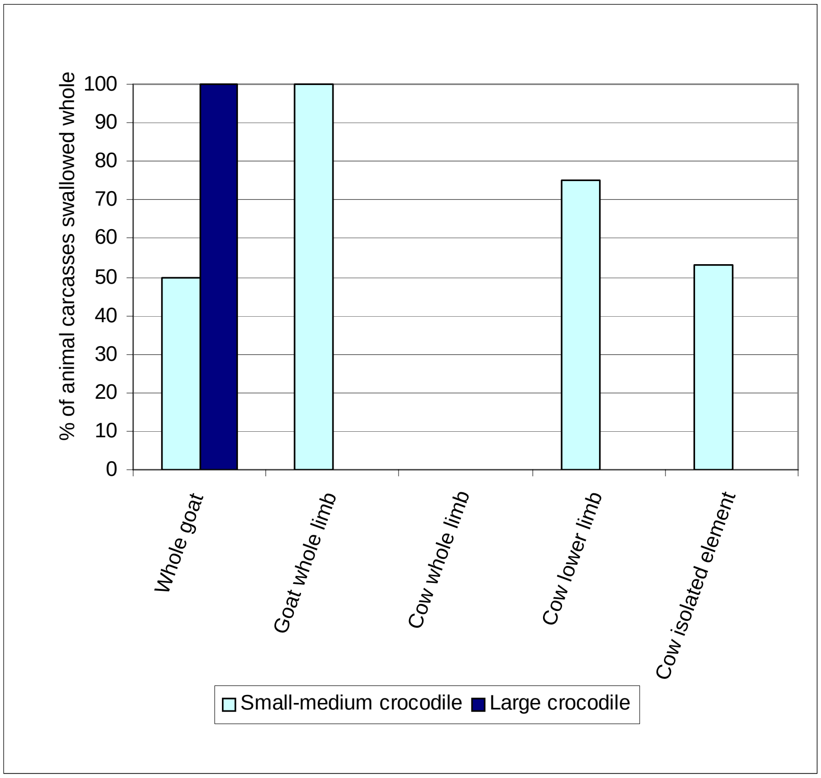


Figure 5.3. Incidence of uningested (surviving) skeletal elements (NISP) bearing at least one tooth mark (data from Table 5.3).

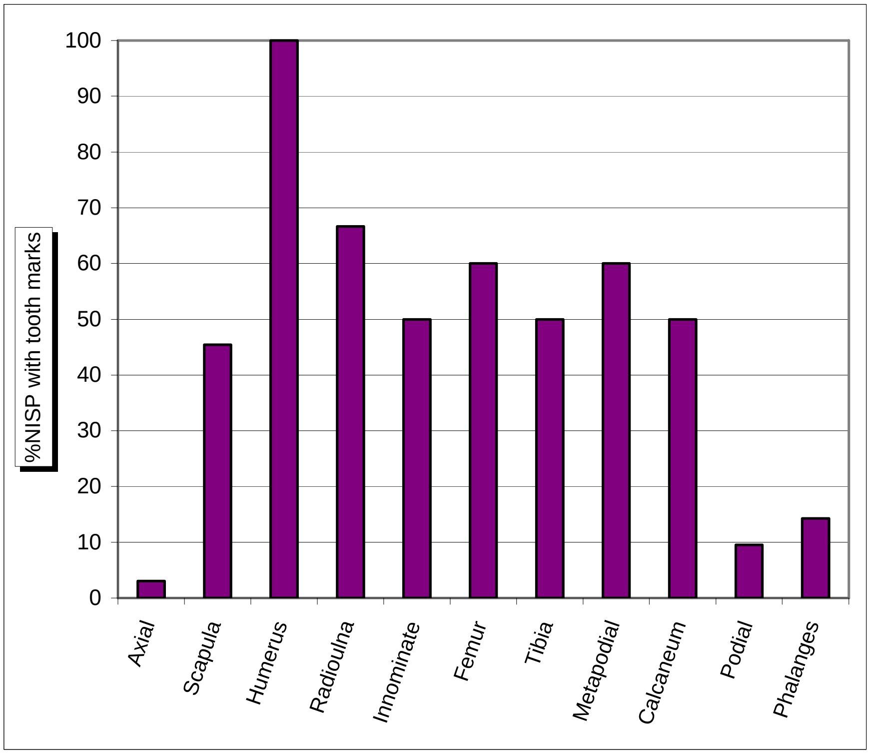
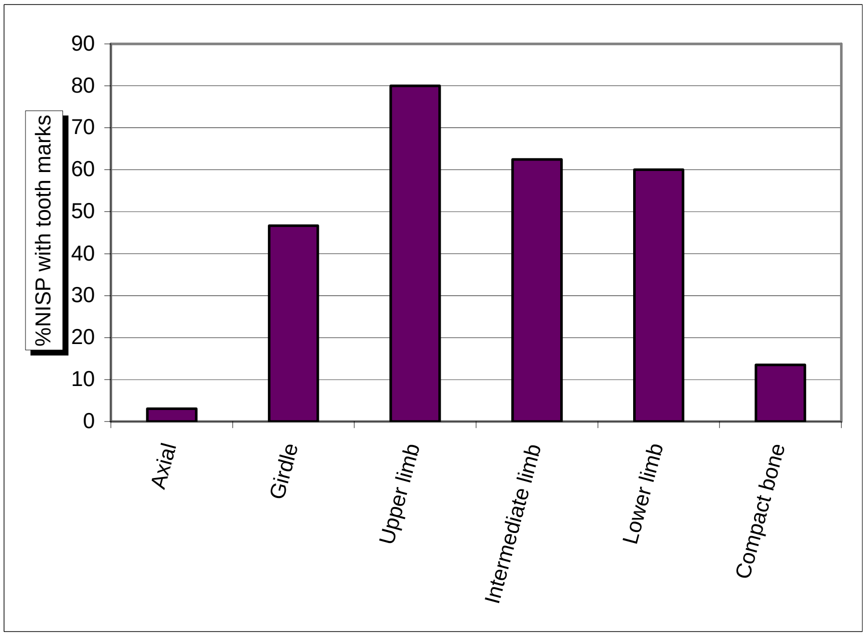


Figure 5.4. Incidence of specimens (NISP) by skeletal groups bearing crocodile tooth marks. Girdle= scapula & pelvis; Upper limb= humerus & femur; Intermediate limb= radio-ulna & tibia; Lower limb= metapodial; Compact= carpals, tarsals, & phalanges (data from Table 5.3).



ii. The impact of crocodile body size

The diet of crocodiles is largely determined by age and size of the reptile. Crocodiles increase the amount of large mammals in their diet as they gain weight and attain larger body size (Cott, 1954, 1961; Pooley, 1989; Alderton, 1991). When crocodiles reach about two meters long they begin to include small and young vertebrates in their diets. The larger they grow the more effective they become in procuring larger prey and ingesting large carcass parts of their prey. Many of large specimens, which are difficult to ingest, are likely to bear tooth marks when abandoned.

Tooth mark data from the control sample shows that small- and medium-sized crocodiles produce tooth marks on very few goat bones (3.5%) and about 32%-34% on bones of mature and immature cow (Table 5.4, Figure 5.5). Usually, large crocodiles swallow goat skeletons whole, so any punctured and crushed bones are swallowed together with flesh. The bones of immature cow are the most affected by large crocodiles, with 46.1% of these bones bearing at least one tooth mark. Bones of mature cow endure forceful bites from large crocodiles, and only 23.5% bear tooth marks. Forceful bites on robust bones may cause premature dislodging of resorbed teeth so this action may be avoided.

While scapulae, humeri, radio-ulnae, metapodials, compact bones, and phalanges are preferentially tooth-marked by small- to medium-sized crocodiles, large crocodiles display a more or less constant pattern of skeletal element modification (Figure 5.6). With the exception of the calcaneum, podials, phalanges and metapodials escaped tooth markings from large crocodiles (Table 5.5, Figure 5.6). The only skeletal region on which large crocodiles inflict more marks than small-medium crocodiles is the trunk region of the cow (Figure 5.6). This behavior can be attributed to the large gape of large crocodiles. The trunk portions of prey skeleton were modeled to bear tooth-damage of crocodiles during defleshing (Table 3.1).

A high proportion of tooth marked upper limbs indicate disarticulation and defleshing activities, while tooth marking on the intermediate and lower limbs reflects disarticulation and breaking attempts (see Figure 5.4). Also, the relatively longirostrine snout of small crocodiles allows this group to rip meat off the bones more effectively than large crocodiles [therefore producing tooth marks on a large number of meatier skeletons such as scapula, humerus and proximal portions of radio-ulna (see Figure 5.6)].

Disarticulation of humerus from scapula or femur from pelvis produces abundant tooth marks on these elements and their articulating lower limbs (radius, tibia, metapodial). In an attempt to detach upper limbs from lower limbs, crocodiles produce tooth marks on metapodials. Pelvic girdles and scapulae provide convenient grasping sites for pulling on the proximal ends of the limbs, whereas radio-ulna, tibiae, and metapodials as well as podials and phalanges provide grasping sites on the distal ends of the limb.

Table 5.4. Proportion of tooth-marked specimens (NISP) stratified by animal size and age, modified by two length-groups of crocodiles. TM= tooth-marked specimen.

Animal Size & Age	Small-Medium Crocodile			Large Crocodile		
	Total n	TM n	TM %	Total n	TM n	TM %
Cow sub-adult	50	17	34.0	13	6	46.1
Cow adult	34	11	32.3	17	4	23.5
Goat sub-adult	57	2	3.5	-	-	-
Goat adult	20	0	0	-	-	-
Total	161	30	18.6	30	10	33.3

Table 5.5. Tooth-marked bones produced by crocodiles on skeletal elements (NISP).

Skeletal element	NISP Tooth-Marked Bones	
	Small-Medium crocodile	Large crocodile
	n	n
Postcranial axial (trunk)	0	2
Podials	4	0
Calcaneum[*]	1	1
Phalanges	4	0
Pelvis	1	1
Scapula	4	1
Femur	2	1
Humerus	4	1
Radio-ulna	6	2
Tibia	1	1
Metapodial	3	0
Total	30	10

[*] Calcaneum is excluded from podial bones

Figure 5.5. Incidence of surviving bone specimens of cow and goat bearing tooth marks after feeding by small-medium and large crocodiles. Goat carcasses were ingested whole by large crocodiles, so no specimens were recovered after feeding. None of the surviving adult-goat specimens fed by small-medium crocodile bears tooth marks (data from Table 5.4).

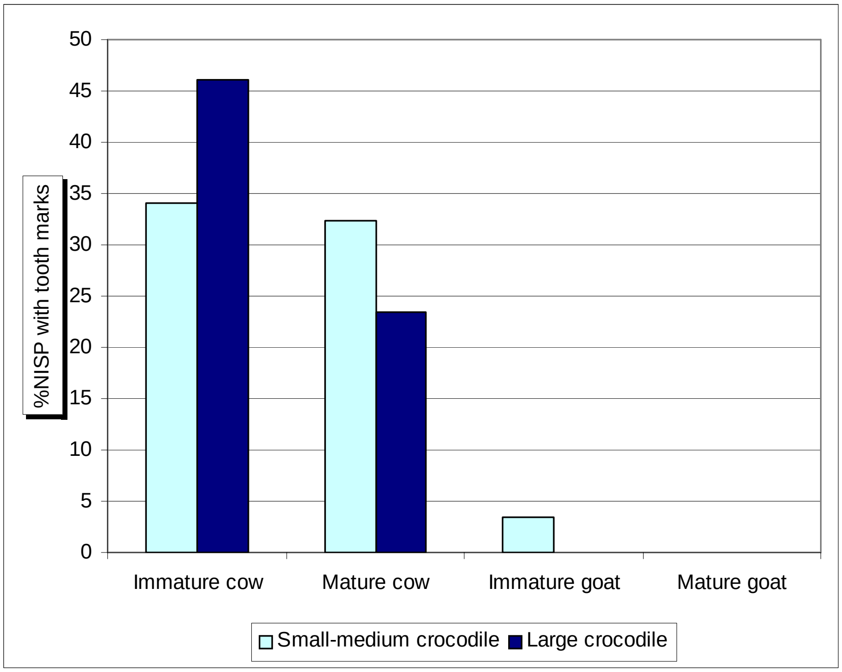
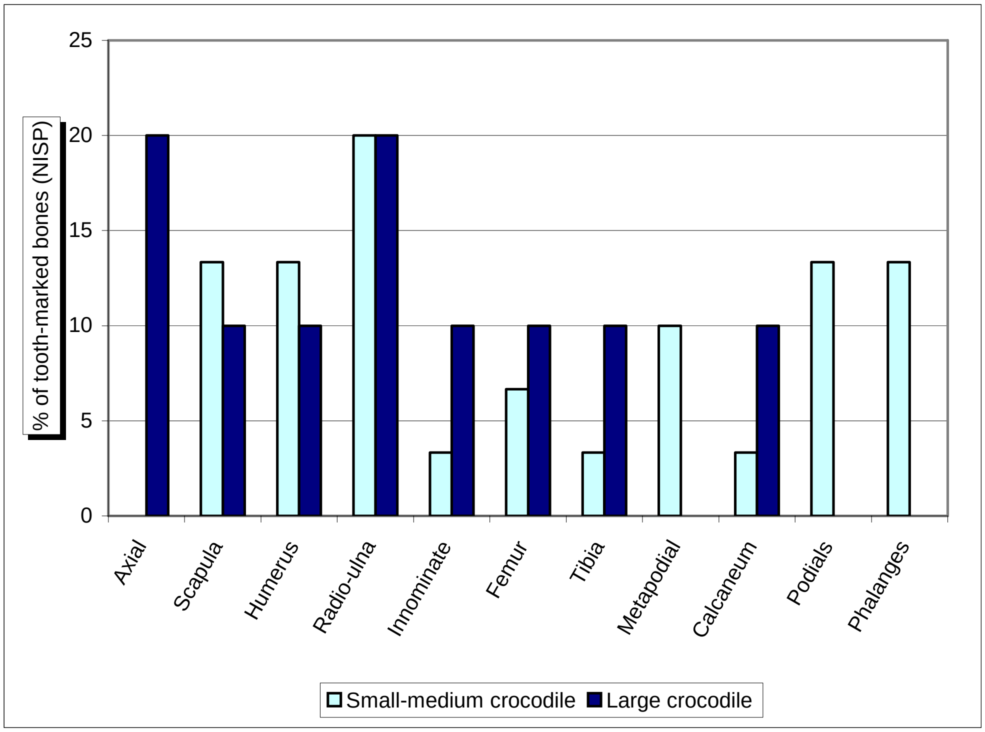


Figure 5.6. Proportion of tooth-marked elements (NISP) produced by small-medium and large crocodiles (data from Table 5.5).



iii. Frequency of tooth marks on bone specimens

Individual tooth marks were counted for each bone specimen that bore at least one tooth mark. Although the incidence of tooth-marked bones in the assemblage produced by crocodiles is low (< 21%), most bone specimens bitten by crocodiles contain a relatively high number of individual tooth marks per bone specimen.

A total of 2,029 individual tooth marks were counted on the forty tooth-marked bone specimens (Table 5.6). Among tooth marked bones, the lower limbs as a group contain the highest density of individual marks per specimen, followed by upper limbs, girdles and intermediate limbs (Figures 5.7a & 5.7b). Some of the individual elements were observed to contain a high concentration of marks, some overlapping each other. The marks are typically distributed over the entire bone surface, although marks tend to concentrate at the grasping sites such as proximal or distal ends of the limb.

Table 5.6. Total number of individual tooth marks counted on each bone specimens (NISP).

Skeletal Part Element	Tooth-Marked Specimens	Number of individual tooth marks				
		Total	Small-Medium		Large	
	NISP	n	NISP	n	NISP	n
Postcranial axial (trunk)	2	11	0	-	2	11
Podials	4	22	4	22	0	-
Calcaneum[*]	2	60	1	31	1	29
Phalanges	4	25	4	25	0	-
Pelvis	2	29	1	16	1	13
Scapula	5	475	4	406	1	69
Femur	3	335	2	235	1	100
Humerus	5	281	4	152	1	129
Radio-ulna	8	388	6	311	2	77
Tibia	2	97	1	7	1	90
Metapodial	3	306	3	306	0	-
Total	40	2,029	30	1,511	10	518

[*] Calcaneum is excluded from podial bones

Figure 5.7a. Average number of individual tooth marks per surviving bone specimen, stratified by skeletal elements (data from Table 5.6).

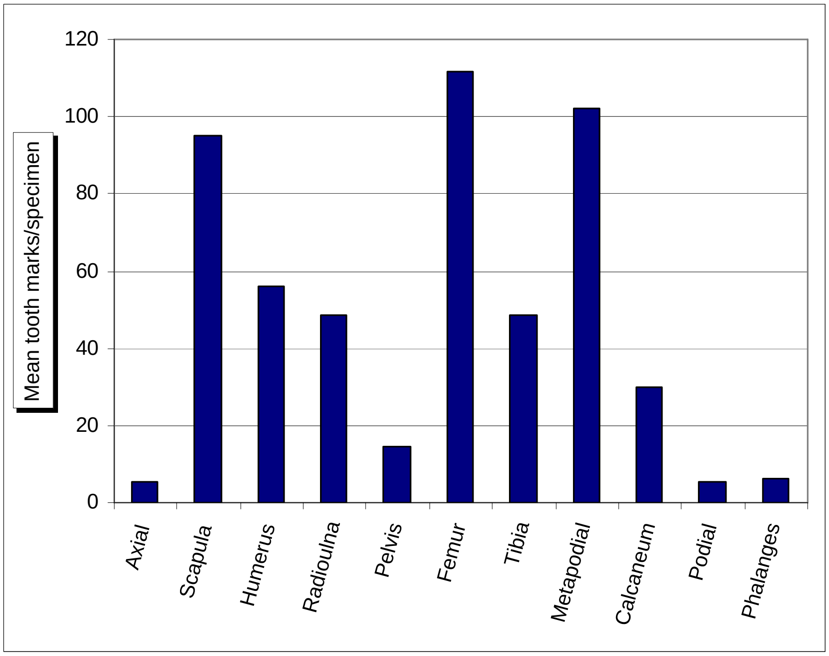
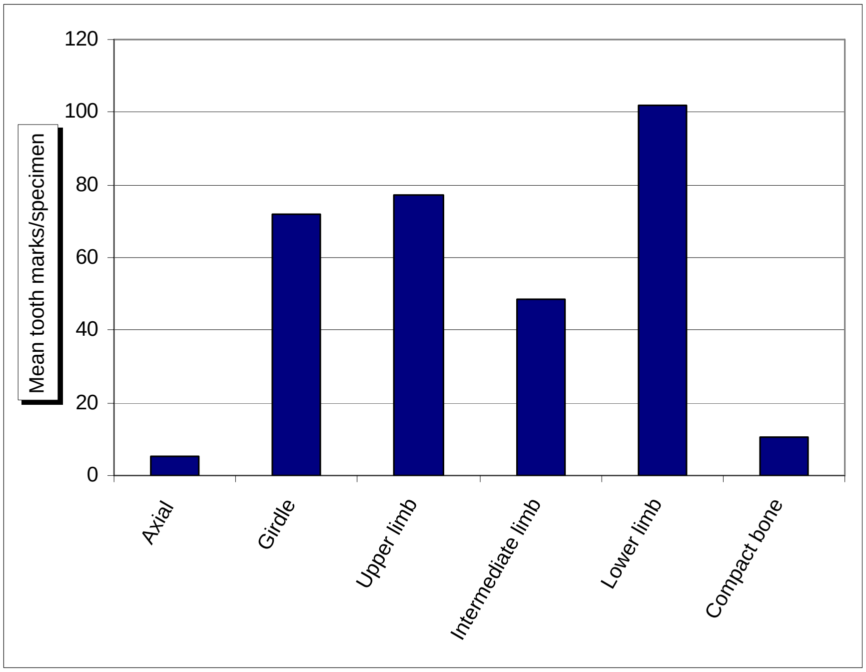


Figure 5.7b. Average number of individual tooth marks per surviving bone specimen, stratified by skeletal groups. Girdle= scapula & pelvis; Upper limb= humerus & femur; Intermediate limb= radio-ulna & tibia; Lower limb= metapodial; Compact bone= carpals, tarsals, & phalanges (data from Table 5.6).



4. Tooth mark morphology

The descriptive morphology of tooth marks provides information on the type of tooth or cusp that produced the marks, and the nature of contact between the tooth and bone surface. Physical variables such as plan form, cross-section and internal features, which are used to describe the morphology of a tooth mark, can be used to distinguish various classes of peri-mortem and post-mortem bone surface modification such as stone knife cut-marking, hammerstone percussion-marking, rodent gnawing, trampling, chemical corrosion (e.g., root-marking), and the exfoliation that accompanies subaerial weathering. Mammalian carnivores produce four major classes of tooth marks on bone surfaces generally known as pits, punctures, scores and furrows (e.g., Maguire *et al.*, 1980; Binford, 1981; Shipman, 1981b). Following this classification system, crocodiles generally produce pits, punctures and scores, which are described below:

1) Pits, which are depressions made on cortical bone, are circular to oval in plan, and bowl-shaped to irregular in cross-section. Depending on the force of the bite, pit depth may range from shallow to deep. Occasionally, a pit may have a short tail (score) emanating from its margin. Some pits are partly or wholly bisected by a sharp linear depression that can exceed the diameter of the pit, showing a V-shaped cross-section across the bisector. This feature is termed “bisected pit” and is not observed in mammalian carnivore tooth markings (Njau & Blumenschine, 2006). The bisected depressions may extend across the whole mark when produced by an unworn tooth that retains the carinae on the apex of the tooth crown, or they may extend in one direction, depending on the angle of the tooth when it contacted the bone. Sometimes the bisected pit may be incomplete, forming a “semi-oval” or “half-bisected pit” shape in plan form.

2) Punctures, which are generally deep and larger than pits, are punctate depressions into trabecular bone. They are circular to oval in plan form and bowl-shaped to irregular in cross-section. Like pits, punctures can also be bisected. A puncture that penetrates thick cortical bone may completely remove the bisected internal mark surface, but there typically remains one or two sharp to rounded triangular projections, formed by the carinae of the tooth, which may extend beyond the puncture's circumference on one or two opposing sides of the puncture (Njau & Blumenschine, 2006).

3) Scores are linear depressions formed into thick cortical bone, resulting from teeth being dragged across the bone surface. The depth of the scores depends on the nature of tooth-bone contact, and/ or the force exerted into bone. Crocodiles produce both shallow and deep scores on the same bone specimen. The length of a score is typically at least twice its breadth, and sometimes may emanate from a well-defined pit. Also, scores may contain one or more internal striae from a chipped tooth crown. Score are U-shaped in cross-section, although in some cases a V-shaped or flat-bottomed cross-section may occur. Scores are parallel and rarely curved in plan form. However, some scores are partially to fully parabolic in plan form, curving between 90° and 180°. This type of score, which has not been observed in mammalian carnivores, is termed a "hook-score" (Njau & Blumenschine, 2006). Some linear scores are basically an elongated pit with a sharp and deep incision extending on one side as a result of "puncture and pull" (*cf.* Erickson & Olson, 1996) by a sharp tooth. These scores are V-shaped in cross-section, and some may be widened, but still the breadth remains less than half of the length.

Virtually all tooth-marked bone specimens (95%) bear pits and scores, whereas only 35% of the specimens have punctures (Table 5.7). Both pelvic bones are punctured, while femora, scapulae, humeri and radio-ulnae are punctured at various rates ranging from 50% to 66.7%. None of the axial, podial, tibia or metapodial bones have puncture marks.

Overall, morphology of crocodile tooth marks is similar to that of mammalian carnivores. Tooth marks of both crocodile and mammalian carnivore exhibit internal surface crushing which is not observed in other classes of bone surface modification such as rodent gnawing, cut-marks, root etching or trample marks. However, due to their differences in masticatory apparatus, crocodiles produce marks with some distinctive features (i.e., bisected marks), which are not observed in mammalian carnivores (Njau & Blumenschine, 2006; see Appendix III).

Table 5.7. Number of tooth-marked specimens (NISP) that bears pits, punctures and/or scores.

Skeletal Part	Pits	Punctures	Scores
	n	n	n
Postcranial axial	2	0	2
Calcaneum*	2	0	2
Podials	4	0	2
Femur	3	2	3
Humerus	5	3	5
Pelvis	2	2	2
Metapodial	3	0	3
Phalanges	3	0	4
Radio-ulna	8	4	8
Scapula	4	3	5
Tibia	2	0	2
Total	38	14	38
Total number of tooth-marked specimens =40			

*Calcaneum is excluded from podial bones

Bisected marks

The occurrences of bisected marks on bone surfaces is typically rare, and usually occur as isolated marks among pits and punctures on bone surfaces. Bisected marks occurred on 33 out of 191 bone specimens analyzed (17%) (Table 5.3 and 5.8). Out of forty bone specimens that bear at least one tooth mark, 33 of them, or 82.5%, bear at least one bisected mark, 27.3% (n=9) of which were made by large crocodiles, while 72.7% (n=24) were made by small-size crocodiles (Table 5.8). Since bisected marks occur on all skeletal elements, there is a good chance that crocodiles may produce this diagnostic feature in 8 out of 10 tooth-marked bone specimens, the being made by small-medium crocodiles due to their sharp, slender teeth.

The number of individual bisected marks are relatively low in comparison to regular marks. Out of a total of 2,029 individual tooth marks produced on 40 bone specimens, only 205 (10.1%) are bisected (Table 5.9). Small-medium size crocodiles produce bisected marks more frequently (7.2%) than large crocodiles (2.9%). These results suggest that the majority of crocodile tooth marks (ca. 90%) cannot be distinguished from mammalian carnivore tooth marks.

Some of the skeletal parts, which are less frequently tooth marked and usually bear few tooth marks, have the highest percent of bisected marks. These include phalanges (28%) and calcanei (25%) (Table 5.9). The pelvis is the only skeletal part that is well tooth-marked [ca. 50% (Table 5.3)] and bears a relatively high percent of bisected pits and punctures (Table 5.9). Radio-ulnae and tibiae account for 11% of bisected pits, and the proportion of bisected marks in other skeletal elements such as scapulae, metapodials and axial vertebrae range from 9.1% to 9.9%. Humeri and femora, which are the most tooth marked elements, bear the lowest proportion of bisected marks (6.4% and 6.9%, respectively).

At least two factors may explain the under-representation of bisected marks in humeri, femora, radio-ulna, tibia and scapula, the most tooth-marked elements: 1) the meatiest portions of skeletons act as a buffer between bone and the short, newly erupted teeth; and 2) bisected marks are produced opportunistically by sharp slender teeth when a crocodile holds a carcass firmly between its jaws prior to ingestion. The over-representation of bisected marks on phalanges and compact bones may be a result of these bones being bitten by small-size crocodiles.

Among the bisected marks, pits and punctures account for 68.3%, while deep scores emanating from well defined pits account for 31.7% of the total number (Table 5.10; Figure 5.8).

Hook-scores

Although hook-scores are rarely observed in the bone assemblages, they are important features diagnostic to crocodile tooth marking. Only 28% (n=11) of all tooth marked bones have at least one hook-score (Table 5.11). This feature is well represented in skeletal regions such as girdles and upper and lower limbs (Figure 5.9), where the reptile holds firmly prior to dismembering the carcass, typically by rolling.

Table 5.8. Incidence of tooth-marked bones (NISP values) with bisected pits, bisected punctures and/ or bisected scores.

Skeletal Element	NISP with Marks only		Bisected Marks	
	n	%	n	%

Postcranial axial (trunk)	2	3.0	1	50.0
Scapula	5	45.5	4	80.0
Humerus	5	100.0	4	80.0
Radio-ulna	8	66.7	8	100.0
Pelvis	2	50.0	2	100.0
Femur	3	60.0	3	100.0
Tibia	2	50.0	1	50.0
Metapodial	3	60.0	2	66.7
Calcaneum	2	50.0	2	100.0
Podials	4	9.5	3	75.0
Phalanges	4	14.3	3	75.0
Total	40	20.9	33	82.5

Table 5.9. Sum of individual bisected tooth marks produced by small-medium and large-sized crocodiles on different skeletal parts.

Skeletal Element	Sum of Bisected Marks Only					Sum of All Marks	Bisected Only
	Large		Small-Medium		Total		
	N	%	N	%	N	N	%
Postcranial axial	1	9.1	0	0.0	1	11	9.1
Scapula	11	2.3	36	7.6	47	475	9.9
Humerus	7	2.5	11	3.9	18	281	6.4
Radio-ulna	5	1.3	39	10.1	44	388	11.3
Pelvis	2	6.9	5	17.2	7	29	24.1
Femur	12	3.6	11	3.3	23	335	6.9
Tibia	11	11.3	0	0.0	11	97	11.3
Metapodial	0	0.0	29	9.5	29	306	9.5
Calcaneum	10	16.7	5	8.3	15	60	25.0
Podials	0	0.0	3	13.6	3	22	13.6
Phalanges	0	0.0	7	28.0	7	25	28.0
Total	59	2.9	146	7.2	205	2,029	10.1

Table 5.10. Proportion of bisected pits/ punctures and bisected scores among bisected marks only.

Skeletal Part	Sum of Bisected Marks Only	Bisected Pits & Punctures	Bisected Scores

	n	n	%	n	%
Postcranial axial	1	0	0.0	1	100
Scapula	47	30	63.8	17	36.2
Humerus	18	11	61.1	7	38.9
Radio-ulna	44	29	65.9	15	34.1
Pelvis	7	7	100.0	0	0
Femur	23	14	60.9	9	39.1
Tibia	11	8	72.7	3	27.3
Metapodial	29	22	75.9	7	24.1
Calcaneum	15	10	66.7	5	33.3
Compact Bones	3	3	100.0	0	0
Phalanges	7	6	85.7	1	14.3
Total	205	140	68.3	65	31.7

Table 5.11. Incidence of tooth-marked bone specimens with at least one "hook-score".

Skeletal element	NISP with Marks	NISP with Hook Score	
	n	n	%
Postcranial axial	2	0	0
Calcaneum	2	0	0
Compact Bone	4	0	0
Femur	3	2	67
Humerus	5	3	60
Pelvis	2	1	50
Metapodial	3	1	33
Phalanges	4	0	0
Radio-ulna	8	0	0
Scapula	5	3	60
Tibia	2	1	50
Total	40	11	28

Figure 5.8. Proportion of tooth marks which are bisected for each skeletal part produced by small-medium and large crocodiles.

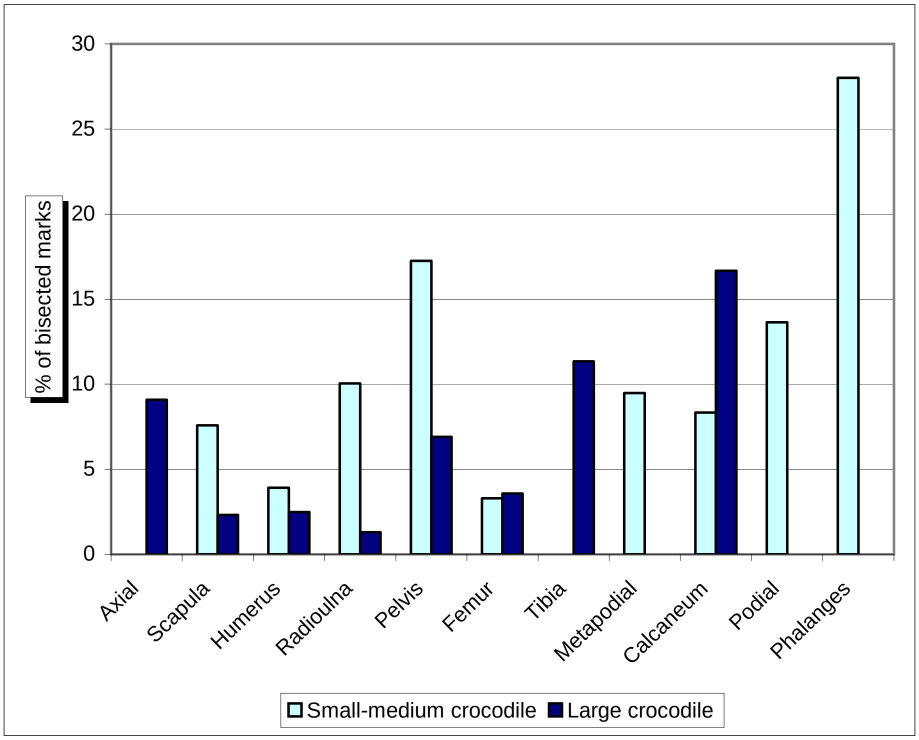
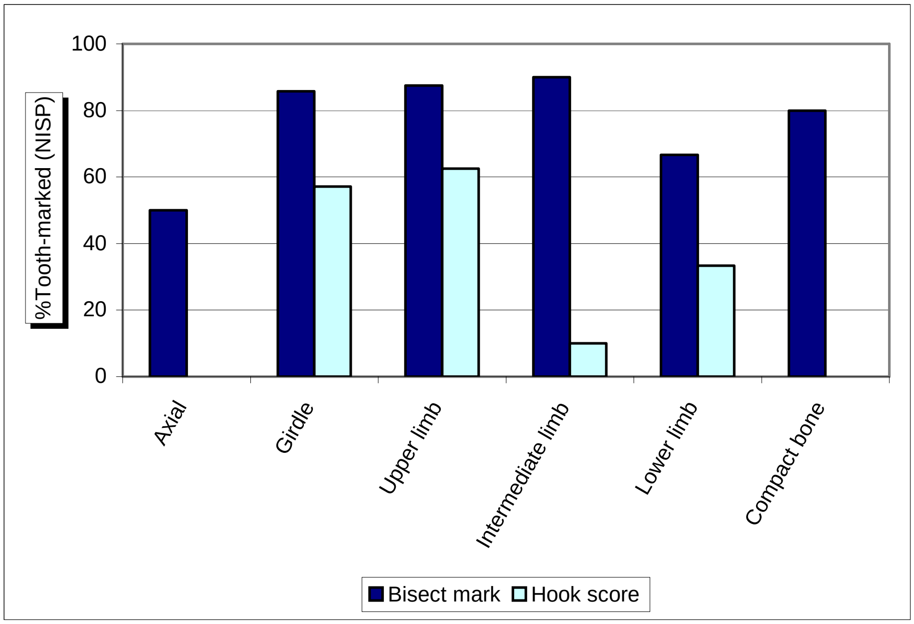


Figure 5.9. Proportion of tooth-marked specimens by skeletal groups that bear at least one bisected mark or hook score (NISP values). Girdle= scapula & pelvis; Upper limb= humerus & femur; Intermediate limb= radio-ulna & tibia; Lower limb= metapodial; Compact= carpals, tarsals, & phalanges (data from Table 5.8, 5.11).



5. Tooth mark size

Pits and punctures

A wide range of pits and punctures with maximum diameters ranging from about 0.1 mm to over 10 mm can be produced on cortical and cancellous bone depending on the size of the crocodile (Njau & Blumenschine, 2006). The smallest pits (pinprick-like), which are usually less than 0.1 mm in maximum diameter, are commonly produced on cortical bone by the sharp and slender teeth of small crocodiles. Small-medium crocodiles can produce pits and punctures of various size ranging from 0.2 mm – 5.9 mm in diameter, whereas the size of similar tooth marks produced by large crocodiles range from 0.2 – 11 mm (Figure 5.10).

Scores

Score size was determined by recording the length of the longest score on each bone specimen. Individual crocodiles produce short to long scores ranging from 1.8 mm – 55 mm with an average length of 13.6 mm (Figure 5.11). The majority of scores, however, range from 5.0 – 30.0 mm in length. The breadth of the widest score on each specimen ranges from 0.1 – 2.8 mm, with average breadth of 1.02 mm (Figure 5.12). All crocodiles are capable of generating scores of various sizes, although the shortest and broadest marks are probably produced by blunt and low crowned lateral teeth of large individuals. Long and narrow scores are likely produced by anterior teeth. Generally, crocodiles produce a wide range of tooth mark size as compared to mammalian carnivores.

Figure 5.10. Maximum pit or puncture diameter produced by large and small-medium crocodiles on individual bones (NISP=38).

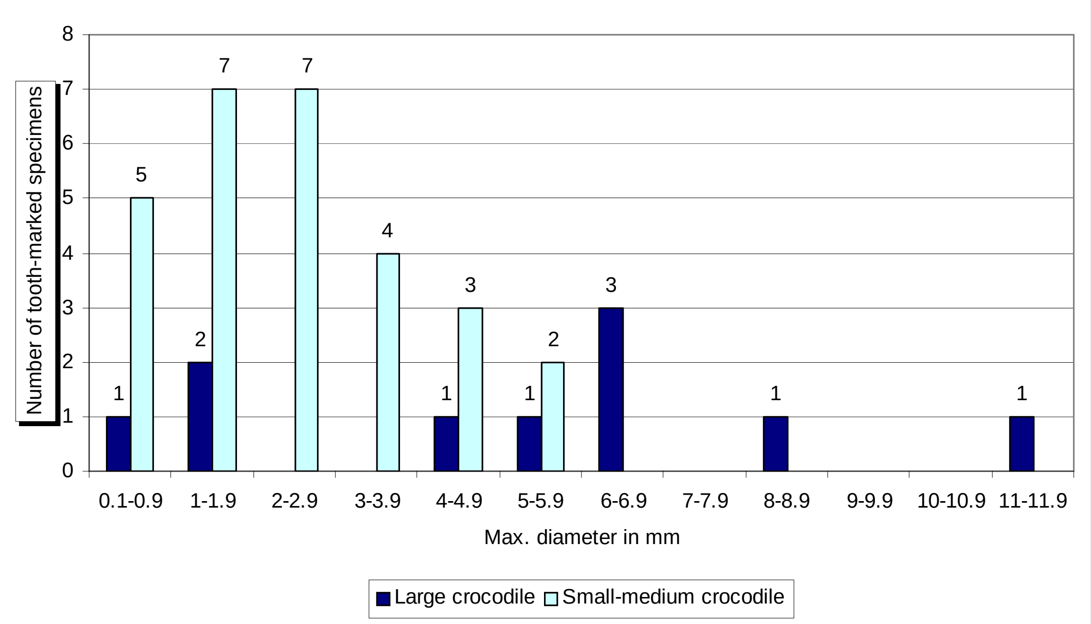


Figure 5.11. Maximum length of scores produced by large and small-medium crocodiles on individual bone specimens. Only the longest score on a specimen is reported here.

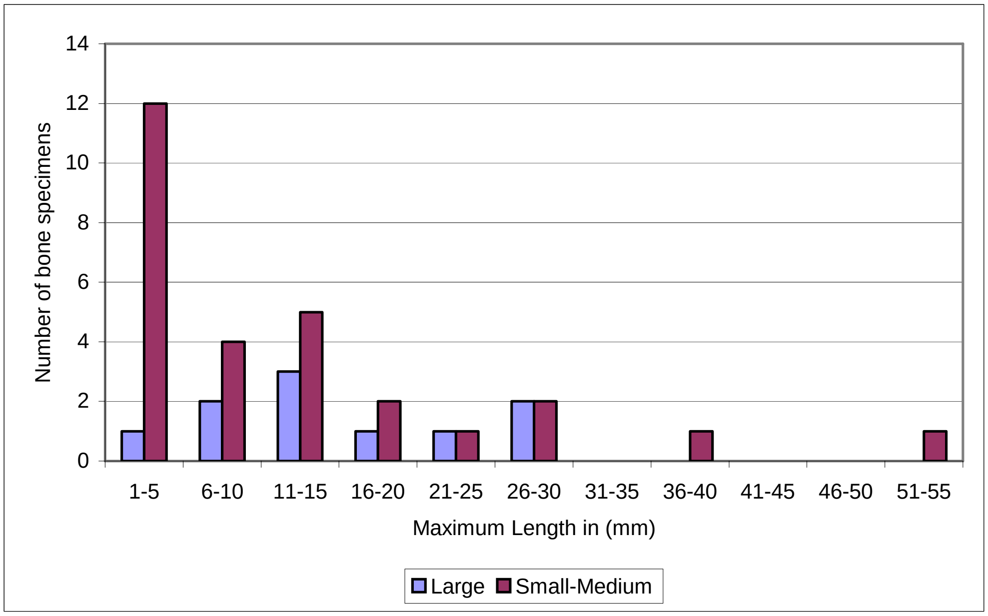
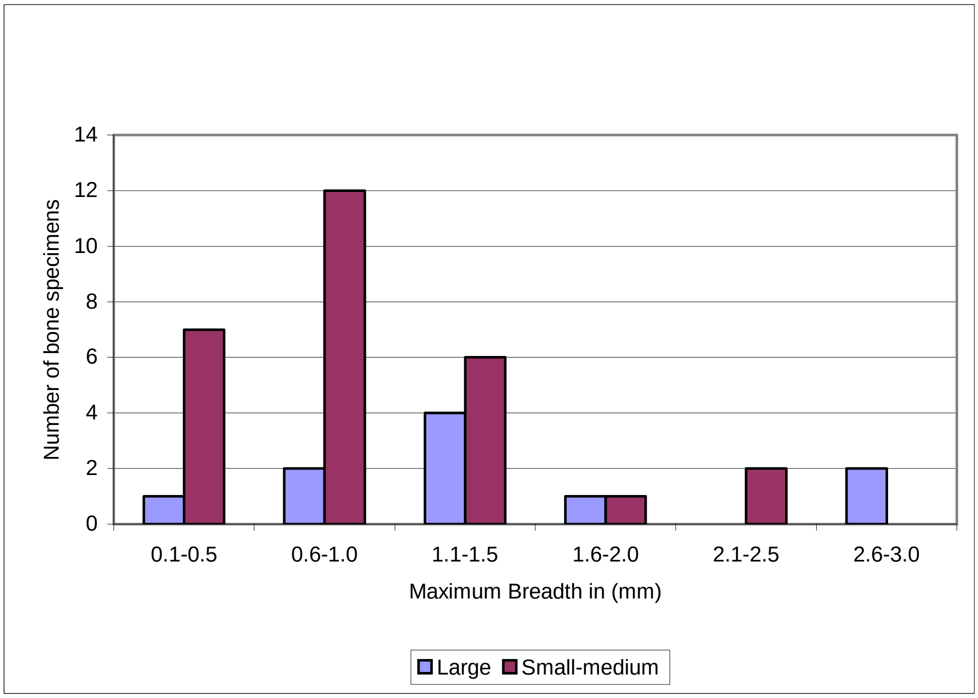


Figure 5.12. Maximum breadth of largest scores produced by large and small-medium-sized

crocodiles on individual specimens.



6. Patterns of tooth marking

Density, location and orientation

Generally, tooth marks occur anywhere on the bone surface, and are usually present in higher densities (number of marks per specimen) when compared to mammalian carnivores. Dozens of pits and sub-parallel scores, some overlaying each other, typically occur on major grasping sites from attempted disarticulation. Although the upper limbs are the most tooth marked elements, followed by intermediate and lower limbs, and the associated girdle elements, the lower limbs have the highest density of marks (Figure 5.7b). High densities of tooth marks are not associated with gnawing. The average number of marks per bone is 50, while the maximum number of marks recorded per specimen is 228, and the minimum number is five (Table 5.6).

Usually the scores are transversely oriented, and marks running obliquely and longitudinally to long bones axes are rare. Both transverse and oblique marks were observed to occur in all bone specimens bearing scores (see Appendix III).

Gross gnawing

Bone gnawing, which is a common feature in mammalian carnivore bone consumption, is absent in crocodile feeding. The "crenulated" or "scalloped" bone margins created by repetitive bites (cf. Binford 1981) are rarely produced by crocodiles during bone utilization. Only a few snapped fracture edges were observed including the end of a scapular spine and on the olecranon process of an ulna as a result of crocodile feeding (Table 5.1). The latter snapped edges are crenulated, probably as a result of a single bite as opposed to continuous gnawing of mammalian carnivores. Most mammalian carnivores, which gnaw cancellous bone portions during and after defleshing to extract grease contained in trabecular bone, inflict deep and large scores, pits and punctures during this process. For complete bones lacking gnawing, mammalian carnivore tooth marks are generally shallower and smaller. Crocodiles cannot chew bones due to lack of precise occlusion, and tooth marking is rarely associated with bone snaps. For detailed description of bone damage produced by crocodiles see Appendix III.

CHAPTER 6. FIELDWORK: METHOD, SAMPLE CHARACTERISTICS, AND RESULTS

1. Introduction

Observation of modern ecosystems, where the kinds of ecological information preserved in vertebrate remains can be precisely defined, is one method for reconstructing paleoenvironments. Many studies have investigated the effects of natural processes on recent mammalian bone assemblages on broad landscapes comprised of variety of environments (e.g., Behrensmeyer *et al.*, 1979; Behrensmeyer & Dechant-Boaz, 1980; Blumenschine, 1989; Sept, 1994a; Tappen, 1995; Dominguez-Rodrigo, 1999). However, studies on wetland environments are relatively rare, and have focused on large areas of swamps and dry lakebeds (e.g., Behrensmeyer & Dechant-Boaz, 1980; Behrensmeyer, 1981, 1983a), river systems (Dechant-Boaz, 1982), and lake margins (Gifford, 1980; West, 1995). Only Capaldo and Peters' (1995) and Njau's (2000) studies, have attempted to sample small land units with the goal of understanding the ecological and taphonomic processes of bone accumulations in lake margin zones. This fine-scale sampling method, advocated by Peters and Blumenschine (1995, 1996), allows observations of natural processes operating at very localized settings, and provides accurate interpretation of processes that are likely to be preserved in potential fossil assemblages.

This thesis extends this approach into riverine, large spring, and lakeshore systems with the aim of understanding processes of bone accumulation and modification by carnivores in wetland environments sub-divided into fine-scale landscape units, or sub-facets level.

2. Study sites

The major fieldwork was conducted in Serengeti National Park, while brief observations were made on land surface bone samples from Ngorongoro Crater, Lake Eyasi and Lake Manyara National Park for comparative purposes (Figures 6.1A and 6.1B). This work was conducted from September to November of 2002 and 2003, at the end of the dry season and prior to onset of the short rains. Landscape bone assemblages were sampled in 24 transects, including 15 on the Grumeti River in Serengeti, one on the lakeshore of lake Magadi in Serengeti, two on the lakeshore of lake Eyasi, two around Ngoitokitok springs in Ngorongoro Crater, two in riverine woodlands of Manyara groundwater forest, and two in Seronera and Wandamu headwaters in Serengeti (Table 6.1).

i) Significance of Serengeti ecosystem in neotaphonomic research

The Serengeti ecosystem provides a unique opportunity for studying modern ecology and natural history of flora and fauna in its largely natural state because it has been protected from the human interference since 1951, when the area was designated a full national park. This status has made the Serengeti a living laboratory for testing various models pertaining to climatic, environmental and faunal change, as well as evolutionary processes in semiarid savanna environments. The ecosystem preserves the last remnants of Late Neogene large vertebrate fauna, including crocodilians.

The Serengeti National Park, where the primary fieldwork was conducted, is part of the ecosystem, which is defined by the annual movements of the migratory wildebeest (*Connochaetes taurinus*) and zebras (*Equus burchelli* Gray). Serengeti is amongst the earth's best studied natural ecosystems and is also recognized as part of Serengeti–Ngorongoro biosphere reserve with the adjoining Maswa game reserve, and its ecology is well published (e.g., Schaller, 1972; Sinclair, 1977; Sinclair & Norton-Griffiths, 1979; Sinclair & Arcese, 1995; and references therein). The ecosystem is bounded by Lake Victoria Basin in the west, and extends to Masai Mara Game Reserve on the north, and Gol Mountains and Angata Sale Plains on the northeast. In the southeast, it extends to the foothills of Ngorongoro highlands and Eyasi escarpments.

The eastern boundary of the current park is situated approximately 40 km west of Olduvai Gorge, where the upstream end of the Main Gorge extends onto the southeastern Serengeti Plains. The history of the Serengeti coincides with the emergence of early bipedal hominins at Laetoli (ca. 3.6 mya) and early large brained *Homo* at Olduvai (ca. 2 mya) (e.g., Leakey, 1960, 1961a, 1961b, 1965, 1971, 1979; Leakey & Harris, 1987).

The assumption that modern African ecosystems are similar to those of the Plio-Pleistocene has been a subject of debate in paleoanthropology since the early 1960s (e.g., Howell & Bourliere, 1963; Bonnefille, 1984). Although Serengeti ecosystem is relatively recent when took its modern form within the past 500,000 years (Peters *et al*., in prep; *contra* Sinclair, 1979), the ecosystem offer an ideal set of conditions for the study of flora and faunal from evolutionary perspective.

It is only in this geographical region that we can still see an abundant fauna community similar to that which populated the area nearly four million years ago. These kinds of ecosystems provide an opportunity for modeling paleocommunity and paleolandscape dynamics (*cf*. Tappen, 2001). The long history of large vertebrate existence has been supported by fossil discoveries from the Pliocene and Pleistocene deposits of Laetoli (e.g., Leakey & Harris, 1987; Maglio & Cooke, 1978; Harrison *et al*., 2005) and Olduvai Basin (e.g., Leakey, 1965, 1971; Leakey *et al*., 1973; Gentry & Gentry, 1978a, 1978b; Blumenschine *et al*., in press).

ii) Modern analogs

The long-term ecological monitoring program in Serengeti provides reliable data, which are paleoecologically relevant and can be compared or tested against the fossil record. These include fauna communities (e.g., Grzimek & Grzimek, 1960; Sinclair & Norton-Griffiths, 1979; Campbell & Borner, 1995; Sinclair & Arcese, 1995; Mduma, 1996), vegetation patterns (e.g., Herlocker, 1975; Schmidt, 1975; Banyikwa *et al*., 1990; McNaughton & Banyikwa, 1995; Copeland, 2004), landscape classification (e.g., Gerresheim, 1974), geomorphology and soil (e.g., Pickering, 1959; Pickering, 1961; Anderson & Talbot, 1965), hydrology (e.g., Norton-Griffiths *et al*., 1975; Pennycuick & Norton-Griffiths, 1976; Gereta & Wolanski, 1998; Wolanski & Gereta, 1999, 2001; Wolanski *et al*., 1999; Gereta *et al*., 2004), and vertebrate taphonomy (e.g., Blumenschine, 1986a, 1986b, 1987, 1989).

Taphonomic studies related to hominin carnivory have been conducted in the Serengeti following Blumenschine’s ground breaking work on ecological contexts that would present scavenging opportunities to stone tool using hominins. His studies together with his colleagues at Serengeti and Ngorongoro (e.g., Blumenschine, 1986a, 1986b, 1988, 1987; 1989; Cavallo & Blumenschine, 1989; Selvaggio, 1994a, 1994b; Capaldo, 1995; Capaldo & Peters, 1995; Njau & Blumenschine, 2006; Blumenschine *et al*., in prep) have provided relevant information for modeling prehistoric behaviors and ecology of hominin-carnivore interactions on paleolandscapes.

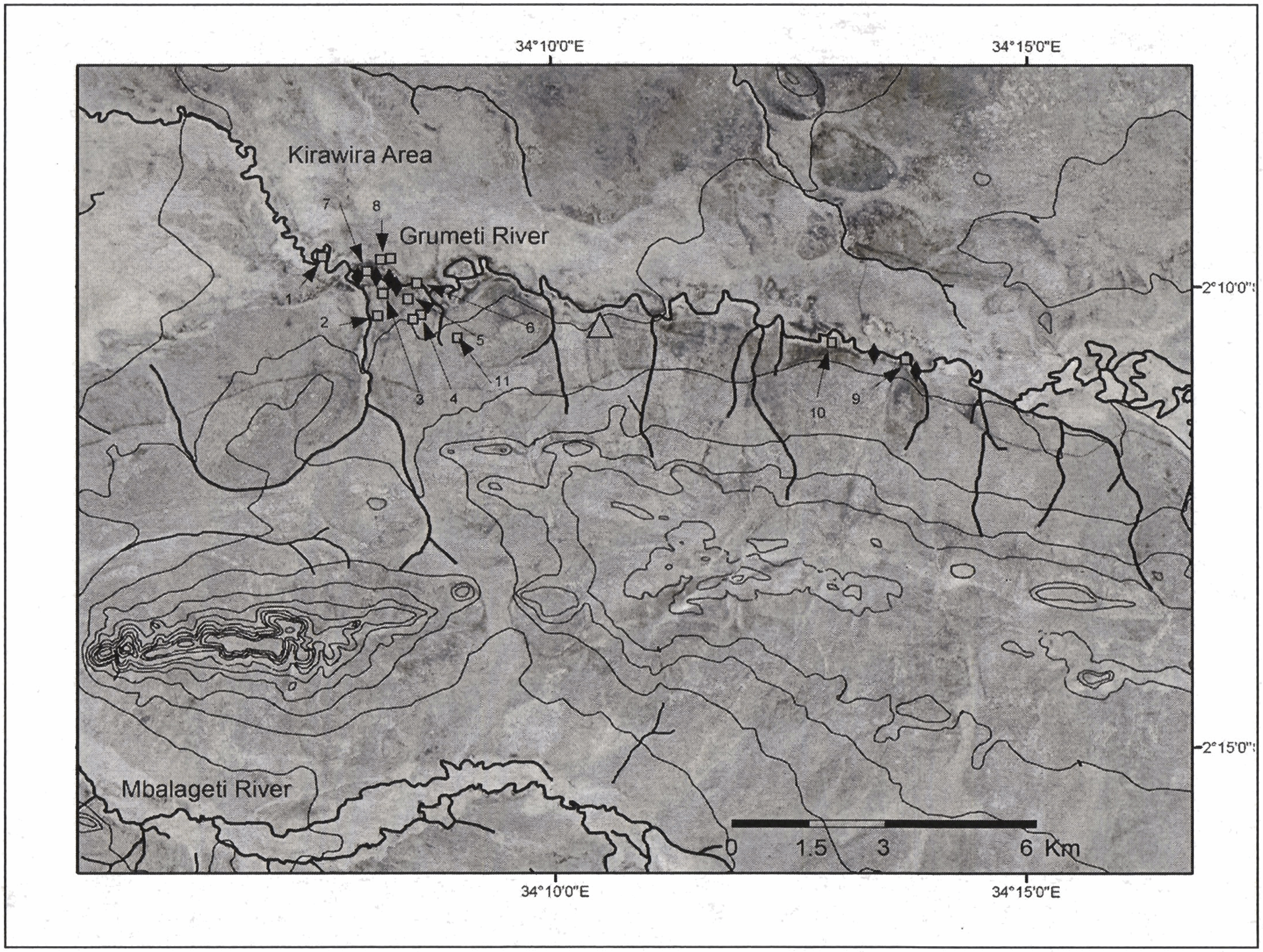
iii) Paleontological evidence

During the early part of the Quaternary period major changes occurred in the Serengeti fauna. Large-bodied mammals such as deinotheres, chalicotheres, Pelorovis, ceratotheres (white rhinos), Hippopotamus gorgops, and Elephas recki (elephant) vanished by Mid-Pleistocene (upper Bed II at Olduvai). The large, brevirostrine crocodiles (C. lloidi), which were dominant among crocodilian species in East Africa during the Miocene, began to disappear from the Olduvai record during this time (Tchernov, 1976, 1986). The Nile crocodiles, which are believed to have speciated from brevirostrine species by Pliocene times, did not appear in Olduvai record until Middle Bed II time, and survived to modern times in the region. Other fauna, which existed in the plains during the late Tertiary but disappeared from the fossil record by the end of Middle Pleistocene, are listed in Appendix IV. Only minor changes took place at the generic level in the Late Pleistocene, with the disappearance of older forms being as important as the appearance of new ones (Maglio, 1978; Maglio & Cooke, 1978).

Based on this paleoecological evidence, the ecological processes that today underlie the basic ecostructure, vegetation, and animal communities are likely to have applied and operated in the past. This assumption has made the Serengeti and the neighboring protected lake basins such as Manyara, Eyasi and Natron among the best living models for reconstructing ancient landscapes of early hominins (e.g., Peters & Blumenschine, 1995, 1996; Copeland, 2004).

Figure 6.1a. Map of northern Tanzania showing the locations of the study sites at Kirawira in Lower Grumeti River, Serengeti National Park; Lake Magadi, Serengeti; Ngoitokitok Spring, Ngorongoro Crater; Kisima Ngeda, Lake Eyasi; and Msasa River area, Lake Manyara National Park.

Figure 6.1b. Map of Lower Grumeti River showing locations of some of the transects in sampled at Kirawira area. The numbers identify the following transects: (1) KRAW4; (2) KRAS5; (3) KRAS1; (4) KRAS6 & KRAS9; (5) KRAS7; (6) KRAS8; (7) KRAS10; (8) KRAN3; (9) GRU1; (10) KRAE1 (see Tables 6.1 and 6.3 for setting descriptions). Solid diamonds= crocodile pools; Triangle= Rangers Post.



3. Descriptions of study sites and sampling procedure

i) Setting descriptions

Three major wetland settings each representing a distinct landscape facet, were defined for this study. They include a river (lower Grumeti River), a lacustrine plain (lakes Magadi and Eyasi), and a large spring associated with a saline lake (Ngoitokitok spring) (Table 6.2). The river was subdivided into three main sub-facets (i.e., pools and dry channel beds, riverbanks, over-banks and/or flood plains). The spring was divided into two sub-facets (i.e., woodland terrace and open lawn), and lacustrine plains into upper and lower lacustrine plains. The terrain morphology, hydrological regime, and vegetation pattern of each wetland setting is described in Table 6.2, and these features are considered to be important factors in the taphonomy of bone assemblages in wetland environments.

Transects were established in order to sample different sub-facets within a wetland landscape (i.e., river, spring, lakeshore) (Table 6.2). Characteristics of each transect were fully described and their sub-facets determined based on terrain, sediments, vegetation cover abundance, live animals sighted, and animal traces (e.g., skeletal remains, burrows, fresh feces, footprints and trails) (Table 6.3). Transect location was based on proximity to water (e.g., dry or active pool, dry channel bed, over-banks, spring edges, or lacustrine plains) and bone visibility (Table 6.3). The length and width of each transect were obtained by measuring tapes or practiced pacing in areas with dense vegetation (Table 6.4). Transects were usually set parallel or perpendicular to the river, spring or lakeshore depending on the physical setting and accessibility of the transect.

Systematic recording of skeletal remains on each transect was used to determine the distribution, composition, and density of bone assemblages in different landscape sub-facets. These small landscape units provide localized conditions in which natural processes operate. Observations of taphonomic processes operating at this level of spatial land analysis is important for interpreting specific landscape contexts of fossil assemblages.

Table 6.1. Transect descriptions listed in order completed indicating field number and identification name, terrain description of landscape facet, and geographical location. The locations of geographical regions are shown in Figure 6.1.a.

#	Transect	Description	Landscape Facet	Locality	Region
1	MAGADI	Narrow, open western lacustrine plains; wind blown side	Lacustrine Plain (Upper-lower)	Lake Magadi	Serengeti
2	SNERA	Head water	Seronera Stream	Seronera	Serengeti
3	WNDAMU	Head water of seasonal stream	Wandamu Stream	Seronera	Serengeti
4	GRU1	Dry riverbed	Lower Grumeti River	Grumeti hunting	Serengeti
5	KRAE1	Open over-bank	Lower Grumeti River	Edgar's Migration cross point	Serengeti
6	KRAN3	Wooded over-bank	Lower Grumeti River	Kirawira	Serengeti
7	KRAS1	Wooded over-bank	Lower Grumeti River	Kirawira	Serengeti
8	KRAST1	Around active crocodile pool, on the dry riverbed	Lower Grumeti River	Kirawira	Serengeti
9	KRAST2	Around active crocodile pool, on the dry riverbed	Lower Grumeti River	Kirawira	Serengeti
10	KRAS7	Wooded riverbank	Lower Grumeti River	Kirawira	Serengeti
11	KRAS10	Dry riverbed with minimal water discharge	Lower Grumeti River	Kirawira	Serengeti
12	KRAS8	Dry riverbed with minimal water discharge	Lower Grumeti River	Kirawira	Serengeti
13	KRAS4	Open over-bank	Lower Grumeti (west of airstrip)	Kirawira	Serengeti
14	KRAS6	Wooded distal floodplains	Lower Grumeti (south of airstrip)	Kirawira	Serengeti
15	KRAS5	Banks of wooded dry channel	Tributary on lower Grumeti	Kirawira	Serengeti
16	KRAS9	Wooded distal flood plains east of KRAS5	Lower Grumeti	Kirawira	Serengeti
17	KRAS11	Distal floodplains	Lower Grumeti (S. airstrip)	Kirawira	Serengeti
18	KRAW4	Vegetated riverbank with breach fan	Lower Grumeti River	Downstream	Serengeti
19	NGO1	Woodland terrace on hippo lawn	Large springs	Ngoitokitok	Ngorongoro Crater
20	NGO2	Open lawn ground	Large springs	Ngoitokitok	Ngorongoro Crater
21	KNGE1	Open upper lacustrine	Upper/ mid lacustrine plains	Kisima Ngeda	Lake Eyasi (east)
22	KNGE2	Open lower lacustrine	Lower lacustrine plains	Kisima Ngeda	Lake Eyasi (east)
23	MSASA	Vegetated stream banks (low banks)	Mid Msasa River (woodland)	Msasa River	Lake Manyara
24	MGA	Vegetated stream banks (low banks)	Mid Mchanga River (woodland)	Mchanga River	Lake Manyara

Table 6.2. Physical and physiognomic features of three wetland systems characterized by landscape sub-facets, following Peters and Blumenschine (1995, 1996; Blumenschine et al., in prep). Riverine: Lower Grumeti River, Serengeti; Spring: Ngoitokitok, Ngorongoro Crater; Lacustrine plains: Lake Magadi, Serengeti and Lake Eyasi, Eyasi. Geographical locations of the systems are shown in Figure 6.1.a.

Physical characteristics	Riverine (Lower Grumeti River)			Spring (Ngoitokitok)	Lacustrine plains	
	Pools & Riverbed	Riverbank	Over-bank/ floodplains	Spring margin	Narrow plains (L. Magadi)	Broad plains (L. Eyasi)
Hydrological regime	Fresh water, relatively fresher downstream; seasonal channel depends mainly on rainfall; drains to the lake; dense concentration of organic matter in pools and logjams on riverbed[1,2,3]	-	-	Fresh perennial marsh drains to the lacustrine plains; groundwater-fed or seasonal stream-fed[4]	Small & shallow saline, alkaline lake	Large lake on rift valley floor, fed by drainage inlets from the escarpments; small stream-fed seepages on mid/ upper lacustrine plains draining into lake
- Wet season	Potable H_2O[1, 3]; high H_2O discharge	Low raised banks are flooded by flowing water	Temporary water stands in wallows in the distal plains	Potable H_2O[4]; high H_2O level[4]	Relatively fresher on the lake edge near drainage inlets	Seepages/ small springs on mid/ upper lacustrine flooded
- Dry season	Poor H_2O quality; potable H_2O found only in stagnant ponds & elephant holes on the riverbed; discharge decreases to base flow maintained probably by groundwater seepage; suspended biogenic matter and bioturbation by hippo[1, 3, 5]	Banks are dry and exposed	-	Relatively good potable H_2O; discharge may be maintained by groundwater seepage[4]	Very saline H_2O	Potable H_2O only on springhead; increase in salinity

Continue

-Table 6.2 continue-

Terrain features	Ponded channel; shallow muddy pools often on point bars, bioturbated & rich of organic matter[1,3,5]; compact foot-printed surface on pool edges[2]; granite boulders, cobbles & well sorted large grain size sediments; low vegetated granitic-boulder islands on the riverbed[2]; meandering increases downstream	High raised granitic banks to low soil banks; breach fans (large trails) on soil banks[2]; large compact gullies developed by trails leading to channel bed/ pools; banks held by tree roots, or granitic rocks; banks flooded during rains[2]	Relatively flat landsurface ca. 3 m above riverbed; fine to coarse granitic sand	Nearly flat 2m above lower lacustrine plains; foot-printed mudflats on marshland margins; small grain size & poorly sorted[4]	Low gradient, ca. 1 m above waterline; fine sediments[5]	Low gradient & broad lacustrine plains, channelized by astonomizing deltas[6]; barren mudflats on lower lacustrine plains
Vegetation cover	Open stands of tall trees fringing the channel; little waterside vegetation; logjams on riverbed, mainly on boulder islands[2, 3]	Dense semi-woody shrubs, forbs & tall trees fringing the channel; grassland reaches right up to the banks; open exits created by large herds of migrating animals; rarely affected by wildfire[2]	Open grassplains with sparse trees and short *A. drepanolobium* (at all stages of growth and regeneration); heavily grazed tall grass (e.g., chloris); wildfire is common in dry season[2]	Open corridor near the pool; thick marshland vegetation (sedge, *Typha* & papyrus) and hippo lawn; closed *A. xanthaphloea*, shrubs on slightly higher ground[4]	Open plains to grazed lawns (salt & Cynodon grass), and *S. consimilis* grass on the lake edge; no trees	Open plains; patches of *S. spicatus* grass only on upper-ecotone zone; dense *Typha capensis, Cyperus articularis, Cyperus laevigatus* & semi woody legume bushes (*Aechymonene*)[7] confined to the springheads & upper part of the drainages; well vegetated ecotone zone by trees (mostly palms) & grass

[1] Wolanski *et al.* (1999), [2] Blumenschine, Peters, Njau, Masao & Stanistreet (in prep), [3] Gereta & Wolanski (1998), [4] Peters & Blumenschine (1996); [5] Wolanski & Gereta (1999), [6] Stollhofen & Stanistreet (pers. comm.), [7] Bamford (pers. comm.).

Table 6.3. Setting description of each transect and corresponding landscape sub-facet, indicating live animals observed by the author and park rangers on or near the transect, the movement of local and migratory animals, and visibility of bone specimens on transect

Landscape Facet	Transect[1]	Sub-facet[2]	Setting description	Live large animals sighted	Migratory status	Visibility[3]
RIVER						
Lower Grumeti	GRU1	RBED	Ponded dry riverbed with series of connected pools previously utilized by crocodiles and hippo. Tree lines & dense vegetation on the riverbank	Large crocodiles and hippo. Impala, vervet, wildebeest, zebra, T. gazelle	Residents in the pools Local residents/ in transit to drink or cross the river	Fair
	KRAE1	OOB	Open short grassplains with scattered *A.arabica* and semi woody bushes. Large scars (breach fan) on riverbank and gullies created by migratory animals. Large boulders and cobbles on the dry riverbed.	Large crocodiles & hippo. Wildebeest, zebra, topi, impala, lion, cheetah, T. gazelle	Local resident in the ponds Local residents/ in transit to drink & crossing. *Migration crossing point*	Good
	KRAS8	RBED	Riverbed with pools previously utilized by crocodiles and hippo. Small ponds connected by basal water flow. Large breach scars on the banks. Small cobbles to large granitic boulders on the channel and riverbank. Logjams on boulder islands.	Large crocodiles & hippo Zebra, impala, buffalo, vervet, giraffe	Residents in the pools Local residents/ on transit to drink or cross the river	Fair
	KRAS10	RBED	Ponded dry riverbed previously utilized by crocodiles and hippo. Tree lines & dense vegetation on the riverbank. Large breach scars on the banks created by migratory animals. Small cobbles to large granitic boulders on the channel and riverbank. Logjams on boulder islands. Tree cover on the riverbank.	Large crocs & hippo. Zebra, impala, buffalo, vervet, giraffe, T. gazelle	Residents in the pools Local residents/ on transit to drink or cross the river	Good
	KRAST1	POOL	On the edge of active crocodile and hippo pools formed on the riverbed. Large breach scars on the banks. Small cobbles to very large granitic boulders on the channel and riverbank. Granitic-boulders islands on the riverbed are densely covered by trees and grass	Large crocodiles & hippo. Baboon, impala, vervet, wildebeest, zebra	Residents in the pool Local residents/ in transit to drink or cross the river	Fair
	KRAST2	POOL	On the edge of active crocodile and hippo pools formed on the riverbed. Large breach scars on the banks. Small cobbles to very large granitic boulders on the channel and riverbank. Granitic-boulders islands on the riverbed are densely covered by trees and grass	Large crocodiles & hippo. Baboon, impala, vervet, wildebeest, zebra	Residents in the pool Local residents/ in transit to drink or cross the river	Good
	KRAS5	RBA	Dense vegetation and tree cover (e.g., *A. xanthaphloea*), thick shrub and grass along the banks of seasonal channel draining into Grumeti	Buffalo, giraffe, impala, baboon	Local residents/ in transit	Fair
	KRAS7	RBA	Dense vegetation, trees, semi-woody shrubs and herbaceous grass on riverbank. Low gradient to steep bank.	Hippo, zebra, wildebeest, impala, buffalo, vervet, hippo, giraffe	Residents/ in transit to drink and minor river crossing	Fair

Continued

Table 6.3 continued

	KRAW4	RBA	Riverbank densely vegetated by tall trees, semi-woody shrubs and herbaceous grass; Large breach fan leading to an open area created by migratory and drinking animals. Reduced size of cobbles and boulders on the riverbed and banks. Decrease number and size of pools	Crocodile, hippo, colobus. (decrease in crocodile body size compared to upper stream) Impala, baboon, elephant	Local residents (Migration crossing point) In transit to drink or cross the river	Fair
	KRAN3	WOB	Short to tall grass with bushes & scattered *A. drepanolobium*. Steep banks with large hippo trail gullies. Coarse to fine granitic sand.	Buffalo, hippo, baboon, hyena	Residents/ in transit to drink and minor river crossings	Fair
	KRAS1	WOB	Short to tall grass with bushes & multi-stem and single-stem trees. Steep banks with large hippo trail gullies. Coarse to fine granitic sand.	Vervet monkey, impala, zebra, wildebeest, baboon	Local residents/ in transit to drink or cross the river	Fair
	KRAS6	WOB	Dense *A. drepanolobium*, short to tall grass, some tall trees	Buffalo, wildebeest, zebra, elephant, giraffe, warthog, vervet, impala, jackals, lion, & hippo (during the night)	Local residents/ in transit	Fair
	KRAS9	WOB	Abundant tree cover of short *A. drepanolobium* & some tall trees. Dense vegetation cover of short to tall grass; a transition between seasonal channel and open grassplains on the distal flood plains.	Buffalo, wildebeest, zebra, baboon, vervet, impala, jackals, lion, T. gazelle. Elephant, giraffe, warthog, & hippo (during the night)	Local residents/ in transit In transit	Fair
	KRAS4	OOB	Over-bank flood plains; open grass plain with sparse semi-wood Acacia trees	Buffalo, wildebeest, zebra, elephant, giraffe, warthog, vervet, impala, jackals, lion, & hippo (during the night)	Local residents near river/ in transit	Good
	KRAS11	INT	Open grassplains with scattered tall single stem trees and short *A. drepanolobium*. Heavily grazed tall grass (e.g., chloris).	Lion, jackals, hyena, buffalo, zebra, wildebeest. Elephant, giraffe, warthog, vervet, impala, and hippo (during the night)	Local resident In transit	Fair
Seronera	SNERA	WHO	Headwater of seasonal stream. Tall sedge & consimilis grass, semi-woody flowering plants along spring orifice and elephant wallows. *A. xanthaphloea* trees on the drainage	Hippo, buffalo, lion, hartebeest, elephant	Residents & brief visits to the ponded wallows and standing water	Poor*
Wandamu	WNDAMU	WHO	Headwater of seasonal stream. Tall sedge & consimilis grass, semi-woody flowering plants along spring orifice and elephant wallows. *A. xanthaphloea* trees cover on the drainage	Elephant, buffalo, waterbuck, topi, lion	Residents & brief visits to the ponded wallows and standing water	Poor*
Msasa	MSASA	WOB	Groundwater forest; Dense vegetation of woodland and semi-woody bushes; minimum water flow	Baboon, elephant, buffalo, sikes monkey	Local resident Large troops of baboon (remains of two baboons killed by leopard	Poor*
Mchanga	MGA	WOB	Groundwater forest; Dense vegetation of woodland and semi-woody bushes, minimum water flow	Bushbuck, baboon, elephant, buffalo, sikes monkey	Local residents/ in transit	Poor*

Continued

Table 6.3 continued

LACUSTRINE PLAINS						
Lake Magadi	MAGADI	SHORE	Narrow strip of barren flats to grazed lawns (salt & cynodon grass) on mid lacustrine plains. Small, shallow & saline lake on Serengeti SE grass plains. Consimilis grass on lake edge.	Hippo & black rhinocerous, jackal, lion. Zebra, hartebeest, giraffe.	Local residents/ In transit	Good
Lake Eyasi	KNGE1	SHORE	Open spring-head; Transition between mid lacustrine plains to barren flats; Spring head and channel vegetated by lavigetus sedge and patches of short grass on footprinted field along the edge of spring that drain into the lake (like Mti Moja). Patch of diminishing *Typha* on stream.	Cattle, dik-dik, vervet. Hyena, leopard but rarely observed	Local residents In transit	Good
Lake Eyasi	KNGE2	BFL	Barren flats on the lower lacustrine plains. Presence of old incised channels on mid lacustrine plains draining into lake created by hippo trails.	Cattle, dik-dik, vervet. Hyena, leopard but rarely observed	Local residents In transit	Good
SPRING						
Ngorongoro-Crater	NGO1	SPR	Transition between hippo lawn densely covered by tall *A. xanthaphloea* and heavily foot printed edge on the east side of spring. Sedges, *Typha* & papyrus on transition between waterline and foot printed field.	Hippo, giraffe, elephant, buffalo, zebra, lion, leopard Complete skeleton of adult buffalo killed by a lion scattered and partially buried in the lawn	Local residents/ in transit	Fair
	NGO2	SPR	As above but it is an open lawn & short grass, no tree cover	As above	As above	Good

[1] Abbreviations and location of transects are provided in Table 6.1

[2] Abbreviations for sub-facets: POOL, crocodile & hippopotamus pool; RBED, Riverbed; RBA, Riverbank; OOB, Open over-bank; WOB, Wooded over-bank; INT, Distal flood plains; SPR, Large springs; BFL, Lower lacustrine plains, or barren flats; SHORE, Upper/mid lacustrine plains; WHO, Head water. Visibility is qualitatively ranked according to the ground cover from good to poor, following Blumenschine (1989).

[3] Good=visibility of bone on ground is not obscured by vegetation cover; Fair= Visibility clear for large specimens although small pieces and fragments may be buried under short grass and boulders, or covered by water; Poor = ground is partially or completely covered by grass, water or large boulders. Small specimens are hard to find, complete and large pieces are likely to be recovered. Ground search more intense in densely vegetated ground.

[*] Transects with poor visibility not included in analysis.

Table 6.4. Lengths and widths of transects and corresponding landscape sub-facets.

Transect ID	Sub-facet ID	Description[1]	Length x Width (m)
MAGADI	SHORE	Narrow, open lacustrine plains	400 x 30
SNERA	WHO	Head water	100 x 50
WNDAMU	WHO	Head water of seasonal stream	400 x 100
GRU1	RBED	Dry riverbed	150 x 30
KRAE1	OOB	Open over-bank	200 x 100
KRAN3	WOB	Wooded over-bank	1200 x50
KRAS1	WOB	Wooded over-bank	400 x 50
KRAST1	POOL	Crocodile/hippo pool	100 x 20
KRAST2	POOL	Crocodile/hippo pool	150 x 40
KRAS7	RBA	Wooded riverbank	300 x 40
KRAS10	RBED	Dry riverbed	150 x 30
KRAS8	RBED	Dry riverbed	200 x 30
KRAS4	OOB	Open over-bank	200 x 300
KRAS6	WOB	Wooded over-bank	300 x 100
KRAS5	RBA	Vegetated dry channel	200 x 50
KRAS9	WOB	Wooded distal flood plains	300 x 50
KRAS11	INT	Distal floodplains	200 x100
KRAW4	RBA	Vegetated riverbank	100 x 20
NGO1	SPR	Woodland terrace on hippo lawn	50 x 20
NGO2	SPR	Open lawn ground	250 x100
KNGE1	SHORE	Open upper lacustrine plains	300 x100
KNGE2	BFL	Open lower lacustrine plains	400 x 300
MSASA	WOB	Wooded stream banks	120 x 30
MGA	WOB	Wooded stream banks	200 x 20

[1] Descriptions and location of transects and sub-facets are provided in Tables 6.1 and 6.2.

ii) Landscape bone inventory

In order to enhance bone recovery, each transect was subdivided into strips running parallel to the length of the transect. The number of strips per transect was determined by transect width and visibility of bone. These rectangular strips were temporarily established by pacing and marking by pin flags. The strip was then searched thoroughly for bones by two observers trained in identifying bones who walked 5-7 m apart over the entire length of the transect. The distance between the observers depended upon ground visibility; in less vegetated landscapes, in which bone specimens could be spotted from a distance, the observers walked 7-10 m apart. This method enhanced bone recovery especially on vegetated ground where visibility was poor.

Bone searches were made systematically, working from left to right along each transect. Once a bone specimen was located the observer made a verbal announcement and the specimen or patch of bones was marked by a pin flag. After locating all bone specimens, the author would begin a bone inventory from strip one and proceed to the last strip. In order to avoid recording one specimen twice the flag pin was removed after the bone was examined and returned to the ground. With the exception of a few specimens that were collected for further study, skeletal specimens were left in place after in-field analysis was completed.

More than eleven attribute states were recorded for each bone specimen upon discovery and coded in fieldwork-forms designed for this particular task [modified from Blumenschine's Zooarchaeological Coding Convention (Appendix I)]. Data collected in the field were later entered into an Excel spreadsheet. For each specimen encountered, skeletal part, portion and segment, and the articulation, fragmentation, and presence of adhering flesh, was recorded according to taxa and estimated size and age of the animal. The specimen were also examined for both carnivore and crocodile damage and for both subaerial and subaqueous weathering conditions. The Grumeti River is the only system surveyed that harbors Nile crocodiles; therefore, it is only those transects from Grumeti that contain traces of crocodiles.

iii) Taphonomic model for large wetland vertebrates

A landscape taphonomic model is developed in this thesis in an attempt to establish criteria for identifying patterns of bone accumulation and modification in riverine, spring and lake margin settings (Table 6.5). Holding preservation biases of bone constant (i.e., fluvial transport, trampling, subaerial and subaqueous weathering), the model considers crocodiles and large mammalian carnivores as dominant predators and major agents of bone modification during the resource-life of bone, in specific wetland settings. Theoretically, the composition of bone assemblages generated under the influence of mammalian carnivores differs from that produced by crocodiles, and that the extent of bone damage by each agent can be determined within a bone assemblage.

Based on the observations made from the lower Grumeti River, the Ngoitokitok groundwater-fed spring, and the lacustrine plains of Lakes Magadi and Eyasi, the physical and physiognomic settings are described for each wetland system in Table 6.2 with the aim of modeling the activities of live crocodiles and terrestrial carnivores, and the composition of bones in wetland settings. Positive and negative affordances that are likely to be encountered by Nile crocodiles, spotted hyena, and felids (mainly lion and leopard) are modeled for the main sub-facets defined in these wetland systems (Table 6.5). The abundance of crocodile, hyena, and felid, and intensity of their activities are modeled for each sub-facet based on the biological capability and survival requirements of each species (Table 6.5). Also the abundance of feeding traces resulting from their activities, and the composition of bone assemblages are modeled for each sub-facet (Table 6.5).

Table 6.5. General activities of crocodiles and large mammalian carnivores (hyaenids and felids) and resulting bone assemblages modeled for landscape sub-facets described for three wetland settings in Tables 6.2 & 6.3 (following Peters & Blumenschine, 1995, 1996; Blumenschine & Peters, 1998).

	Riverine			Spring	Lacustrine Plains	
Composition of live fauna & bone assemblage	Pools & Riverbed*	Riverbank/ over-bank	Over-banks/ floodplains		Narrow plains	Broad plains
Live crocodile suite	++++	+[1, 2, 4]	+[2, 3?]	+[5]	0[5]	0[5]
[†]Live hippopotamus	++++	+[3]	++(grazing)	++++	++[3]	+[3]
Live terrestrial carnivore suite						
- Spotted hyena	+[1]	+	++++	++[1, 3]	++++	++++
- Large felids (lion, leopard)	+[1]	++[4, 6]	+	++++	+[3]	+[3]
[‡]Hominin activities	+[1, ¶]	++++[3, 6, 7, 8]	+[3]	++[8, 9]	0	0
Crocodile skeletal remains	++++[10]	+[11]	+[11]	-	-	-
Hippopotamus skeletal remains	++++[10]	0/+	++[11]	++[11]	+	+
Presence of bone modification by						
- Crocodile	++++	+	0/+	-	-	-
- Spotted hyena	+	0/+	++++	+	++++	++++
- Large felids (lion, leopard)	++	++++	++	++++	++	++
Completeness of long bone elements						
- NISP/MNE	++++[12, 13]	++	+[14]	++++[13]	+[14]	+[14]
Density of bone occurrence	++++[12, 13, 15]	++	+[14]	++	+[14]	+[14]
Voorhies' transport groups	III >II>>I[10]	II=III >I	I/III > II	-	-	-
- Abrasion/rounding	++++	0/+	0	-	-	-
- Fragmentation	++++	0/+	0	-	-	-
- Weathering stage	0-2	0-3	3-4	0-2	3-4	4-6

++++ = Abundant; ++ = Moderate; + = Low to rare; 0 = None

[1]Opportunistic scavenging; [2]Basking and/ or nesting site near riverbanks; [3]In transit; [4]Hunting along breach fans/ crocodile scavenging from lion kills; [5]Lack of raised ground near H_2O suitable for locating nesting sites, and high predation risk to eggs, hatchlings and/ or juveniles; [6]Leopard tree-stored kills; [7]Posts for sighting safe drinking/bathing spot (in wet seasons); [8]Refuge trees; [9]Foraging root stocks; [10]Lag deposits (e.g., skull, mandible, pelvis, teeth, long bones, and large bones), large individuals die in water, small crocodile predation; [11]Individuals killed by lions or hyenas, or natural death; [12]Due to active crocodile predation and low hyena activities, crocodile behavior of abandoning near complete carcasses unutilized; [13]Mainly animal stuck in the mud or whole bones pushed into mud by hippos; [14]Bone exposure to hyena ravaging & subaerial processes (e.g., weathering, trampling); [15]Mass drowning, hydraulic concentration.

*Home to crocodile and hippo. High predation risk to variety of animals including ungulates, primates, terrestrial carnivores, juvenile crocodiles or isolated baby hippos.

[†]Hippopotamus are large aquatic mammals usually sharing the same pools and channels in the Lower Grumeti

[‡]Based on Blumenschine & Peters (1998).

[¶]In dry season=extreme predation risk from crocodiles, and poor H_2O quality.

a. Hypotheticalland use patterns of crocodile, hyena, and large felids

The population density of crocodiles is modeled to be relatively high in the channel bed, especially in areas where the water is relatively fresh, calm and shallow. In the case of the lower Grumeti, the river flow is minimal during dry years, and dries out tremendously during the dry seasons, leaving behind a series of heavily eutrophied stagnant ponds formed on the channel bed (Gereta & Wolanski, 1998; Wolanski & Gereta, 1999, 2001). Even in wet years surface water is ponded most of the year, creating the larger pools that are occupied by hippopotami and crocodiles (Blumenschine *et al.*, in prep).

Crocodiles

Crocodile hunting and feeding is modeled to concentrate in the pools, the only source of water for wildlife during the dry seasons. These pools are used repeatedly although during the wet seasons crocodiles and hippopotami tends to disperse towards the upper stream. Activities are modeled to decrease in the adjacent riverbank/over-bank settings, and are limited to nesting, opportunistic hunting or scavenging (Cott, 1961). Sometimes crocodiles can scavenge from lion kills located close to water (e.g., Pitman, 1931; Attwell, 1959). The open areas on the riverbanks, breached by big-game trails, also offer basking grounds for crocodiles. These game-trail bank breaches, which originate from the over-banks, sometimes form small alluvial fan-like features, referred to as “breach fans” by Blumenschine *et al.* (in prep). Generally, the soil-banks are stabilized by tree and shrub roots, which are often exposed on the steeper trail breaches. Basking is preferred in open, sandy grounds, or on large rocks on the riverbed and riverbank.

Since crocodile nests are preferentially located on the raised sandy ground with good shade, near the channel but free of flooding (e.g., Grabham, 1909; Modha, 1967), over-banks are modeled to offer conducive nesting sites (Table 6.5).

Positive affordances to crocodiles are considered to be the highest in the pools, but decrease in riverbanks and over-banks. The mortality rate of this species increases on land, especially in the distal flood plains. Characteristics and composition of bone assemblages is therefore expected to reflect crocodile activities in different sub-facets.

The absence of crocodiles in spring and lakeshore sites is partly attributed to an abundance of negative affordances, such as lack of adequate nesting sites, and/or the expected high mortality rates of hatchlings and juveniles due to predation by birds and terrestrial carnivores (Table 6.2, 6.5).

Spotted hyena (Crocuta crocuta)

Hyena density and activities are modeled to be relatively high in less vegetated settings such as lakeshores and distal over-banks or floodplains (Tables 6.2, 6.5). Although game may be abundant in riverines and springs, hyena activities in these settings is limited to brief scavenging trips or when commuting between landscapes. This is because riverine and wooded spring margins support dense tree cover, which hinders sight of the aerial clues provided by vultures and used by hyenas for discovering kills on the ground (e.g., Kruuk, 1972; Blumenschine, 1987). Also, hyena activities are less frequent in the channel because crocodiles can pose potential danger. Bone ravaging is therefore considered to be low in channels occupied by crocodile (Table 6.5).

Large felids

Large springs, riverbanks and over-banks are modeled to provide good tree cover for lion activities (Table 6.2). Trees also facilitate arboreal storage for leopard kills (Cavallo & Blumenschine, 1989). With the exception of rare incidences when crocodiles can access carcasses on the ground, kills made by lions and leopards persist longer in riverine woodlands before being discovered by other terrestrial carnivores (e.g., Blumenschine, 1986b, 1987; Cavallo & Blumenschine, 1989). Although distal floodplains may provide abundant game to felids, lack of good vegetation cover may lead to high competition from other terrestrial and aerial scavengers.

The lacustrine plains are modeled to provide fewer resources to felids, due to exposure and lack of good ambushing sites. Presence of adult crocodiles in ponded channels may also hinder felid activities in or near pool settings.

The activities of these large carnivore guilds are paleoanthropologically important because they are major competitors as well as providers of scavenging opportunities for hominins (Peters & Blumenschine, 1995, 1996). Blumenschine and Peters (1998) proposed that landscapes located near potable water sources are likely to support greater tree-cover abundances and associated resources such as plant foods and scavengeable carcasses. These settings were likely to attract foraging hominins due to reduced hyena activities or predator encounter risk, thus yielding abundant hominin trace fossils in bone assemblages. Theoretically, in settings with few trees, terrestrial carnivore density and potential competition among large carnivores for carcasses would be higher, as would hyaenid to carcass ratios (Blumenschine, 1986b, 1987).

Following Blumenschine and Peter's predictive models, the predator encounter risk for hominins is also greater in settings inhabited by crocodiles adjacent to tree covered riverbank/over-bank settings (Tables 6.2, 6.5). Therefore, in a lower Grumeti-like setting, the riverbanks and proximal over-banks would provide arboreal refuge trees for hominins traversing the riverine landscapes.

4. Characteristics of the sample

A total of 2,051 bone specimens were analyzed in the field (Table 6.6). Initially 31 transects were established at my field sites, but only twenty of them that contained at least one bone specimen are reported here. Seven transects were established in different regions as part of feasibility studies and were discarded due to either presence of dangerous animals (such as hippopotamus, crocodiles, buffalo, elephants, or lions) along the riverine settings, or presence of dense vegetation, water, a mucky surface or large rocks that obscure access to bones and/or visibility of bones on the ground. There were no bone specimens encountered in two of the Serengeti and two of the Lake Manyara transects in spite of thorough searching, due to poor visibility (Table 6.3); therefore these are not included in the analysis.

All transects were designed to be as linear as possible, and with the exception of a few transects the length varied from 100 m to 400 m, while width ranged from 20 m to 100 m (Table 6.4). In most cases the size of a transect was determined by the morphology and the setting of the landscape facet. Good visibility on the ground was expected to enhance bone discovery regardless of type of landscape sub-facet; therefore the visibility for each transect is reported qualitatively in order to give a picture of the landscape in which bones were recovered.

The sample is stratified by three main wetland landscapes consisting of river, lake and freshwater spring. A total of fifteen transects were sampled for various sub-facets in the Grumeti River. Only three transects were sampled on lacustrine plains of Lake Eyasi and Lake Magadi, and two at Ngoitokitok Spring (Table 6.6). 1,556 bone specimens were recorded in the riverine landscapes with a total area of 272,000 m^2, while 349 bones were sampled in 162,000 m^2 of lacustrine plains, and 146 from springs with a total area of 26,000 m^2. Thirteen transects containing 1,362 bones were sampled along the lower Grumeti River in the Kirawira area, while only two samples (GRU1 and KRAE1) comprised of 194 bones came from farther upstream, near the Grumeti Hunting Camp bridge.

Table 6.6 Sample characteristics of three major wetland landscape facets stratified by sub-facets, including the area, and number of bone specimens (NISP) for each transect. POOL: crocodile & hippopotamus pool; RBED: Riverbed; RBA: Riverbank; OOB: Open over-bank; WOB: Wooded over-bank; INT: Distal flood plains; SPR: Large springs; BFL: Lower lacustrine plains, or barren flats; SHORE: Upper/mid lacustrine plains; WHO: Head water.

Landscape Facet	Sub-facet	Transect	Area m^2	NISP
GRUMETI RIVER				
Lower Grumeti	RBED	*GRU1	4,500	21
	OOB	*KRAE1	20,000	173
	RBED	KRAS8	6,000	39
	RBED	KRAS10	4,500	100
	POOL	KRAST1	2,000	44
	POOL	KRAST2	6,000	205
	RBA	KRAS5	10,000	50
	RBA	KRAS7	12,000	60
	RBA	KRAW4	2,000	29
	WOB	KRAN3	60,000	148
	WOB	KRAS1	20,000	41
	WOB	KRAS6	30,000	27
	WOB	KRAS9	15,000	167
	OOB	KRAS4	60,000	356
	INT	KRAS11	20,000	96
SERONERA RIVER	WHO	SNERA	5,000	0
WANDAMU RIVER	WHO	WNDAMU	40,000	0
MSASA RIVER	WOB	MSASA	3,600	0
MCHANGA RIVER	WOB	MGA	4,000	0
Sub-total				1,556
LACUSTRINE PLAINS				
Magadi lacustrine plains	SHORE	MAGADI	12,000	64
Eyasi Upper/spring heads	SHORE	KNGE1	30,000	25
Eyasi barren flats	BFL	KNGE2	120,000	260
Sub-total				349
NGOITOKITOK SPRINGS	SPR	NGO1	1,000	68
	SPR	NGO2	25,000	78
Sub-total				146
GRAND TOTAL		24		2,051

*Transect located farther upstream

5. Results

This section reports the taphonomic characteristics of bone assemblages recorded in twenty transects at the Grumeti River, Ngoitokitok Sring, and the lacustrine plains of lakes Magadi and Eyasi. The analysis focuses mainly on the early biostratinomic or nutritive phase of bone assemblage information, although some of the potential physical processes such as fluvial transport, weathering and trampling are discussed. Results from transects are grouped by sub-facet, with the aim of contrasting these smallest landscape units in terms of density of bone occurrences, composition of animal species, and bone modification profiles. Grumeti is the only study site used by both crocodiles and mammalian carnivores. Therefore, patterns of crocodile and mammalian carnivore bone modification in bone assemblages are established from this site. Tooth mark and bone completeness data are used to quantify the distribution of crocodiles and mammalian carnivore activities across adjacent landscape sub-facets.

i). Density of bone occurrences

The processes involved in concentrating and dispersing bone specimens can be evaluated by documenting the number of specimens per unit area of each landscape sub-facet. The concentration of bones measured by both NISP/ha and MNI/ha is quantified for twenty transects (Table 6.7). The mean densities (NISP/ha and MNI/ha) are quantified for corresponding sub-facets in Table 6.8 and Figure 6.2.

Generally, the crocodile pools contain among the highest concentration of bone specimens and individuals per unit area compared to the sub-facets away from the channel, such as the over-banks and riverbanks (Table 6.8). With the exception of over-bank sub-facet, the number of transects for other sub-facets is insufficient to support statistical testing (see Tables 6.7 and 6.8). Nonetheless, the density (NISP/hectare) in over-banks is not significantly different from that in the adjacent riverbanks (Mann-Whitney U = 6.000, P> 0.05).

The high mean densities of specimens reported from two pool sub-facets (NISP/ha and MNI/ha) reflects: 1) the crocodile’s behavior in carcass utilization and discard, and 2) preservation potential of bones in pools at least over the short term. Usually, skeletal regions uningested by crocodiles are deposited in the pool after disarticulation and are trampled into bottom of the pool by hippopotamus and crocodiles (see Table 6.5).

Crocodiles tend to leave unattended, articulated skeletal regions or large bones (e.g., pelvis, scapula, skull) of larger prey relative to their size. The complete and broken parts can be shaken off the carcass and thrown out of pool to the pool margins/riverbed, increasing the intermingling of bones between pools and riverbed. Due to proximity and probable mixture of bone specimens between the pools and riverbed, these two sub-facets are combined in a number of analyses.

Lacustrine plains record the lowest values of mean densities (Table 6.8, Figure 6.2). The very high mean density in springs is a result of nearly complete two buffaloes deposited in a small area (Transect NGO 1). There is no significant difference in terms of bone densities (NISP/ha and MNI/ha) between lacustrine plains and spring sub-facets, or between Grumeti river sub-facets and springs or lacustrine plains, due to the small sample size of transects representing springs (N=2) and lacustrine plains (N=3) (Table 6.7).

The over-bank and lacustrine plain sub-facets were modeled to contain relatively low densities of bones due to increase in concentration of hyena activities, and exposure to subaerial weathering and trampling (Table 6.5). Riverbanks and springs contain more bones per unit area (Table 6.8), as expected due to low hyena ravaging and minimum bone damage by weathering (Table 6.5).

Table 6.7. Density of occurrences of large vertebrate bones recorded in each transect and corresponding sub-facet as NISP/m^2 and MNI/ha. Fish and bird bones are excluded. MNIs for KRAS4 and KRAS6 are combined. Setting description for each transect is provided in Table 6.3.

Transect	Sub-facet	Area		NISP	MNE	MNI	Density		
		m^2	Hectare				NISP/m^2	NISP/ha	MNI/ha
KRAST1	Pool	2,000	0.2	43	38	3	0.0215	215.0	15.0
KRAST2	Pool	6,000	0.6	205	184	14	0.0342	341.7	23.3
GRU1	Channel bed	4,500	0.45	21	17	4	0.0047	46.7	8.9
KRAS8	Channel bed	6,000	0.6	38	35	3	0.0063	63.3	5.0
KRAS10	Channel bed	4,500	0.45	100	67	4	0.0222	222.2	8.9
KRAS5	Riverbank	10,000	1	50	24	2	0.0050	50.0	2.0
KRAS7	Riverbank	12,000	1.2	60	42	3	0.0050	50.0	2.5
[†]KRAW4	Riverbank	2,000	0.2	29	23	5	0.0145	145.0	25.0
KRAE1	Over-bank	20,000	2	173	68	4	0.0087	86.5	2.0
KRAN3	Over-bank	60,000	6	148	88	7	0.0025	24.7	1.2
KRAS1	Over-bank	20,000	2	41	29	6	0.0021	20.5	3.0
KRAS6	Over-bank	30,000	3	27	21	-	0.0009	9.0	-
KRAS9	Over-bank	15,000	1.5	166	118	6	0.0111	110.7	4.0
KRAS4	Over-bank	60,000	6	356	219	10	0.0059	59.3	1.7
KRAS11	Over-bank	20,000	2	96	54	6	0.0048	48.0	3.0
[‡]NGO1	Spring	1,000	0.1	68	49	1	0.0680	680.0	10.0
NGO2	Spring	25,000	2.5	66	47	4	0.0026	26.4	1.6
MAGADI	Lacustrine	12,000	1.2	64	20	2	0.0053	53.3	1.7
KNGE1	Upper Lacustrine	30,000	3	15	14	1	0.0005	5.0	0.3
KNGE2	Lower Lacustrine	120,000	12	229	61	4	0.0019	19.1	0.3
				1,995	1,218	89			

[†] Bone concentration eroding out of a gully, held by tree roots

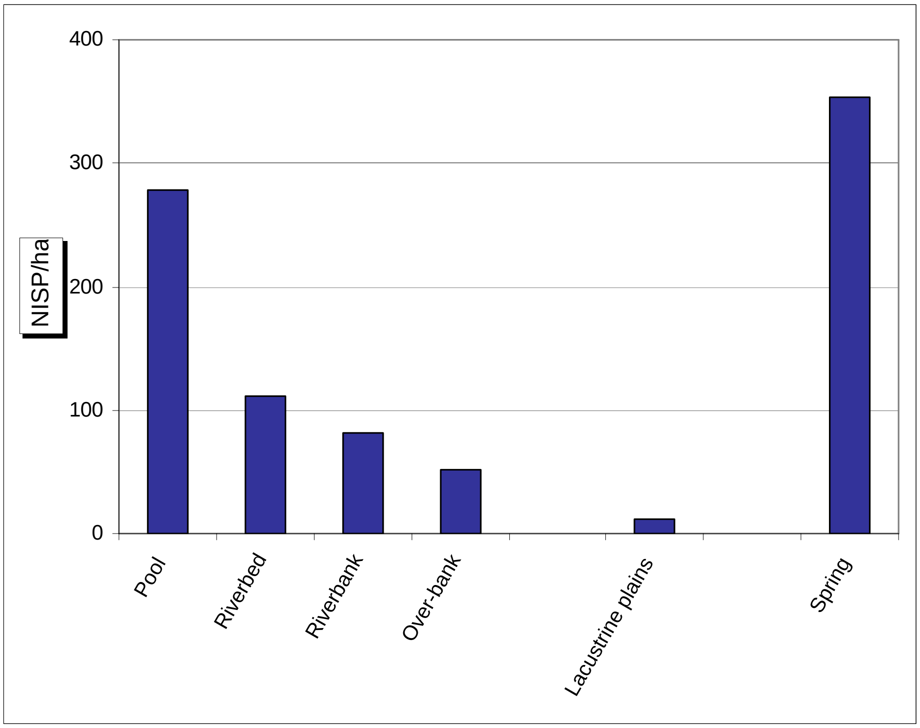
[‡] Bones of one individual concentrated within a small area

Table 6.8. Mean densities of large vertebrate bones for each sub-facet recorded in twenty transects (data from Table 6.7).

Sub-facet	Transect N	Mean NISP/ha	Std. Deviation	Mean MNI/ha	Std. Deviation
Pool	2	278.3	89.5	19.1	5.8
Riverbed	3	110.7	96.8	7.6	2.2
Riverbank	3	81.6	54.8	9.8	13.1
Over-bank	7	51.2	37.1	2.1	1.3
†Spring	2	353.2	462.1	5.8	5.9
Lacustrine plains	3	12.0	9.9	0.7	0.8
Total	20				

†Bones derived from one individual (high Std. Deviation value)

Figure 6.2. Mean densities of large vertebrate bones for sub-facets recorded in twenty transects (data from Table 6.8).



ii). Species composition

The faunal remains represented in the bone assemblages closely correspond to the live animals sighted or known to live around sampled sites (see Table 6.3). Habitat-specific animals, in particular crocodiles, are well represented in sites where they live (Table 6.9a, 6.9b; Figure 6.3). Crocodile skeletal remains are proportionately most common in pools and riverbeds, and are rarely represented in transects located farther away from the channel bed, such as riverbanks and over-banks (Table 6.10a). Crocodile scutes, and cervical and abdominal ribs are excluded from the analysis due to their overrepresentation in an individual. The mean percentages of crocodile specimens calculated for each transect are 23.9% in crocodile pools, 11.9% in riverbeds, 1.1% on riverbanks, and 0.8% on over-banks (Table 6.10b). No remains of this species were observed in the distal flood plains.

The number of crocodile specimens (NISP) from the pool/riverbed sub-facet is significantly higher than the combined number of specimens from riverbanks and over-banks ($X^2 = 323$, df = 1, $P < 0.001$). Crocodile skeletal remains are, therefore, a good indicator of pools in Lower Grumeti River where they live. Crocodile feeding and predation of juveniles by large crocodiles are among factors contributing to the concentration of crocodile skeletal material in pools (Table 6.5).

Bones of hippopotami, which were observed to share many of the pools in Grumeti with crocodiles, are not as common as those of crocodiles in pools/riverbeds (8.1%), and rarely represented in riverbanks and over-banks (0.1%) (Table 6.9b). Contrary to my expectations, however, hippo are less common than crocodiles in pools and riverbanks/over-banks (Figure 6.3). Skeletal remains of hippopotamus were expected to be as abundant as crocodiles in the ponded channel bed assemblages because they share the same habitats and because they possess large robust bones (see Table 6.5). Generally, hippo bones are common in springs (9%), and rare in lacustrine plains (5.9%).

Although live giraffe, elephants and large mammalian carnivores and olive baboons are common in all study sites, their skeletal remains are rarely represented on landsurfaces (Table 6.9a). Very few skeletal remains of catfish (*Clarias*) were found, restricted to drying pools in the riverbed and the channelized deltas on the lower lacustrine plains of Lake Eyasi (Table 6.9a). Pelican and flamingo bones were observed only in the lacustrine plains, while Marabou stork bones were observed only in two of the Grumeti River transects (Table 6.9a).

Generally, the medium-sized ungulates (size 3) such as wildebeest and zebra are well represented in all bone samples, as expected from their high live biomasses (Table 6.9a). Bones of small-sized animals (size 1-2), such as gazelles, impala and warthogs, are represented in all landscapes, but are less common than medium-sized ones in all sub-facets except for the barren lacustrine plains. In addition to high live biomass, the overrepresentation of medium-sized herbivore bones in the Grumeti sub-facets partly reflects crocodile predation on herds of wildebeest and zebra crossing the river during annual migrations in this area. The size 4 mammal bones (mainly buffalo) are represented in all sub-facets. The disproportionately high NISP of buffalo in the spring assemblage reflects the remains of two partial skeletons of buffaloes, which had been killed by lions.

Table 6.9a. Observed taxonomic composition of bone assemblages (NISP values) from the Grumeti River, Ngoitokitok Springs, Lake Magadi and Lake Eyasi, recorded by sub-facets.

Composition of faunal and bone assemblage	Riverine[1]						Spring[2]		Lacustrine Plains			
	Pool/riverbed		Riverbank		Over-bank/Flood plains		Marshland margin		L. Magadi[3]		L. Eyasi[4]	
	n	%	n	%	n	%	n	%	n	%	n	%
Live carnivore suite												
[5]Nile Crocodile	>100	-	<100	-	<5	-	None		None		None	
[5]Terrestrial carnivores	<5[6]	-	<5[6]	-	>50	-	<5	-	>5[7]	-	<5[8]	
Species (skeletal remains)												
Crocodile	113	27.6	1	0.7	3	0.3	-	-	-	-	-	-
Hippopotamus	31	7.6	0	0.0	1	0.1	12	8.2	0	0.0	12	4.2
Bovid size 1-2	40	9.8	18	12.9	106	10.5	7	4.8	22	34.4	65	22.8
Bovid size 3	163	39.9	85	61.2	650	64.5	11	7.5	36	56.3	46	16.1
Bovid size 4	14	3.4	6	4.3	37	3.7	102	69.9	0	0.0	10	3.5
Zebra	22	5.4	23	16.5	105	10.4	2	1.4	1	1.6	11	3.9
Warthog	1	0.2	0	0.0	1	0.1	0	0.0	0	0.0	1	0.4
Giraffe	0	0.0	1	0.7	1	0.1	0	0.0	0	0.0	0	0.0
Elephant	1	0.2	0	0.0	1	0.1	0	0.0	0	0.0	0	0.0
Baboon	1	0.2	0	0.0	15	1.5	0	0.0	0	0.0	0	0.0
Mammalian carnivore	3	0.7	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Indeterminant mammals	18	4.4	5	3.6	87	8.6	0	0.0	5	7.8	99	34.7
[9]Aves	1	0.2	0	0.0	1	0.1	12	8.2	0	0.0	34	11.9
Clarias	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	7	2.5
NISP=2051	409	100.0	139	100.0	1008	100.0	146	100.0	64	100.0	285	100.0

[1] Lower Grumeti River, Serengeti National Park

[2] Ngoitokitok Springs, Ngorongoro Crater

[3] Narrow and open lacustrine plains, Lake Magadi

[4] Broad and open lacustrine plains (lower-mid/ upper), Lake Eyasi

[5] Live crocodiles (small to large) and mammalian carnivores (lion, hyena, leopard, jackals) observed by the author or park rangers in or near the study areas

[6] In transit, crossing the channel, ambush hunting by lions, leopard stalking baboons & monkeys, brief scavenging trips on dry channel by hyenas & canids

[7] Hyenas and canids; occasionally lions in transit

[8] Few hyenas, domestic dogs, and probably jackals; lack of large felids due to expansion of onion farms and human settlements

[9] Aves= Marabou stork[1], flamingo[3, 4], pelican[4], Guinea fowl[2]

Table 6.9.b. Proportion of animal species represented by skeletal remains (NISP) in four major sub-facets. Fish, bird, indeterminate mammal bones, and crocodile scutes, cervical and abdominal ribs are excluded. Primate and mammalian carnivore bones are disproportionately underrepresented in the sample (Table 6.9a) and are not included in this analysis. GIR, giraffe; ELE, elephant.

Species	Pool/ Riverbed		Riverbank/ Over-bank		Spring		Lacustrine Plains	
	NISP	%	NISP	%	NISP	%	NISP	%
Crocodile	113	29.4	4	0.4	0	0.0	0	0
Hippo	31	8.1	1	0.1	12	9.0	12	5.9
Bovid	217	56.4	902	86.8	120	89.6	179	87.7
Zebra	22	5.7	128	12.3	2	1.5	12	5.9
Warthogs	1	0.3	1	0.1	0	0.0	1	0.5
GIR & ELE	1	0.3	3	0.3	0	0.0	0	0.0
Total	385		1039		134		204	

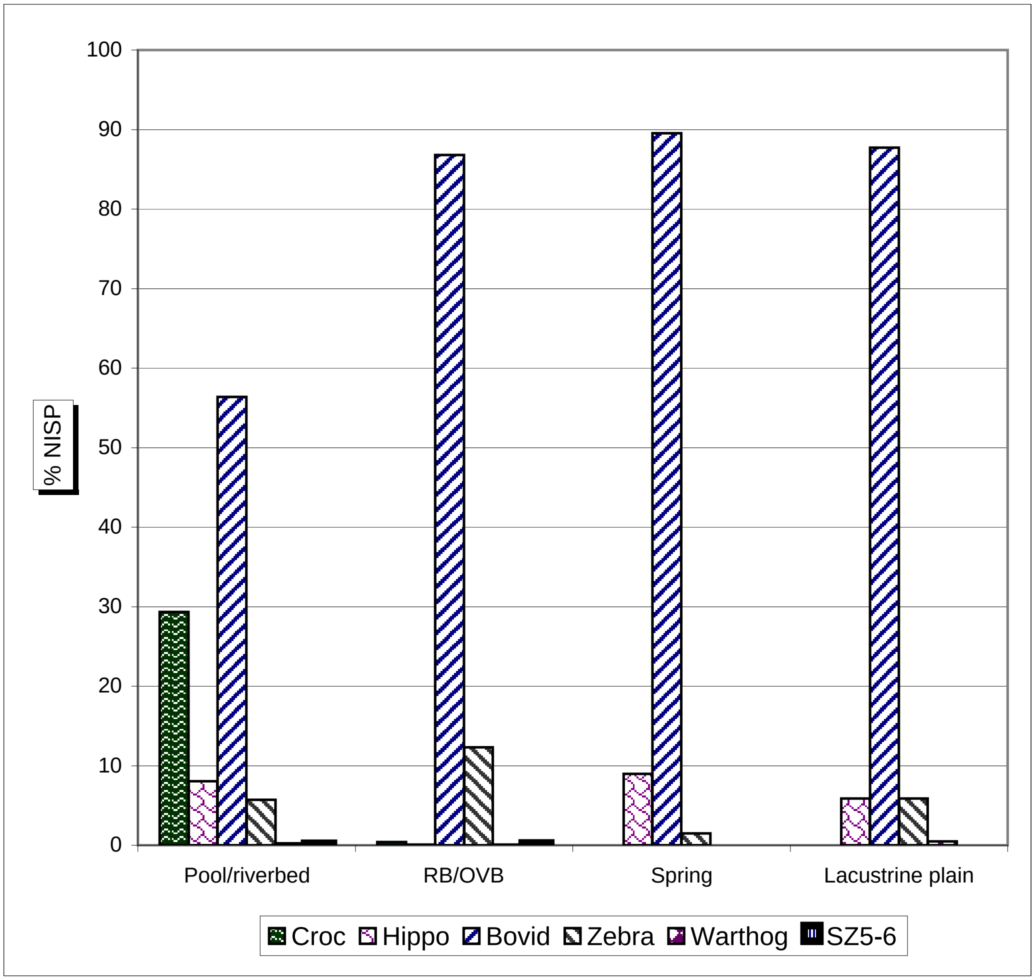
Table 6.10a. Proportion of crocodile skeletal specimens recorded as a percentage of large vertebrate specimens represented in each transect at Grumeti River (data from Table 6.7).

Transect	Sub-facet	Crocodile only		Total
		NISP	%	NISP
KRAST1	Pool	2	4.6	43
KRAST2	Pool	89	43.4	205
GRU1	Riverbed	2	10.5	21
KRAS8	Riverbed	4	10.3	38
KRAS10	Riverbed	16	16.0	100
KRAS5	Riverbank	0	0.0	50
KRAS7	Riverbank	0	0.0	60
KRAW4	Riverbank	1	3.4	29
KRAE1	Over-bank	0	0.0	173
KRAN3	Over-bank	1	0.7	148
KRAS1	Over-bank	2	4.9	41
KRAS6	Over-bank	0	0.0	27
KRAS9	Over-bank	0	0.0	166
KRAS4	Over-bank	0	0.0	356
KRAS11	Over-bank	0	0.0	96

Table 6.10b. Mean percent of crocodile bone specimens represented in each sub-facet in the Lower Grumeti River (data from Table 6.10a

Sub-facet	Transect N	Mean %	Std. Deviation
Pool	2	23.9	27.5
Riverbed	3	11.9	3.5
Riverbank	3	1.1	1.9
Over-bank	7	0.8	1.7
Total	20		

Figure 6.3. Proportion of species represented in each sub-facet (NISP). Croc=crocodile, Hippo=hippopotamus, SZ5-6=giraffe and elephant. RB/OVB= riverbank/over-bank. Primates, carnivores, indeterminant mammals, birds, and fish not included (data from Table 6.9b).



iii). Bone completeness and skeletal representation

Generally, bones are well preserved in pools inhabited by crocodile and in the wooded settings of springs than in other sampled settings (Table 6.11). Pools/riverbeds contain the highest proportion of complete (undamaged) bone elements relative to the total minimum number of specimens (57.6%). Intact bones are also common in springs (51.5%). The low degree of bone fragmentation in pools/riverbeds and springs is partly attributed to low ravaging activities usually performed by hyenas in non-wooded open settings. In addition to lack of hyenas in the channel, the tendency of crocodiles to discard uningested skeletons leads to deposition of complete sets of articulating skeletal groups. The assemblage from lacustrine plains is relatively fragmented due exposure of bones to physical subaerial processes such as trampling and weathering, and occasional ravaging by non-resident hyenas.

In Grumeti, the number of complete bone elements is significantly higher in pool/riverbed sub-facets than in riverbank/over-bank sub-facet ($X^2 = 53.7$, df = 1, $P < 0.05$). The degree of bone completeness was expected to be relatively higher in the settings inhabited by crocodiles as compared to adjacent riverbanks and over-bank, where crocodiles are less active compared to mammalian carnivores (Table 6.5).

Skeletal part profiles presented in Table 6.12 show that, with the exception of lacustrine plains, post-cranial axials (vertebra and ribs) predominate all assemblages (Figure 6.4a). Long bones are also well represented in all assemblages, although not to the degree of axial elements. Crania, scapulae and pelves are moderately represented, while compact bones (carpals, tarsals and phalanges) are underrepresented.

The overrepresentation of axials in the pool/channel, over-bank, and spring assemblages reflect the abundance of ribs and vertebra in an individual (see Table 4.2), rather than selective concentration of bones by high-energy water. Axial and compact bones, which belong to fluvial transport group I (see Table 2.1), have the highest tendency to transport by flotation. Therefore, their abundance in bone assemblages may indicate the effect of fluvial process. Since axial bones are over-represented and compact bones are underrepresented both in channel and non-channel environments, transport by high-energy water is unlikely to be major taphonomic factor in the formation of these assemblages (see discussion). On the other hand, the overrepresentation of long bones in lacustrine plain assemblages (Figure 6.4a) reflects the survivorship of this skeletal group due to their high structural density.

When the degree of bone completeness is expressed as the frequency of complete bones relative to total minimum number of elements (MNE), pool/channel and spring sub-facets generally preserve the highest proportions of complete elements for each skeletal group (Table 6.12; Figure 6.4b). For example, whole long bones are proportionately more common in pools (64.1%) than in riverbank/over-bank sub-facets (43%). Complete long bone elements are also common in springs (52.1%) and lacustrine plains (40.4%).

Complete skulls display similar patterns, while axial elements are proportionately most common in all landscapes ranging from 61.1% to 83.6%. Complete girdles are proportionately more common in springs (57.1%) and pools/riverbeds (51.3%), and less represented in riverbanks/over-banks (43.5%) and lacustrine plains (33.3%). Most of the compact bones recovered were complete in all sub-facets except in springs (Table 6.12, Figure 6.4b).

The proportion of complete long bone elements represented in an assemblage was predicted to be relatively high in the crocodile pools compared to the adjacent riverbank and over-bank sub-facets due to crocodile predation, lack of hyena activities, and burial of whole bones in pools (see Table 6.5). The proportion of complete long bone elements observed in pool/riverbed sub-facets is significantly higher than that observed in riverbank and over-bank sub-facets as expected (X^2 =40.3, df= 1, P < 0.05). Fragmentation of long bone specimens was expected to increase in the riverbanks and over-banks due to an increase in bone utilization by mammalian carnivores.

Table 6.11. Frequency of complete elements (undamaged bones) of large vertebrates relative to NISP for each sub-facet. Non-identified specimens and isolated teeth are not included.

Sub-facet	Complete elements		Grand Total
	NISP	%	NISP
Pool/riverbed	217	57.6	377
Riverbank	37	28.2	131
Over-bank	368	37.1	993
Spring	69	51.5	134
Lacustrine plains	41	14.7	279
Total	732	38.2	1914

Table 6.12. Proportion of bone specimens (NISP values) categorized by skeletal group in each sub-facet, expressed as percentage of skeletal group in an assemblage (percent values are italicized). The occurrence of complete (intact) elements in each skeletal group is reported as percentage of complete elements (CO) relative to the total Minimum Number of Elements (MNE) in each skeletal group (percent values are bolded). Non-identified specimens and isolated teeth are not included. CRA= cranium, GIR= girdle, AXL= axial elements, LBN= long bone, CBN= compact bone (carpals, tarsals and phalanges), CO= complete elements.

Sub-facet	CRA		GIR		AXL		LBN		CBN		Total
	N	%	N	%	N	%	N	%	N	%	N
Pool/riverbed											
CO	17	**42.5**	19	**51.3**	112	**82.9**	59	**64.1**	10	**100.0**	
MNE	40		37		135		92		10		
NISP	50	*13.3*	43	*11.4*	169	*44.8*	105	*27.9*	10	*2.7*	377
Riverbank/ over-bank											
CO	15	**20.8**	34	**43.5**	228	**76.5**	75	**43.0**	53	**98.1**	
MNE	72		78		298		173		54		
NISP	93	*8.3*	100	*8.9*	552	*49.1*	325	*28.9*	54	*4.8*	1124
Springs											
CO	0	**0.0**	4	**57.1**	51	**83.6**	12	**52.1**	2	**50.0**	
MNE	1		7		61		23		4		
NISP	2	*1.5*	7	*5.2*	96	*71.6*	25	*18.7*	4	*3.0*	134
Lacustrine											
CO	1	**14.2**	4	**33.3**	11	**61.1**	17	**40.4**	8	**100.0**	
MNE	7		12		18		42		8		
NISP	11	*3.9*	12	*4.3*	101	*36.2*	147	*52.7*	8	*2.9*	279

Figure 6.4a. Frequency of bone elements represented in each sub-facet categorized by skeletal groups. RB/OVB= Riverbank and Over-bank; CRA=cranial, GIR=Girdle, AXL=Axial, LBN=Long bone, CBN=Compact bone. Data from Table 6.12.

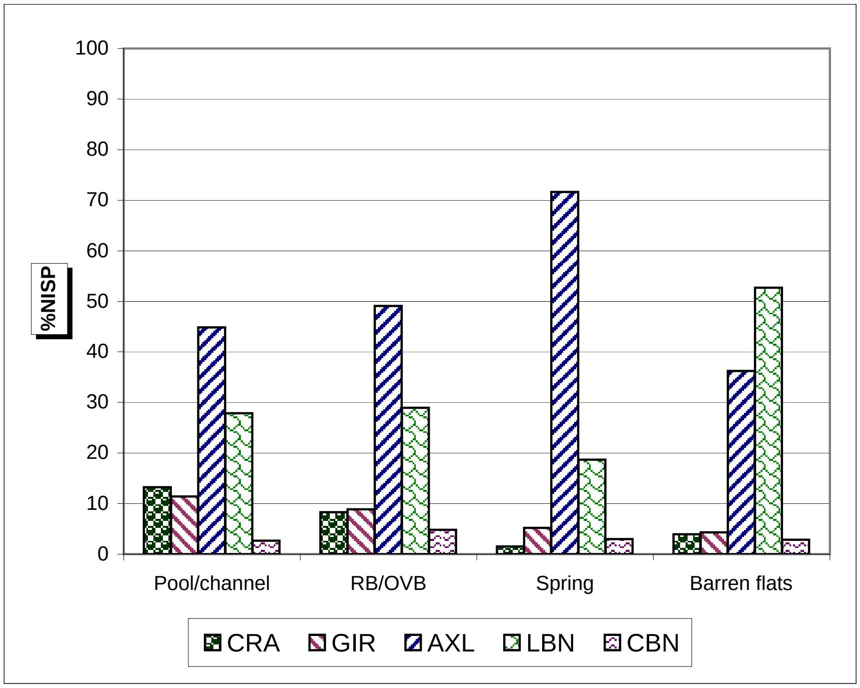
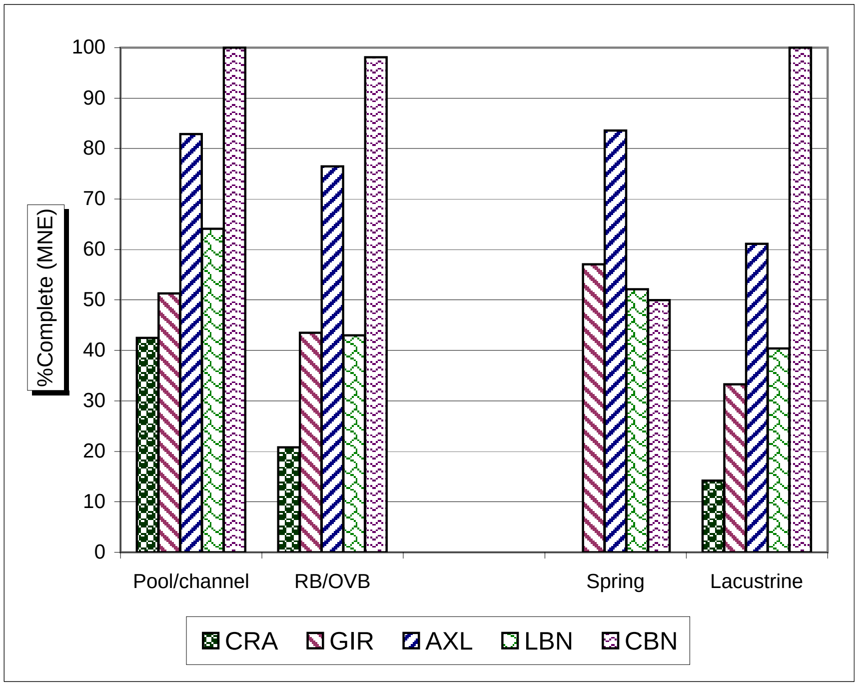


Figure 6.4b. Frequency of complete bones relative to Minimum Number of Elements (MNE) for each skeletal groups. RB/OVB= Riverbank and Over-bank; CRA=cranial, GIR=Girdle, AXL=Axial, LBN=Long bone, CBN=Compact bone. Data from Table 6.12; MNE values.



iv). Bone modification

A total of 1,914 bone specimens were analyzed for surface bone modifications in four landscape sub-facets. Tooth-marked specimens are proportionately more common in springs (85.1%) and riverbanks and over-banks (62.2%), and less common in pools/riverbeds (38.2%) and lacustrine plains (27.2%) (Table 6.13). In Lower Grumeti the number of bone specimens bearing at least one tooth mark is significantly lower in crocodile pools/riverbeds than in riverbanks/over-banks (X^2 =66.3, df =1, $P < 0.05$). This observation suggests that tooth marking is less common in assemblages derived from crocodile dominated settings (pools/riverbed) as compared to assemblages formed away from the channel, where mammalian carnivores are more active.

Under controlled conditions, captive crocodiles produce tooth marks on approximately 21% of bones they are unable to ingest (Table 5.2), while mammalian carnivores typically produce tooth marks to more than 50% of bones they leave behind after consumption (e.g., Blumenschine, 1988; Capaldo, 1995). The proportion of tooth-marked bones in the Grumeti crocodile pool/riverbed assemblage is, therefore, relatively higher (38.2%) than that expected for crocodiles alone (21% in control sample) but lower than that expected for mammalian carnivores alone, suggesting that bones were modified by both carnivores in the channel.

Crocodiles are not present in the sampled spring and lacustrine plain sub-facets. Therefore, all bone modification is attributed to mammalian carnivores in these settings. The underrepresentation of tooth-marked specimens in lacustrine plains is partly due to fragmentation and poor preservation conditions of skeletal materials on the open lacustrine plains and rarity of carnivores at Lake Eyasi.

Table 6.13. Proportion of bone specimens bearing at least one tooth mark for each sub-facet.

Sub-facet	Tooth-marked bones NISP	%	Total NISP
Pool/riverbed	144	38.2	377
Riverbank/over-bank	700	62.2	1124
Springs[§]	114	85.1	134
Lacustrine plains[§]	76	27.2	279
Total	1034	54.0	1914

[§]No live crocodiles

a. Bone modification by mammalian carnivores and crocodiles in the Grumeti assemblages

Both mammalian carnivores and crocodiles are considered as agents of bone modification along the Grumeti River, and have been observed or reported to consume carcasses of large vertebrates there. Crocodilian bone modification is distinguished from that of mammalian carnivores by using criteria developed in chapters four and five. Since the majority of tooth marks produced by crocodiles (ca. 90%) are morphologically indistinguishable from those made by mammalian carnivores (Table 5.9), only “bisected marks” are used to identify crocodilian bone modification. Since at the time of analysis the variability in crocodilian tooth marks and the nature of associated damage on a full range of skeletal elements (see Appendix III) was not fully understood, I recorded only bisected pits and punctures and not hook scores.

This conservative estimate also excludes some ungnawed complete specimens with dense concentrations of tooth marks, resulting in underestimates of the overall frequency of bones tooth-marked by crocodiles. Also, the nature of crocodile traces enhanced by occurrence of bisected marks in only 80% of bones fed by this reptile under controlled condition (Table 5.8), adds to conservative nature of results on the impact of crocodiles feeding traces.

A bone specimen bearing at least one bisected pit or puncture was tallied as crocodile modified. If the specimen bore a bisected mark and was also grossly gnawed, or contained tooth notches on the medullary surface etc., both groups of carnivores were tallied. Modified specimens attributed to mammalian carnivores were those that lacked bisected marks, or were grossly gnawed, or fragmented.

Among the tooth-marked specimens in crocodile pools/channel beds, 60.4% bear at least one bisected mark (Table 6.14a, Figure 6.5). Among tooth-marked specimens in this sub-facet, 24.3% were attributed to mammalian carnivores and 15% had traces of both carnivores. Generally, 75.7% of all tooth-marked bones in pools/riverbeds bear at least one bisected mark, while 39.6% have traces consistence with mammalian carnivore feeding (Table 6.14a). This pattern changes in the riverbank/over-bank sub-facets, where among the tooth-marked bones, 99.4% are produced by mammalian carnivores, while only 0.9% are produced by crocodiles (Table 6.14a). The results show that the number of bones modified by crocodiles is significantly higher than those modified by mammalian carnivores in pools/riverbeds, and significantly lower in adjacent riverbanks/over-banks ($X^2 = 492.6$, df =1, $P < 0.001$).

Long bone specimens display a similar trend (Table 6.14b). Among the tooth-marked long bones in pools/riverbeds, 76.7% bear at least one bisected mark, while 50% bear damages consistence with mammalian carnivore (Table 6.14b). Among the tooth-marked long bone specimens in the riverbank/over-bank sub-facets, 99% are produced by mammalian carnivores while only 1.4% are produced by crocodiles (Table 6.14b).

Table 6.14a. Proportion of tooth-marked bones inferred to have been modified by mammalian carnivores, crocodiles or both. Unidentified specimens and teeth are excluded.

Sub-facet	Mammalian carnivore		Crocodile		Both		Total Tooth-marked
	NISP	%	NISP	%	NISP	%	NISP
Pool/riverbed	35	24.3	87	60.4	22	15.3	144
Riverbank/ over-bank	694	99.1	4	0.6	2	0.3	700
Springs[§]	114	100.0	-	-	-	-	114
Lacustrine plains[§]	76	100.0	-	-	-	-	76
Total	919	88.9	91	8.8	24	2.3	1034

[§]No live crocodiles in the system and no evidence of crocodile tooth marking on tooth-marked specimens

Table 6.14b. Proportion of tooth-marked long bones only inferred to have been modified by mammalian carnivores, crocodiles or both.

Sub-facet	Mammalian carnivore		Crocodile		Both		Total Tooth-marked
	NISP	%	NISP	%	NISP	%	NISP
Pool/riverbed	13	23.2	28	50.0	15	26.7	56
Riverbank/ over-bank	212	98.6	2	0.9	1	0.5	215
Springs[§]	24	100.0	-	-	-	-	24
Lacustrine plains[§]	44	100.0	-	-	-	-	44
Total	293		30		16		339

[§]No live crocodiles in the system and no evidence of crocodile tooth marking on tooth-marked specimens

b. Completeness of tooth-marked bone specimens

Crocodile pool assemblages tend to contain a high proportion of whole bones, the majority of which bear crocodile modification. 58 bone specimens, or 66.7% of bones bearing crocodile tooth marks were complete, while only 28.6% of bone specimens modified by mammalian carnivores were intact (Table 6.15a, Figure 6.6). All of the bone specimens bearing bisected marks in riverbank and over-bank assemblages were intact (100%), while only 32.2% specimens bearing mammalian carnivore damage were complete in these sub-facets (Figure 6.6). The number of whole bones modified by crocodiles is significantly higher than those modified by mammalian carnivores in pools and riverbanks/over-banks ($X^2 = 202.2$, df = 1, $P < 0.001$). These results are consistent with observations from controlled observations of mammalian carnivore's ability to ravage large mammal bones (e.g., Blumenschine, 1988; Spencer & Marean, 1991; Capaldo, 1995). It has been demonstrated in Chapter Five that a bone assemblage modified by crocodiles under controlled conditions is predominated by complete bone specimens (Njau & Blumenschine, 2006).

The tooth-marked bones that are complete are common in springs, reflecting the rarity of hyenas in this setting (Figure 6.6.). Complete elements tooth marked by mammalian carnivores in lacustrine plains occur infrequently (17.1%), probably due to exposure to subaerial processes that fragment bone.

Tooth-marked complete long bones

The complete long bone specimens display a similar pattern (Table 6.15b). None of the long bone specimens tooth-marked by crocodiles was broken (Figure 6.7). All long bones bearing bisected marks in pool/riverbed and riverbank/over-bank sub-facets were intact. In contrast, long bones are often fragmented during consumption by mammalian carnivores. With the exception of spring sub-facets, the long bone specimens that are abandoned without being broken during consumption by mammalian carnivores are proportionately less common (13%-17%) in all sub-facets (Table 6.15b, Figure 6.7). Six out of fifteen (40%) specimens bearing both crocodile and mammalian carnivore tooth marks in pool/riverbed are complete. Generally, the number of whole long bones modified by crocodiles is significantly higher than those modified by mammalian carnivores in pool/riverbed and riverbank/over-bank sub-facets ($X^2 = 46$, df = 1, $P <$

0.05). These observations are consistent with results from the control sample, which shows that assemblages produced by crocodiles are composed primarily by whole long bones (see Table 5.1).

Table 6.15a. Proportion of tooth-marked bones that are complete, inferred to have been modified by mammalian carnivores, crocodiles or both.

Sub-facet	Mammalian carnivore		Crocodile		Both	
	NISP	%	NISP	%	NISP	%
Pool/riverbed	10	28.6	58	66.7	11	50.0
Riverbank/over-bank	224	32.2	4	100.0	0	0
Springs[§]	51	44.7	-	-	-	-
Lacustrine plains[§]	13	17.1	-	-	-	-

[§] No live crocodiles and no evidence of crocodile tooth marking on chewed specimens

Table 6.15b. Proportion of tooth-marked long bones only that are complete, inferred to have been modified by mammalian carnivores, crocodiles or both.

Sub-facet	Mammalian carnivore		Crocodile		Both	
	NISP	%	NISP	%	NISP	%
Pool/riverbed	2	15.3	28	100	6	40
Riverbank/over-bank	36	16.9	2	100	0	0
Springs[§]	11	45.8	-	-	-	-
Lacustrine plains[§]	6	13.6	-	-	-	-

[§] No live crocodiles and no evidence of crocodile tooth marking on chewed specimens

Figure 6.5. Tooth-marked specimens only (NISP), inferred to have been modified by mammalian carnivores, crocodiles, or by both agents for each sub-facet. RB/OVB= Riverbank and Over-bank. Live crocodiles not present in Spring and Lacustrine plains (data from Table 6.14a).

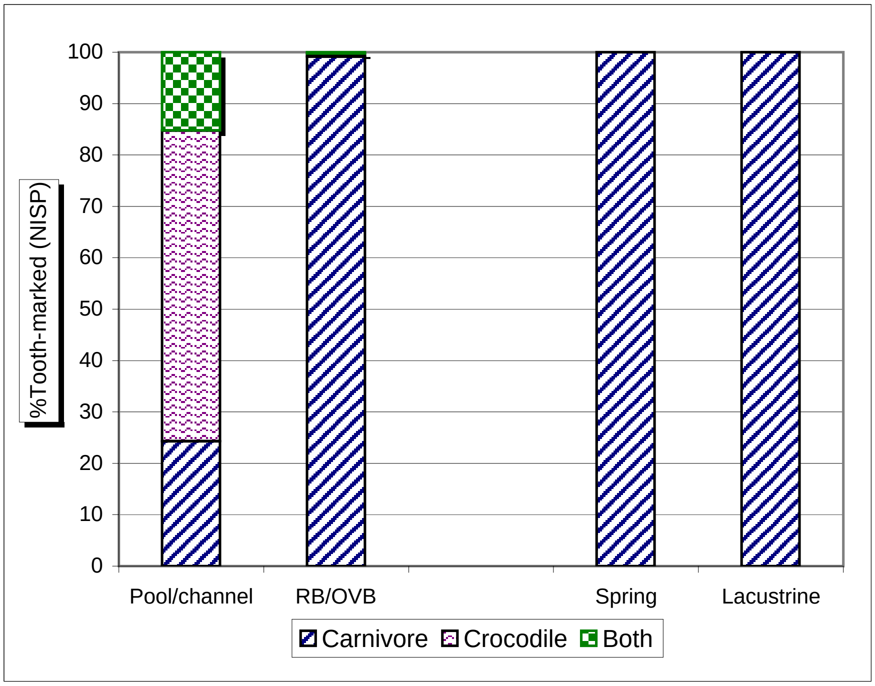


Figure 6.6. Proportion of tooth-marked whole bones (NISP) inferred to have been modified by mammalian carnivores, crocodiles, or both (data from Table 6.15a) RB/OVB= Riverbank and Over-bank.

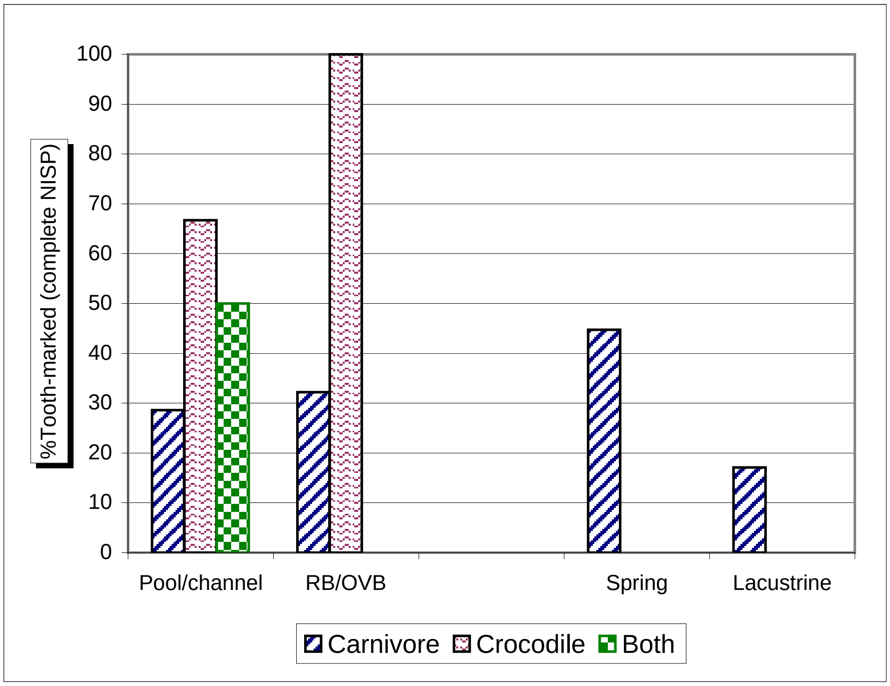
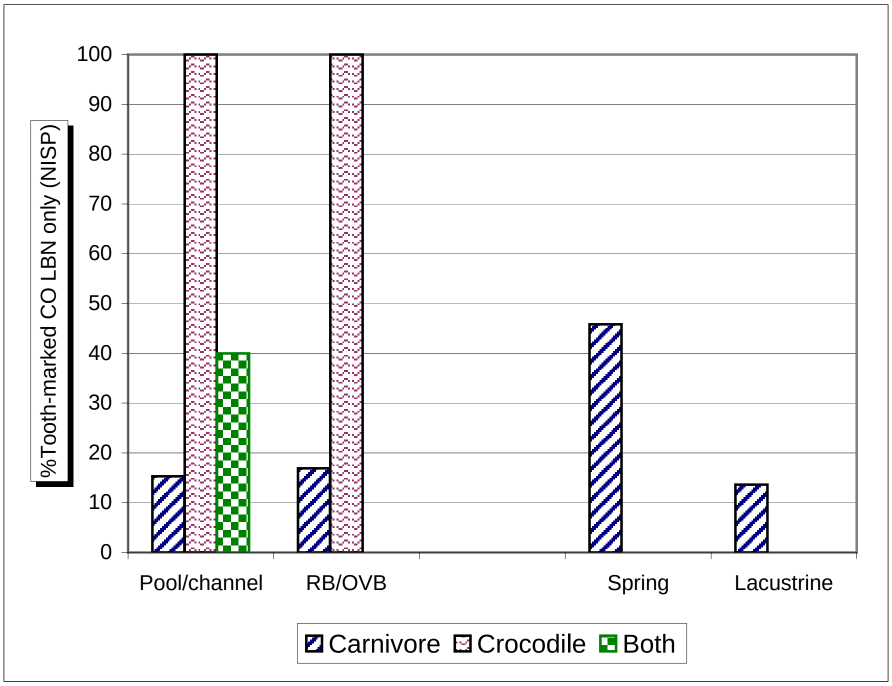


Figure 6.7. Proportion of tooth-marked long bones that are complete (NISP), inferred to have been modified by mammalian carnivores, crocodiles, or both. RB/OVB= Riverbank and Over-bank (data from Table 6.15b).



CHAPTER 7. OLDUVAI CASE STUDY: METHODS, ANALYTICAL SAMPLE, AND RESULTS

1. Introduction

Many of the stone artifact and fossil bone assemblages recovered from the paleo-Olduvai Basin have been interpreted as sites where Oldowan hominins manufactured stone tools and processed animal food (e.g., Isaac, 1971, 1983; Leakey, 1971). These rich stone-bone assemblages were deposited in or near fresh and saline, alkaline wetland settings in the Eastern Lake-Margin zone (Hay, 1976). However, the socioeconomic contexts in which these assemblages were formed have been questioned by various researchers (e.g., Binford, 1981; Potts, 1984; Blumenschine, 1987). The recent landscape paleoanthropological work conducted by OLAPP at Olduvai demonstrates that the lake margins contained a complex mosaic of landscape settings, affording various resources and predation risks to early hominins. The exposure to predation risk, particularly in wetland settings where mammalian carnivores and crocodilians (as evidenced by their body fossils) were present, was predicted to condition the intensity and nature of hominin activities, and the resulting trace fossils (Peters & Blumenschine, 1995, 1996; Blumenschine & Peters, 1998).

This chapter investigates the nature of hominin activities in wetland settings by examining the composition and characteristics of some of the Oldowan fossil assemblages. The analysis is guided by the results obtained from two neotaphonomic studies. The goal of the first study (Chapters Four and Five), which was conducted under controlled conditions, was to determine signature criteria of crocodile feeding traces in bone assemblages. The results from the control study were applied in order to characterize bone assemblages formed under the influence of both crocodiles and mammalian carnivores in modern riverine settings (Chapter Six). The goal of this study was to develop taphonomic criteria for determining patterns of crocodile and mammalian carnivore predation in different sub-facets within a riverine system. Density of bone occurrences, frequency of crocodile skeletal remains, frequencies of crocodile tooth marks, and completeness of skeletal elements are signature criteria established for determining the nature and composition of bone assemblages in environments inhabited by crocodiles. The occurrence of crocodile tooth marks on complete, ungnawed fossil bones is a primary taphonomic feature used in this chapter to assess the intensity of crocodile predation in paleo-wetland settings at Olduvai. Also, the distribution of crocodiles of different size across the paleo-basin landscapes is provided.

2. Defining the Olduvai sample

Only fossil materials from wetland deposits of Bed I and lowermost Bed II were sampled. In addition to sedimentological evidence, the following taphonomic evidence also indicates presence of wetland settings during the accumulation of some of the Oldowan fossil assemblages.

1) The occurrence of crocodilian body fossils, in particular shed teeth, is a good indicator of the aquatic habitat where the animal lived. Leakey (1971: 249) inferred that the abundant crocodile teeth, especially near the “occupation floor” at DK site, were shed by living crocodiles. Because crocodiles shed teeth in water, occurrences of these elements indicate presence of wetland inhabited by crocodiles.

2) The presence of bone specimens bearing crocodile tooth marks or damage, as first reported here in this chapter, provide direct evidence of crocodilian feeding, which is typically performed in water. Since crocodiles do not transport prey items long distances from kill sites, feeding is usually restricted to water or the water's edge. Diagnosing crocodilian feeding traces in the fossil record is a new paleoecological method of identifying ancient wetland environments.

To maximize the chance of finding bone modified by crocodile, the analysis focused on assemblages reported to contain crocodilian body fossils (Leakey, 1971; Potts, 1988; West, 1995; Blumenschine *et al*., in prep). These include the assemblage from FLKNN3, in which the OH 7 parietal fragments were inferred by Davidson & Solomon (1990) to have been modified by crocodiles.

The Olduvai sample was categorized into two sets: 1) assemblages excavated by Mary Leakey between 1960-1963, and 2) assemblages excavated by OLAPP between 1989-2001. The analytical sample includes the following assemblages, which were interpreted as "living sites" by Leakey: DK levels 1-3, FLK NN level 3, FLK level 22 (*Zinjanthropus*), and HWK E levels 1 and 2 (Table 1.1, Figure 1.1). The OLAPP sample examined here includes assemblages from FLK, VEK, HWK E, HWK W, MCK, TK-Loc 20, JK-WK, Loc 60 and Loc 64.

3. Analytical procedures

Numerous studies have provided partial or complete lists of large vertebrate taxa and skeletal remains from Bed I and Bed II (e.g., Leakey, 1971; Bunn, 1982; Potts, 1988; Blumenschine *et al*., unpublished). Therefore, my major focus was to examine bone surfaces for traces of postmortem biotic processes that influenced assemblage formation. Previous studies of bone modification have identified mammalian carnivore, rodent and hominin stone tool damage on the bone specimens from Olduvai collections (e.g., Bunn, 1981; Potts & Shipman, 1981; Bunn & Kroll, 1986; Blumenschine & Selvaggio, 1988, 1991; Oliver, 1994; Blumenschine, 1995; Monahan, 1996; Capaldo, 1997; Dominguez-Rodrigo, 1997). None of these studies, however, identified crocodilian damage to bones.

A systematic search for carnivore tooth marks was performed with the aim of generating data on the incidence of crocodilian tooth marks in the bone assemblages. Only bones of large mammals and crocodiles were analyzed. The analysis was guided by my experience with control samples of bones modified by Nile crocodiles, published criteria of bone damage by mammalian carnivores, and my own experience of examining control assemblages modified by known mammalian carnivores. Procedures and criteria for identifying crocodilian tooth-damaged bones are described in detailed in Chapter Four, while criteria for identifying mammalian carnivore tooth marks are described in various published accounts (e.g., Haynes, 1980, 1982a, 1982b, 1983a; Binford, 1981; Bunn, 1981; Shipman, 1981b; Shipman & Rose, 1983; Blumenschine *et al*., 1996).

Each specimen was systematically inspected on the cortical surface of complete elements and on the cortical and internal surfaces of bone fragments, using a low magnification 16 x hand lens, under a 100 watt table light, following Blumenschine's (1995) procedure. Located marks were examined for the morphological features distinguishing crocodilian from known mammalian carnivore tooth marks and stone tool butchery marks (Table 7.1). Guided by results from the control sample, whole long bone specimens were preferentially selected for this study.

After a specimen was examined carefully, attribute states were coded using a bone coding system modified from the Zooarchaeological Coding Convention (developed by Blumenschine; Appendix I) and entered into the Excel spread sheet. Along with corresponding locality and stratigraphic levels of specimen recovery, the following relevant attributes were coded: taxon; estimated animal size and age (e.g., Bunn, 1982; Capaldo, 1995); skeletal element, portion and segment; circumference of the bone shaft; weathering stages; root etching and other types of chemical or physical factors that may exfoliate or adhere to bone surface and obscure marks; type of fracture; presence of recent breakage (post-depositional); presence of butchery damage (cut marks and percussion marks) and tooth marks; and inferred agent of tooth-marking (i.e., mammalian carnivore, crocodile or rodent). The basic quantitative unit used for this analysis is NISP, the number of specimens identified to at least general skeletal part.

i) Tooth mark identification

Bone modification is expressed as an occurrence of at least one tooth mark per bone specimen. Carnivore tooth marks are further identified as pits, punctures, scores or furrows (Table 7.1). Bones were identified as crocodile-modified only if a bisected mark was present.

Table 7.1. Criteria for diagnosing mammalian carnivore tooth marks and butchery marks on bone surfaces. Carnivore damage patterns are established from observations of carnivore feeding in natural and captive settings (Blumenschine *et al*., 1996).

Features	Tooth mark (hyena & lion production)	Cut-mark (metal knife)	Stone tool-percussion mark
Plan form	Pit= Circular to polygonal, variable size Score= linear, straight usually broader than cut marks Puncture= Circular, usually large Furrow= Linear, usually large and linear	Linear, usually narrower than tooth scores	Pit= carnivore tooth pit Groove= Deeply embedded patch of parallel microstriations
Cross section	Pit = Bowl-shaped to irregular Score & Furrow = U-shaped; Rarely V-shaped Puncture =Bowl-shaped	V-shaped	Pit= Bowl-shaped to irregular Groove= Individual striae are V-shaped
Orientation to bone's long axis	Score= tending to transverse Furrows= perpendicular to break edge	Oblique= filleting Transverse= disarticulation	Groove= Transverse
Associated microstriations in internal surface	Microstriations uncommon, distinctly broader, occur in patches significantly less dense than percussion produced	Contain multiple, fine, linear striations which cut into, and orient longitudinally	Microstriations are shallower, narrower, and usually shorter occurring in dense unidirectional patches
Other features on inner surface	Internal surface crushed	Lacks internal crushing	Lacks internal crushing

ii) Analytical sample

Leakey's sample

A total of 622 bone specimens were examined for surface condition in the paleontology laboratory at the National Museum of Kenya. The sample is from four sites excavated by Leakey on the Eastern Lake Margins of Bed I and lower Bed II (Table 7.2). All fossil materials recovered from these large excavations had been exported by Leakey to Nairobi, where they are currently curated in the National Museum of Kenya.

The collection in the museum is organized taxonomically with specimens stored in wooden trays and secured on metal shelves. Each tray has an identification number and is arranged in shelves according to sites and lithological levels. In most cases, bones of individual skeletal groups (e.g., limbs) from the same site and level are sorted into one tray, therefore simplifying the task of locating specimens from the shelves. Each specimen has an accession number labeled on the bone surface. In order to be able to locate any particular bone specimen for further analysis, I recorded both the specimen identification number, and the tray and shelf numbers from which the specimen derived. For sites such as DK, in which more than one excavation was conducted, the number of each excavation strip was indicated. After bone specimens were carefully dusted off with a soft brush, and examined for the surface marks, they were placed back in the tray and covered by a plastic sheet before being returned to the shelves.

Leakey’s collection, especially the large and extensively well-preserved assemblages such as FLK 22, has received extensive analysis from that focusing on taxonomy and systematics to functional anatomy, taphonomy and zooarchaeology. Most zooarchaeological studies have aimed to understand the formational history of the juxtaposition of fossils and stone tool artifacts. Following Leakey's (1971) general description of the Bed I and Bed II Olduvai fauna, the analysis of bone specimens has expanded from taxon and skeletal identification (e.g., Tchernov, 1976, 1986; Gentry & Gentry, 1978a, 1978b; Bunn, 1982, 1983; Potts, 1982, 1988; Stewart, 1994) to identification of classes of biotic damage to bone such as: 1) mammalian carnivore induced tooth marks and fragmentation; 2) hammerstone-induced impact and fracture marks; and 3) cut marks (e.g., Bunn, 1981; Potts & Shipman, 1981; Shipman, 1981a, 1981b, 1983, 1986a; Blumenschine & Selvaggio, 1988, 1991; Oliver, 1994; Blumenschine, 1995; Capaldo, 1997; Dominguez-Rodrigo, 1997).

Similarly, skeletal part profiles have been quantified to evaluate the degree of carnivore involvement in the assemblages (e.g., Bunn, 1982, 1986; Bunn & Kroll, 1986; Bunn & Ezzo, 1993; Potts, 1988), while subaerial weathering of bone surfaces have been examined to assess burial and preservation processes acting on bones (e.g., Potts, 1986, 1988). Among the specimens sampled in the current study, 493 come from FLK 22, FLK NN and DK sites in Bed I, while 129 specimens come from HWK E in Lowermost Bed II (Table 7.2).

Table 7.2. Number of bone specimens analyzed for bone surface modification from Olduvai Gorge sites excavated by Mary Leakey (1971).

Strata	Site		N
Lower BED II	HWK E	Level 2	42
	HWK E	Level 1	87
BED I	FLK	Level 22	203
	FLK NN	Level 3	44
	DK	Level 1	13
	DK	Level 2	146
	DK	Level 3	87
Total			622

OLAPP Sample

The OLAPP collection is curated at the National Natural History Museum in Arusha, Tanzania. The materials are organized in trays and cabinets according to trench number and year of excavation. Each specimen has an accession number and is bagged according to trench and lithological level. This system enables individual specimens to be accessed from the shelves. The analysis focused on long bones excavated from seventeen trenches that were reported to contain crocodilian body fossils or traces of crocodile feeding (Table 7.3), with the exception of Trench 34, which contains no crocodile specimens.

Table 7.3. Trenches examined for traces of crocodilian bone modification.
The trenches were selected based on the occurrence of crocodilian body fossils.

Geographical locale/ Associated Outcrop	Trench
FLK	18, 47, 112B
VEK	21[§], 22, 45, 72, 110, 111
HWKW	23, 44
HWKE	24, 43, 104.2, 104.4, 104.18
HWKEE-KK	107
MCK	27, 34[*], 53
TK-LOC20	41
JK-WK	125
Western Basin: LOC 60	71
Western Basin: LOC 64	57 (Upper Bed I)

[§] Evidence of crocodile modification (Njau & Blumenschine, 2006)
[*] Crocodile body fossil not present

4. Tooth-marked hominin specimens

An analysis of surface marks was conducted on the early *Homo* specimens OH 7 and OH 8, using similar analytical procedures described above, with slight modification to suit the study. The study was conducted together with Dr. Robert Blumenschine at the National Museum of Tanzania in Dar es Salaam. These fossil remains were recovered from FLK NN level 3 by the Leakeys in early 1960s (Leakey, 1960, 1961a, 1961b). OH 7, which is represented by the juvenile hand, jaw and skull fragments, became the holotype of *Homo habilis* (Leakey *et al*., 1964; Leakey & Leakey, 1964). OH 8, which is comprised of foot bones of a sub-adult individual (Susman & Creel, 1979; Susman & Stern, 1982; *contra* Day & Napier, 1964; Leakey, 1961a, 1971), became part of the paratype. The hominin remains were found scattered over the "occupation floor" in conjunction with other faunal remains of obligate drinkers (i.e., reduncini), indicating that the site was formed close to a marsh in the lake margin (Leakey, 1971: 229). This interpretation was in part based on the presence of crocodilian body fossils and the abundance of *Kobus* sp. in the assemblage.

Carnivore tooth marks have been reported to exist on the right parietal bones of OH 7 and talus of OH 8 by various researchers (e.g., Leakey, 1971; Davidson & Solomon, 1990). The marks were inferred to have been produced by large-size carnivore other than hyena because hyena would have totally ravaged the soft bones of these immature hominins (Leakey, 1971; Tobias, 1991). However, on the basis of the scattering nature of the remains, Reader (1981: 185) argued that the remains reflect typical hyena behavior of bone ravaging and dispersal. More recently, crocodiles have been inferred to have produced the tooth marks on the parietal bones of OH 7 (Davidson & Solomon, 1990). The marks are conspicuous and roughly parallel scores. They are very large, wide and shallow (Davidson & Solomon, 1990: 197; Leakey, 1971:228). The breakage on the tips of OH 8 metatarsal bones have been attributed to gnawing by mammalian carnivores (Susman & Stern, 1982).

An extensive search for marks was performed for each specimen, first by the author and then together with Blumenschine, at which time we described the damage features. Analyses were repeated for the marks that seemed to be of great interest or those displaying some ambiguity as to agent of production. A detailed and full description for each tooth mark was recorded and photographed by digital camera (Nikon 8 Mega-pixels with built-in macrolens).

Although the foot bones (OH 8) were found to articulate with OH 35 specimens (tibia and fibula), and thus were inferred to derive from a single individual (Susman & Stern, 1982), no tooth marks have been reported on the OH 35. If the foot bones, tibia and fibula belonged to the same individual, then it is most likely that the tibia and fibula would have been tooth marked, at least on the distal portions were they articulate with the talus and cuboid bones.

Investigations made on the OH 35 casts show that these specimens bear tooth mark damage, including pits, punctures, and scores on the distal parts of tibia and fibula. However, in order to determine the specific carnivore responsible for the bone modification, a detailed and full description of individual tooth mark from the original specimens is required. This detailed analysis will allow precise comparison of tooth marks inflicted on OH 8 and OH 35. If OH 8 and OH 35 bones preserve similar patterns of tooth marking as expected for an articulated hominin ankle, then the specimens will be confirmed independently to derive from a single individual, as proposed by Susman and Stern (1982).

The goal of our analysis was to conduct a systematic search for crocodile tooth-marks, by using the referential framework developed from my control sample of crocodile feeding traces.

5. Results

i) Leakey Sample

The analysis of fossil material excavated by Mary Leakey involved the initial taxonomic identification of bone specimens in order to determine groups of animals that were most affected by crocodilian predation. Taxonomic assignments were possible for most complete skeletal elements or fragments with diagnostic anatomical landmarks. The analyzed sample was comprised of larger mammalian and crocodilian bone specimens (Table 7.4). Size 1 animals identified included *Antidorcas recki*, small antilopini, unidentified bovid and mammals, and young size 2 animals. Size 2 animals included large antilopini, indeterminate bovids, suids and mammals, and young size 3 animals. Size 3 animals include *Parmuliaris altidens, Kobus sigmoidalis, Kobus* sp., tragelaphini, reduncini, hippotragini, alcelaphini, indeterminate bovids, indeterminate suids, and indeterminant mammals and young size 4 animals. Size 4 animals include *Megalotragus*, indeterminate equids, indeterminate bovid, indeterminant mammals and young size 5 animals.

Surface bone modification

A total of 468 (75.2%) of specimens in analytical sample are tooth-marked (Table 7.5). Only 26 specimens among the tooth-marked bones bear at least one bisected tooth mark, a diagnostic trace of crocodile feeding. Since at the time of analysis I did not possess my current understanding of the variability in crocodilian tooth marks and the nature of associated damage on a full range of skeletal elements (see Appendix III), I was recording only bisected pits and punctures as indicative of crocodile feeding. This conservative estimate, that excludes some potentially crocodile-modified bones, such as ungnawed complete specimens with dense concentrations of tooth marks or bones possessing hook scores, underestimates the overall frequency of bones tooth marked by crocodiles.

All other tooth mark damage to bones was therefore attributed to mammalian carnivores unless marks were bisected. Tooth marks produced by mammalian carnivores occur on 442, or 71%, of the bone specimens analyzed (Table 7.5). Bone damage attributed to mammalian carnivores among the Leakey assemblages is generally higher compared to crocodilians, ranging from 46% – 86%, whereby bones modified by crocodiles account for only 1% – 9% of the analytical sample. Table 7.6, which describes the skeletal type and completeness of specimens bearing at least one bisected mark, indicates that they are all virtually complete and lack gross gnawing. The incomplete specimens possess postdepositional breaks. This observation is consistent with samples from both captive setting and crocodile pools along the Grumeti River (Table 5.1, 6.15a, 6.15b).

The majority of bone specimens (91%) examined in the analytical sample for surface modification are long bones (Table 7.7). In the following sections, I will report the tooth-mark data recorded on long bone specimens so that they can be compared with mammalian carnivore tooth marks reported by other workers from the same assemblages (e.g., Blumenschine, 1995; Capaldo, 1995, 1997; Monahan, 1996). A total of 122, or 60.7% of all long bone specimens from HWKE levels 1 and 2 were examined, whereas only 180 specimens (24.6%) were analyzed from FLK level 22 (Table 7.7 & 7.8). All of the long bone specimens from FLK level 3 (N=43) were analyzed, while 212 (75.2%) long bone specimens from DK levels 2 and 3 were analyzed.

Crocodile tooth marks occur on only 22 long bone specimens, 13 of which are complete elements, seven are ends with intact epiphyses, and two are midshaft cylinders (Table 7.6). The broken specimens have evidence of recent breaks. None of the long bone fragments broken prior to fossilization examined contained bisected marks. Other specimens that contain at least one bisected mark but are not included in this analysis include one complete phalanx, two complete calcanea, and one broken iliac bone (Table 7.6).

DK has the highest proportion of long bones modified by crocodiles in the analytical sample (6.7%), followed by HWKE level 2 (5.7%), FLKNN3 (4.6%), HWKE level 1 (1.1%) and FLK 22 (1.1%) (Table 7.8, Figure 7.1).

The majority of tooth-marked long bones bearing crocodile modification belong to small and medium sized mammals (size 1-3), while only one specimen (4.5%) belongs to a size 4 mammal, and five specimens (22.7%) to crocodiles (Table 7.6). The abandonment of carcasses by crocodiles depends on the size of crocodile relative to prey size, and also the abundance of prey. Adult crocodiles are known for preying on young crocodiles, and this behavior is reflected in the crocodile bone specimens bearing bisected marks.

Table 7.4. Number of bone specimens (NISP) analyzed for surface modification, indicating the proportion of animals of different size and taxon represented for each sampled assemblage.

Site & Level	Mammalian Size Class								Crocodile Size Class				Total
	1		2		3		4		Large		Small-Med		
	n	%	n	%	n	%	n	%	n	%	n	%	n
HWKE Level 2	1	2.4	29	69.0	11	26.2	1	2.4	0	0	0	0	42
HWKE Level 1	11	12.6	16	18.4	55	63.2	5	5.7	0	0	0	0	87
FLK Level 22	64	31.5	8	3.9	78	38.4	53	26.1	0	0	0	0	203
FLKNN Level 3	4	9.1	6	13.6	28	63.6	6	13.6	0	0	0	0	44
DK Level 1	0	0.0	0	0.0	11	84.6	2	15.4	0	0	0	0	13
DK Level 2	16	11.0	30	20.5	62	42.5	14	9.6	3	2.1	21	14.4	146
DK Level 3	11	12.6	21	24.1	37	42.5	11	12.6	0	0	7	8.0	87
Grand Total	107	17.2	110	17.7	282	45.3	92	14.8	3	0.5	28	4.5	622

Table 7.5. Analytical sample: Proportion of bone specimens (NISP) bearing at least one tooth mark produced by mammalian carnivores, crocodiles or rodents.

Site & Level	Carnivore		Crocodile		Rodent		Total
	NISP	%	NISP	%	NISP	%	NISP
HWKE L2	28	66.7	3	7.1	1	2.4	42
HWKE L1	75	86.2	1	1.1	2	2.3	87
FLK 22	157	77.3	3	1.5	18	8.9	203
FLKNN L3	28	63.6	2	4.5	4	9.1	44
DK L1	6	46.2	0	0.0	0	0.0	13
DK L2	99	67.8	13	8.9	4	2.7	146
DK L3	49	56.3	4	4.6	1	1.1	87
Grand Total	442	71.1	26	4.2	30	4.8	622

Table 7.6. Skeletal parts modified by crocodiles listed by site and level from which they derive, and indicating completeness, taxon and age.

Site & Level	Element[1]	Completeness	Taxon & Size	Age
HWKE L1	TIB	Complete	Antilopini size 1-2	Adult
HWKE L2	HUM	Complete	Alcelaphini size 3	Adult
HWKE L2	HUM	Complete distal end	Bovid size 2	Adult
HWKE L2	CAL	Complete	Bovid size 2	Juvenile
FLK 22	INNO	Iliac fragment	Bovid size 3	Juvenile
FLK 22	ULN	Complete proximal end	Antilopini size 1-2	Adult
FLK 22	MCM	Complete	Antilopini size 1-2	Adult
FLKNN L3	MCM	Complete	Antilopini size 1-2	Adult
FLKNN L3	MCM	Complete proximal end	Bovid size 2	Adult
DK L2	HUM	Complete	Parmularius *sp.*	Adult
DK L2	HUM	Complete	Crocodile (small)	Juvenile
DK L2	RAD	Complete	Parmularius *sp.*	Adult
DK L2	RAD	Proximal end plus shaft	Crocodile (small)	Juvenile
DK L2	RAD	Complete distal end	Bovid size 1	Adult
DK L2	MCM	Complete	Parmularius *sp.*	Adult
DK L2	MCM	Complete	Tragelaphini size 3	Adult
DK L2	FEM	Complete shaft	Crocodile (small)	Juvenile
DK L2	TIB	Complete	Bovid size 3	Juvenile
DK L2	FIB	Complete shaft	Crocodile (small)	Juvenile
DK L2	FIB	Complete distal end	Crocodile (small)	Juvenile
DK L2	MTM	Complete	Alcelaphini size 3	Juvenile
DK L2	PHA	Complete	Bovid size 2	Adult
DK L3	HUM	Complete	Suid size 3	Adult
DK L3	HUM	Complete proximal end	Bovid size 4	Juvenile
DK L3	CAL	Complete	Bovid size 3	Juvenile
DK L3	MTM	Complete	Tragelaphini size 3	Adult

[1] Element abbreviations are defined in Appendix I

Table 7.7. Skeletal part composition of samples analyzed from each assemblage. LBN CO= Complete long bone; LBN END= Long bone end with complete circumference; LBN SH= Long bone shaft portions; CBN= Compact bone; NID= indeterminate.

SITE & LEVEL	RIB NISP	GIRDLE NISP	LBN CO NISP	LBN END NISP	LBN SH NISP	CBN NISP	NID NISP	TOTAL NISP
HWKE L2	0	2	7	25	3	5	0	42
HWKE L1	0	0	16	60	11	0	0	87
FLK 22	16	3	10	49	118	4	3	203
FLKNN L3	1	0	4	26	13	0	0	44
DK L1	0	0	0	7	0	4	0	13
DK L2	0	0	22	95	15	14	0	146
DK L3	0	0	13	58	9	7	0	87
Sub Total	17	5	72	320	171	34	3	622

Table 7.8. Incidence of tooth-marked long bones bearing at least one bisected mark, measured as a percent of the total number of long bones in the analytical sample. Tooth-marked specimens lacking bisected marks are attributed to mammalian carnivore damage.

Site & Level	[1]Total	Bisected tooth marks		Carnivore tooth marks		[2]Other studies		
						Total	Tooth-marked	
	NISP	NISP	%	NISP	%	NISP	NISP	%
HWKE L2	35	2	5.7	25	71.4	201[¶]	59	29.3
HWKE L1	87	1	1.1	75	86.2	-	-	
FLK22	180	2	1.1	139	77.2	731[†]	444	60.7
FLKNN3	43	2	4.6	28	65.1	43[*]	-	
DK2/3	221	15	6.7	140	63.3	282[*]	-	
Total	566	22	3.8	407	71.9			

[1] Total number of long bones in recorded in this study

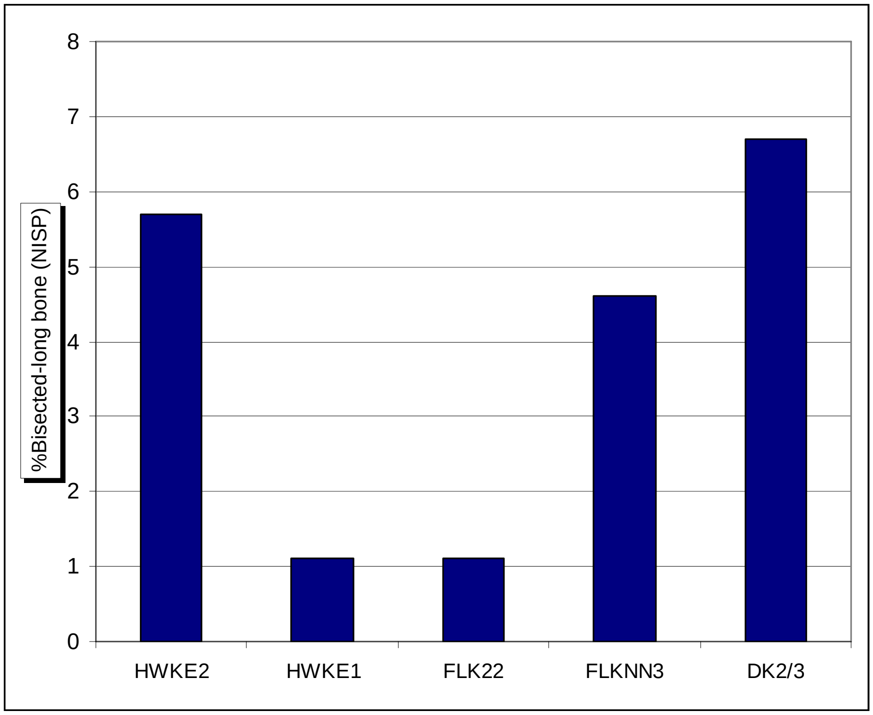
[2] Total number of long bones from Mary Leakey assemblages reported by other researchers

[¶] Combined number of HWKE levels 1 and 2 reported by Monahan (1996), for incidence of carnivore tooth marks, cut marks and percussion marks on long bones

[†] Analytical sample reported by Blumenschine (1995) on incidence of tooth marks and percussion marks on long bones (excluding intact elements). The original number tallied by Bunn (1982) is 1,450, but included fragments with recent breaks, poor surface condition, <2 cm long, and larger animals > size 5

[*] Number tallied by Potts (1988)

Figure 7.1. Incidence of tooth-marked long bones bearing at least one bisected mark, measured as a percent of the total number of long bones in analytical sample (data from Table 7.8).



ii) OLAPP Sample

a. Bone specimens modified by crocodiles

Two specimens excavated from stratigraphic units that contain crocodile specimens, fossils of obligate drinkers, and Oldowan stone artifacts in lowermost Bed II have been described by Njau and Blumenschine (in press) to contain crocodilian tooth marks. They include a tibia of a juvenile eland-sized bovid and an adult equid (zebra-sized) femur from Trench 21 in VEK. Both specimens are complete with the exception of the bovid tibia, for which the unfused proximal epiphysis was not located in excavation. The bones are heavily and conspicuously tooth-marked, but none are gnawed. Investigation of other OLAPP trenches that contain shed teeth has yielded few specimens with crocodile tooth marks. Only three specimens, each from a different trench, have crocodile tooth marks (Table 7.9).

These include a complete radius of an adult Grant's gazelle-sized bovid from hominin Trench 57 in Bed I, a femur midshaft (with recent breaks) of a size 3 bovid from HWKW, and a broken scapula (recent breaks) from MCK in lowermost Bed II. The radius, with its ungnawed ends, bears dozens of deep to narrow, mainly transversely oriented scores all along the shaft and at least one bisected pit. The femur fragment (~60 mm long) has a good surface condition with minor waterlogged cracking. In addition to one bisected pit, there are two scores transversely oriented and one pit on the cortical surface but no tooth marks on the medullary surface. The scapula glenoid end portion (~ 80 mm long) from MCK is post-depositionally broken, slightly weathered (stage 2) and has minor surface exfoliation, rounding and waterlogged cracking. There is one bisected pit (ca. 1 mm) located on the medial side. The internal surface of the mark is slightly smoothed by rounding. Two tiny and shallow pits (half-bisected) are located on the same side towards the cranial end of the scapula. Also two sharp, narrow but shallow curved scores run parallel near the bisected pit. The specimen bears one short cut mark on the lateral ventral side of the glenoid end, and a few trample marks and insect traces.

Table 7.9. Bone specimens modified by crocodilians from Lowermost Bed II

Outcrop	Trench	Taxa	Skeletal Part Portion
HWKW	44	Bovid size 3	FEM shattered midshaft
VEK	21[§]	Bovid size 3	Tibia complete
VEK	21[§]	Equid size 3-4	Femur complete
MCK	34	Equid size 3-4	Glenoid end of scapula
LOC 64	57[*]	Bovid size 2	Radius complete

[§] Njau & Blumenschine (in press)
[*] Hominin level (Upper Bed I)

b. Distribution of crocodiles across paleolandscapes

Crocodilian body fossils are documented throughout the basin during lowermost Bed II times (Tables 7.10; Figures 7.2). In the Western Basin, crocodile were recorded in Localities 60 and 64 (Trench 57). One trench (# 71) out of two excavated at Locality 60 (Western Lowermost Bed II) yielded crocodile material, while none of the nine trenches dug in the Naisiusiu Complex yielded any crocodile material (Figure 7.3). With the exception of MCK, crocodile specimens are well represented in all geographic locales in Eastern Lake Margin and distal Eastern Alluvial Fan. Generally, the frequency of crocodile specimens in bone assemblages from Olduvai localities is relatively higher than that observed in modern pool/riverbed samples from lower Grumeti River (Tables 6.9a, 6.9b, 7.10, 7.11).

The occurrence of crocodile body fossils is relatively higher in FLK, HWK and VEK suggesting substantial stable crocodile habitats in this area during lowermost Bed II times. These locales also present evidence of crocodilian feeding traces (Table 7.9; Figure 7.2). Observations of modern crocodile settings indicate feeding traces of crocodiles occur more frequently in crocodile living sites. Although the occurrence of crocodiles is rare in HWKEE-KK, TK-LOC 20, and JK-WK fossil deposits, this species predominates the large vertebrate assemblages (Table 7.11, Figure 7.4). In the absence of preservation biases, predominance of crocodile in these bone assemblage indicates wetland contexts.

In addition to understanding the location of crocodile occurrences, the size of crocodiles (body lengths) were assessed in order to determine parts of the landscapes that accommodated the largest individuals. Crocodile lengths were estimated from the size of the largest tooth recovered in a trench. In this study, tooth size is determined by maximum length of its crown (Table 7.10). The body sizes of Olduvai crocodiles are estimated from the largest teeth measured from the known body size of living Nile crocodiles.

Morphometric studies of crocodilians demonstrate that the skull and total body lengths of young and adult crocodiles are strongly correlated, and that sexual variation is negligible (e.g., Poole, 1961; Greer, 1974; Webb & Messel, 1978; Webb *et al*., 1983; Woodward *et al*., 1995). Based on this method, cranial material has been used to reconstruct total body lengths of fossil crocodilians, including the giant species such as *Deinosuchus, Sarchosuchus,* and *C. lloidi* (or *R. llyoidi*) (e.g., Erickson & Brochu, 1999; Sereno *et al*., 2001; Schwimmer, 2002; Storrs, 2003). However, the criteria for determining body length directly from tooth size remains poorly developed, despite Poole’s (1961) indication that tooth enlargement in crocodiles during growth may correspond to the increase in the length of the tooth row (jaws). The great variation in tooth enlargement within a socket during replacement (Poole, 1961; Erickson, 1996a, 1996b), and variations in growth rate of individuals (e.g., Kalin, 1933; Iordansky, 1973; Dodson, 1975), may hinder direct correlations between tooth size and body-length. Nonetheless, conservative estimates of crocodile jaw and ultimately body length can be made from the size of the largest tooth of an individual (e.g., Davidson & Solomon, 1990).

Following this preliminary method, the largest tooth measured from a 5 m long dead crocodile encountered in one of the study sites at Grumeti River is about 41 mm (crown length) (Table 7.10). Most of the functional teeth were still embedded in the jaws, and the series of successional teeth observed in the jaws suggests that this animal died prematurely, and was still growing. Other measurements were obtained from the largest shed teeth collected from Bagamoyo farm. The size of the largest tooth from the *bandas* that housed large crocodiles (maximum body length = 4 m) and small-medium sized (maximum body length = 2.5 m) crocodiles are ca. 33.7 mm and 21.8 mm, respectively (Table 7.10).

The tooth sizes from a dead Grumeti crocodile and living Bagamoyo crocodiles provide rough estimates of the minimum crocodile body lengths in fossil assemblages. Based on these preliminary estimates the largest crocodile at HWKE, VEK and Trench 57 exceeded 5 m (Figure 7.5). A crocodile that possesses a tooth this large can kill a buffalo-sized animal and can swallow a gazelle-sized animal whole without leaving behind many remains of the prey. Crocodiles probably as large as 4 m long existed in HWKW. Although the number of tooth specimens are underrepresented in FLK, HWKEE-KK, MCK and TK these data suggest that crocodiles large enough to prey upon small land mammals like gazelles and hominins were present in these locales. Generally, HWK and VEK complexes supported large and probably stable wetland systems sufficient to accommodate large crocodiles greater than 5 m long (Figure 7.5). Variation in tooth size is high within the Olduvai assemblages (Figure 7.5). This pattern is also common in modern crocodiles, and is partly attributed to the great variability of tooth size within individuals (see above).

Table 7.10. Distribution of crocodiles across Olduvai paleolandscapes expressed as frequency of crocodile specimens relative to total number of large mammal and crocodilian specimens recorded in OLAPP trenches (NISP values). Size of the largest crocodile shed-teeth recorded from OLAPP trenches, and live and dead Nile crocodiles of known body lengths from Bagamoyo and Lower Grumeti River are provided in columns five and six. Tooth size is obtained by recording the maximum length of the crown. The maximum diameter of the base of the teeth is also provided. TTH= Tooth; BYO= Bagamoyo; GRU= dead crocodile from lower Grumeti River.

Olduvai Site	Trench #	Crocodile body fossil NISP	Crocodile body fossil %	Maximum Crown Length (mm)	Maximum Basal Breadth (mm)
FLK	18	1	-	11.8	7.3
FLK	47	2	66.7	22.1	12.2
FLK	112B	13	92.9	28.8	14.9
VEK	22	1	50.0	12	7
VEK	72	*2*	66.7	15.3	10.3
VEK	45	12	53.8	28	16
VEK	21	19	40.4	38.6	15.6
VEK	111	26	46.4	45.1	22.2
VEK	110	11	78.6	-	-
HWKW	23	6	75.0	23.8	12
HWKW	44	26	51.0	32.8	14.7
HWKE	24	1	100.0	24.5	11.5
HWKE	43	9	33.3	32.3	14.4
HWKE	104.2	24	50.0	38.5	18.8
HWKE	104.18	12	80.0	56.7	25.4
HWKE	104.4	33	60.0	69.2	33.3
HWKE	104.5	2	9.5	-	-
HWKE	104.6	1	4.5	-	-
HWKEE	107	1	100.0	10.6	7.2
TK-LOC20	41	2	100.0	14.8	7
MCK	27	1	14.3	24.3	13
MCK	53	1	50.0	-	-
JK-WK	125	1	100	-	-
WEST	71	2	40.0	16	11
[¶]LOC64	57	8	40.0	40.7	19.1

Modern crocodile	Known Body Length (m)	Modern TTH NISP	-	Maximum Crown Length (mm)	Maximum Basal Breadth (mm)
Live – BYO	2.5[*]	268		21.8	12.0
Live – BYO	4.0[*]	89		33.7	19.3
[†]Dead –GRU	5.02	61		41.0	25.0
[†]Large –GRU	>> 5.0	12		54.3	29.5

[¶] Hominid trench from Upper Bed I

[*] Estimated body length of the largest crocodile in the *banda*

[†] Shed teeth found on the drying crocodile pool in lower Grumeti River. The size of the largest teeth indicates the animal was larger than 5 m.

Figure 7.2. Distribution of crocodiles across Olduvai paleolandscapes expressed as frequency of crocodile specimens relative to total number of large mammal and crocodilian specimens recorded in OLAPP trenches (NISP values). TM= evidence of bone specimens bearing crocodilian tooth mark-damage. Data from Table 7.10.

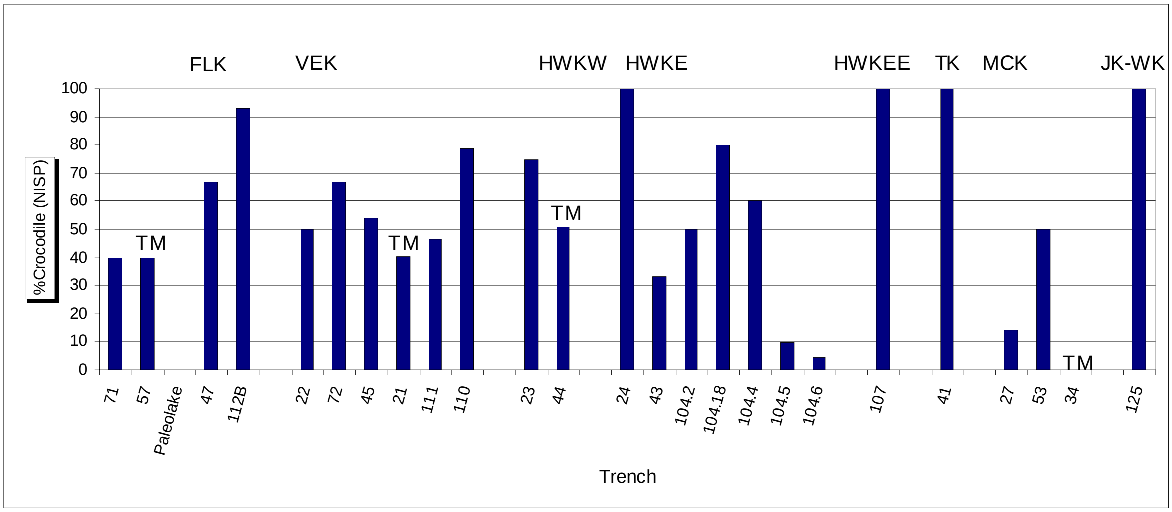


Figure 7.3. Map of Olduvai Gorge, showing the location of OLAPP trenches (boxes) and the geographic locales into which they are allocated (Figure from Blumenschine *et al.* 2005a).

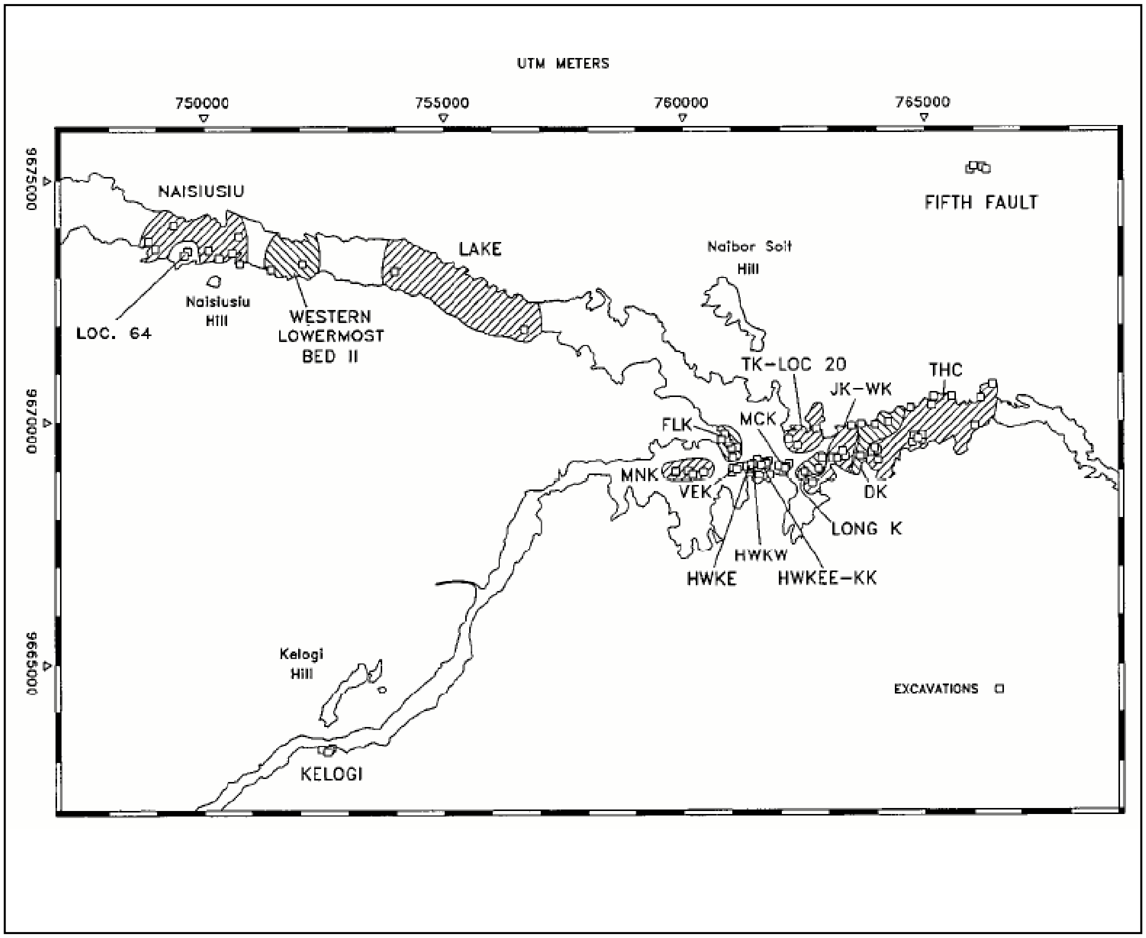


Table 7.11. Frequency of crocodile specimens from each geographic locale (see Figure 7.2).

Locality	Crocodilian Body Fossil NISP	%	Total Large Vertebrate NISP
LOC 64 (Trench 57)	8	40.0	20
WEST (Trench 71)	2	40.0	5
FLK	15	88.2	17
VEK	73	49.3	148
HWKE	79	54.1	146
HWKEE	1	100.0	1
TK LOC20	2	100.0	2
MCK	2	22.2	9
JK-WK	1	100.0	1

Figure 7.4. Frequency of crocodile specimens from each geographic locale or outcrops (data from Table 7.11).

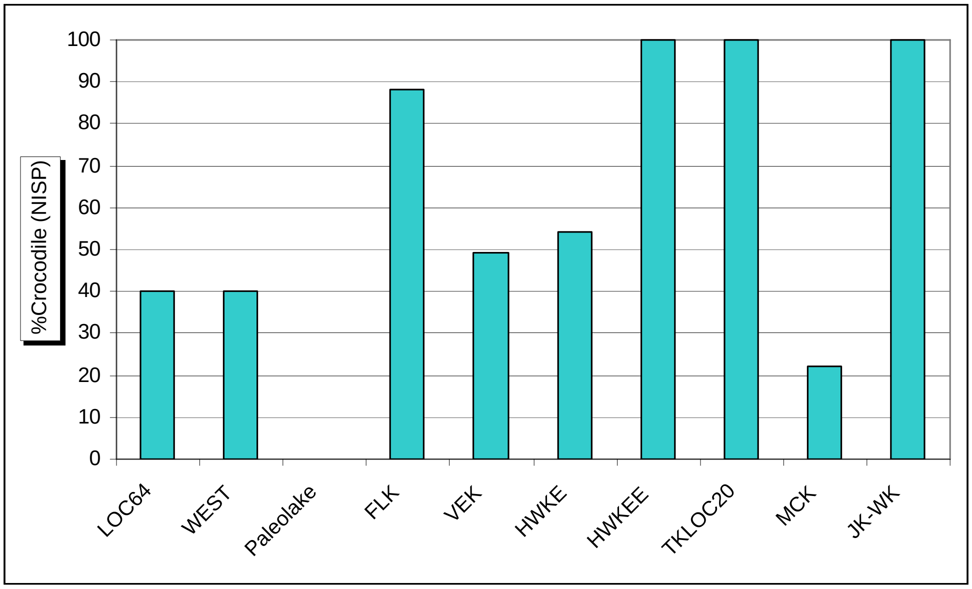
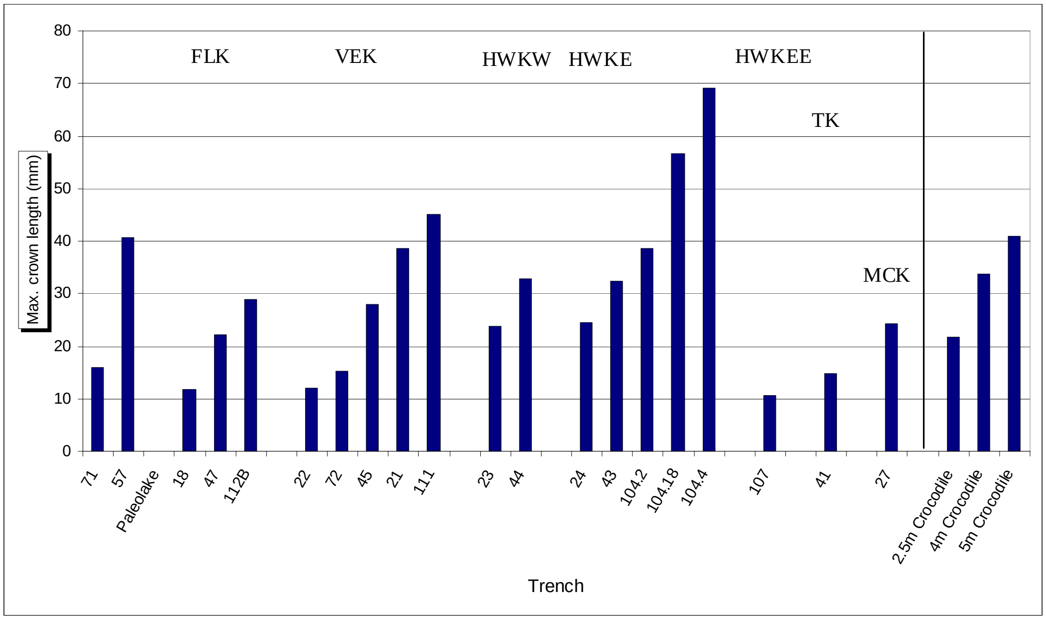


Figure 7.5. Distribution of crocodile size (body-length) inferred from the largest teeth recorded in each OLAPP trench. Teeth from modern crocodiles of known body sizes are presented to give an idea on the size of the fossil crocodiles recorded at Olduvai (data from Table 7.10).



CHAPTER 8. DISCUSSION AND APPLICATION OF THE NEOTAPHONOMIC-DERIVED INFORMATION TO THE PLIO-PLEISTOCENE OLDUVAI CASE STUDY

1. Introduction and summary

Results from captive crocodile feeding observations and lower Grumeti River bone samples provide a taphonomic framework for interpreting fossil assemblages, particularly those formed in wetlands contexts utilized by multiple sets of carnivores, such as crocodiles and terrestrial carnivores. While the control sample establishes the first diagnosis of crocodilian tooth marks, which distinguish this species from mammalian carnivores in bone assemblages, the Grumeti sample establishes patterns of bone assemblages in terms of bone modification, degree of bone completeness, and composition of species in wetland settings. Results from these neotaphonomic studies are used as a referential framework for analyzing bone modification in fossil materials from Oldowan assemblages, as well as for determining the proximity of these assemblages to aquatic habitats.

Data from the control sample indicate that bone assemblages modified by crocodiles are composed primarily of complete elements, and relatively few specimens (ca. 20%) are tooth marked (Table 5.2). Often the tooth-marked bones bear a high density of shallow to deep pits and scores, some overlapping each other, without fracturing the bone. Relatively small or less dense bones that are crushed during consumption are ingested together with flesh (see Table 3). In addition, assemblages produced by crocodiles lack gross gnawing and are characterized by the retention of both low- and high-density bone portions (Njau & Blumenschine, 2006).

Since the majority of crocodile tooth marks are indistinguishable from mammalian carnivore in terms of morphology, the bisected marks and hook scores are the most definitive features of crocodile feeding traces. About 80% of the tooth-marked specimens produced by crocodiles under controlled condition bear at least one bisected mark (Njau & Blumenschine, 2006). Hook scores, however, are rarely observed in the control sample (see Chapter Five). Generally, mammalian carnivore feeding traces are distinguished from those left by crocodiles by the following characteristics of bone assemblages: 1) lack of bisected marks or hook scores, 2) presence of gross gnawing and fragmentation of bones, 3) presence of furrows and tooth notches, 4) higher frequency of high-density bone elements and portions, and 5) fewer articulating specimens than those abandoned by crocodiles, except when carcasses are large relative to carnivore size and when feeding competition for carcasses is low. A detailed description on the differences and similarities between crocodile and mammalian carnivore feeding traces is provided in Appendix III.

Bisected marks together with a lack of gnawing and fragmentation of bones is the diagnostic feature that distinguishes crocodile feeding traces from those left by mammalian carnivores in modern and fossil assemblages (Njau & Blumenschine, 2006). These criteria are applied in order to model bone modification profiles of crocodiles and mammalian carnivores in Grumeti River landscapes, where both carnivore groups are presently common.

Contemporary observations from Grumeti show that crocodile predation, and feeding in particular, are confined in the channels (pools and riverbed). Typically, carcasses encountered by crocodiles on the riverbank or near/proximal over-bank settings are dragged into the nearby pool for complete dismemberment and consumption. In contrast, bone ravaging by mammalian carnivore is low in the channel, but increases in riverbank and over-bank landscapes, where crocodile are not active (in terms of feeding). Whole (undamaged) bones are more common in crocodile pool assemblages than in adjacent over-bank landscapes where assemblages are frequently fragmented by mammalian carnivores.

The Grumeti sample also establishes criteria for diagnosing crocodile living habitats in terms of abundance of crocodilian skeletal remains in bone assemblages. Conversely, crocodile skeletal remains are rarely represented on adjacent riverbanks/over-banks.

In light of current knowledge of crocodile taphonomy, the wetland model advanced in this study (Table 6.5) predicted that in the absence of physical preservation biases, crocodile specimens and feeding traces are expected to concentrate in the pools, marshlands and channels where crocodiles live, and decrease in adjacent dry land zones, usually formed by raised terraces or banks. Depending on the morphology of the wetland system, a low, raised terrace/bank (e.g., Ngoitokitok-like marshlands) will support a transition of vegetation cover from short/lawn-grass near the water’s edge to bushes and tree belts on the upper zone (see Table 6.3), and riparian corridors/riverine woodlands if there are streams supplying the marsh. Relatively steep, raised banks (e.g., lower Grumeti-like) supports riverine woodlands/riparian corridors (Table 6.3). These kinds of settings set a precedent for understanding the nature of hominin-mammalian carnivore-crocodile interactions in paleo-wetland landscapes.

Inferences regarding the landscape contexts of Oldowan assemblages from HWKE levels 1 and 2, FLK level 22, FLKNN level 3 and DK levels 1–2 , are drawn from the crocodile taphonomy model developed in this study, and the land use models by Peters and Blumenschine's (1995, 1996) and Blumenschine and Peters' (1998). Theoretically, the composition of crocodilian trace fossils (body fossils and feeding traces) in Oldowan archaeological assemblages predicts the proximity of scavenging hominin activities to aquatic setting utilized by predatory crocodiles. In this view, hominin trace fossils are expected to decrease with the increasing proximity to water bodies inhabited by crocodiles.

In this chapter, the relationship between the modern Grumeti and Oldowan fossil samples is established based on the taxonomic composition of the large vertebrates, the effects of crocodile and mammalian carnivore damage to long bones of large vertebrates, and completeness of long bones. The aim here is to determine the location and proximity of fossil assemblages to water, guided by the fine-scale landscape sub-facets established for the Lower Grumeti. Butchery data were also recorded for the fossil sample in order to determine the degree of hominin activities in presumably dangerous crocodilian contexts.

The crocodile taphonomy model developed for this study keeps constant the effects of postdepositional processes on bones, such as hydraulic transport, weathering or trampling, partly due to the differences in depositional conditions between Olduvai and modern Grumeti setting. The Olduvai assemblages came primarily from relatively undisturbed wetland settings adjacent to lake-margin deposits (Hay, 1976). Some of the assemblages such as DK and FLK NN3 have been inferred to occur close to marshy settings, due to the abundance of crocodile and *Kobus* sp., and the presence of fossil rhizomes of papyrus in sediments (Leakey, 1971; Hay, 1976).

Although the Olduvai and Grumeti wetlands are not identical in terms of terrain morphology and depositional environments, Grumeti provides a significant or partial analog for modeling ecological contexts of bone occurrences in landscapes utilized by crocodiles and mammalian carnivores.

Physical processes in channels

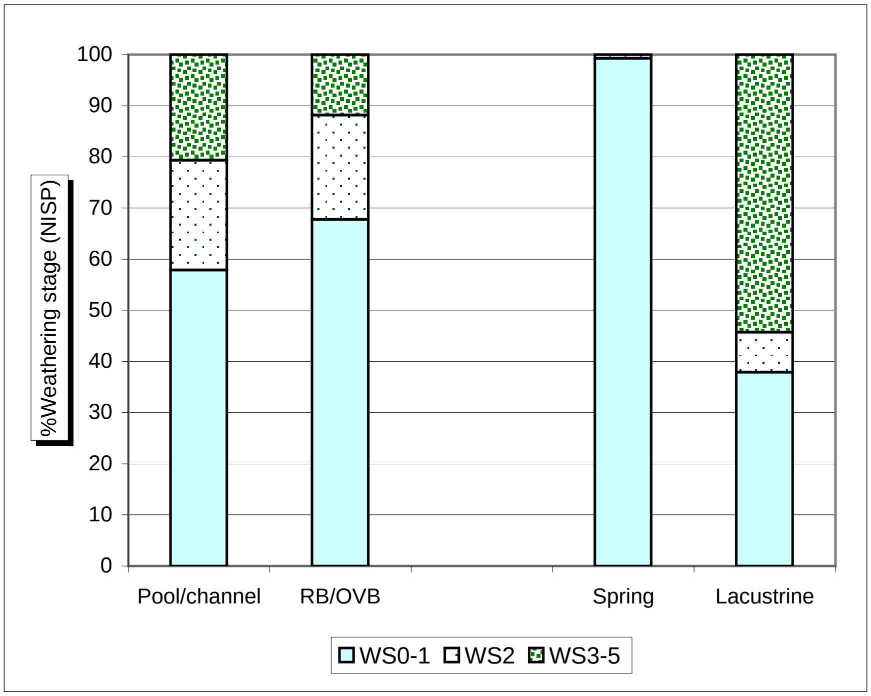
The hydrologically based taphonomic model developed for fluvial systems by Behrensmeyer (1988) was applied to the channel in the lower Grumeti by Blumenschine *et al* (in prep.). The bone assemblages in the lower Grumeti, indicate an overlap between channel-lag and channel-fill taphonomic modes, reflecting characteristics of the channel displayed by episodic flow (e.g., Gereta & Wolanski, 1998; Wolanski *et al*., 1999). According to Behrensmeyer (1988), the “channel-lag” assemblage is more allochthonous, composed of abraded fragmented bones. Larger and heavier elements are more common. This mode represents active drainages with recurring energetic flow and reworking of banks and bedload sediments. The “channel-fill” assemblage is composed of more autochthonous, unabraded, complete skeletons. This taphonomic mode reflects an abandoned channel, which has sporadic, waning flow with minor reworking of bank and bedload sediments.

Vertebra and ribs (Voorhies’ transport group I) and long bones (Voorhies’ transport group II) are preferentially represented in both pool/channel bed and riverbank/over-bank settings in the lower Grumeti (Figure 6.4a). Compact bones (Voorhies' group I), and cranial elements (group III) are underrepresented in both pool/channel and riverbank/over-bank assemblages. The overrepresentation of axial bones (group I) and disproportionate representation of compact bones (group I) in the pool/channel and over-bank assemblages reflect the abundance of these elements in an individual, rather than selective preservation of bones by active flow. Also, lack of any significant difference between pools/channel beds and riverbanks/over-banks in terms of frequency of long bone and cranial elements is inconsistence with hydraulic concentration (Figure 6.4a).

The preponderance of complete bones in the pools/channel beds compared to riverbanks/over-banks (Table 6.11) may suggest channel-fill assemblages. The good preservation of bone assemblages indicates an attritional mode of bone deposition in both landscape contexts. The proportion of fresh bones (weathering stage 0-2) is 58% and 68% for pools/channel beds and riverbanks/over-banks, respectively (Figure 8.1).

The skeletal part representation, bone completeness and weathering suggest a more autochthonous assemblage for both pools/channel beds and riverbanks/over-banks with respect to the dry channel setting, although potential overlap between channel-lag and channel-fill taphonomic features exists (e.g., Blumenschine *et al*., in prep.).

Figure 8.1. Weathering stages of bone assemblages in the Lower Grumeti categorized in three groups. WS0-1= stage 1-0 or relatively fresh, unweathered; WS2= stage 2, slightly weathered; WS3-5= stages 3-5, weathered bones. RB/OVB= riverbank/overbank. Large vertebarte bone specimens only, excluding teeth.



Sub-facet	WS0-1 NISP	WS2 NISP	WS3-5 NISP	Grand Total NISP
Pool/channel	221	82	79	382
RB/OVB	769	232	134	1135
Spring	133	1	0	134
Lacustrine	106	22	152	280
Total	1229	337	365	1931

2. Relevance of crocodile taphonomy in modeling paleo-wetland landscapes

Crocodiles depend on aquatic environments, and prefer wetland settings that provide them with basic survival requirements such as: 1) calm water necessary for food acquisition, feeding and breeding, 2) basking sites on the water's edge or open sandy grounds on the banks or islands, 3) raised terrace and vegetated sandy terrain located a short distance from water (over-banks) for nesting, and or 4) strategic locations for ambushing land mammals (e.g., animal crossing or trail).

Scientific and historical accounts show that adult crocodiles are major predators in many African inland waters such as rivers, marshes, and lake edges (e.g., Selous, 1908; Pitman, 1941; Cott, 1961; Guggisberg, 1972; Graham & Beard, 1973; Deeble & Stone, 1993), and the body fossils of this species have been recovered in numerous East African Neogene and Pleistocene fluvial, floodplain or lacustrine deposits (Patterson *et al*., 1970; Leakey, 1971; Tchernov, 1976, 1986; Tchernov & Van Couvering, 1978; Feibel *et al*., 1991; Leakey *et al*., 1996). Recent discovery of crocodile feeding traces associated with Oldowan hominin trace fossils at Olduvai (Njau & Blumenschine, 2006) suggests that crocodilians are taphonomic agents that may provide useful information on the contexts of bone accumulation.

Since only one species of crocodile (*C. lloidi*) lived at Olduvai during Oldowan times (Tchernov, 1986), the body fossils and feeding traces are attributed to this species. Although *C. lloidi* was relatively large reptile, possessing robust and broad snouts, its postcranial and tooth morphologies were similar to that of extant *C. niloticus*. The tooth-damage observed on Olduvai fossil specimens is fully consistent with that produced by captive Nile crocodiles. This brevirostrine form relied more on larger terrestrial mammalian prey (Tchernov, 1986) than *C. niloticus*, which includes more fish in the diet.

i) Crocodilian body fossils

The most frequently preserved crocodile materials in the fossil record are shed teeth. Usually, the most advanced resorbed teeth fall off when making forceful contact with a bone surface during feeding, or when holding heavy struggling prey. As a result, shed teeth are accumulated and deposited on the bottom of the pools. The occurrence of crocodile specimens in banks, where crocodiles are less active, reflects attritional mortality. A fresh adult crocodile carcass that I observed on the riverbank at lower Grumeti probably died naturally since there was no damage to the carcass. Also, individuals, which are injured from combat, usually die under tree bushes in the banks. Holding the preservation biases constant (i.e., hydraulic transport, trampling), the occurrence of skeletal remains, in particular shed teeth, provides unique information on the nature of a landscape in relation to proximity to crocodilian living sites.

The frequency of crocodiles relative to large vertebrates in the Grumeti bone assemblage is 29.4% in pool/channel setting, and 0.4% in riverbank and over-bank settings. Applying this actualistic model to the Olduvai fossil sample, some of the Oldowan assemblages are likely to have been accumulated near crocodile habitats (Table 8.1, Figure 8.2).

With the exception of HWKE level 1, crocodilian body fossils are represented at varying proportions (2.4% - 79.7%) in all of the Leakey assemblages studied. While crocodiles are rarely present at FLK level 22 (2.4%) and FLK NN level 3 (4.5%), they are well represented at DK (79.7%) and HWKE level 2 (13.6%).

The DK assemblage has the highest proportion of crocodilian materials (over 90% being shed teeth), even more than the modern crocodile pool sample. The preponderance of crocodilian body fossils (>4,500 teeth) may reflect a large and stable marsh, or a series of marshlands on the lake margin, repeatedly utilized by crocodiles. The DK site contains at its bottom level (level 3) a dense concentration of stone artifacts and bones on a paleosol, in some places lying on underlying basalt. A pile of stones roughly in the shape of a circle, which was interpreted by Leakey (1971: 24) as a foundation for a shelter constructed by early hominins, was exposed at the base of this level.

In the basis of the quantity of crocodile body fossils, DK and HWKE2 assemblages are likely to have been accumulated in the marsh-like wetland/pool, while HWKE1, FLK22 and FLKNN3 were more like deposited in adjacent banks (Table 8.1, Figure 8.2). The landscape settings in which these assemblages were deposited, and their proximity to crocodile living site are hypothetically represented in Figure 8.3. This model place DK and HWKE2 assemblages generally in pools or near pool margins. The exactly location of archaeological assemblages in the marshland area depends on the level of climate-driven lake fluctuations.

The relatively low proportion of crocodile specimens at FLKNN3 indicates that the assemblage was probably located in an area of fluctuating marshlands, whereby during the wet seasons the high water level expanded near to the terraces/banks. The FLK22 assemblage is inferred to have accumulated on the terrace/banks farther away from the pools. The occurrence of crocodile shed teeth suggests that at one time this setting was utilized by crocodiles, probably when the marshes expanded during the wet seasons.

The HWKE level 1 assemblage lacks crocodile specimens. Therefore, it looks very much like an assemblage that have been formed on the distal floodplains or a setting rarely utilized by crocodile (Figure 8.3). However, OLAPP excavations have yielded about 79 crocodilian specimens from this level constituting about 54% of the assemblage (Table 7.11), indicating a considerable crocodile population in this locale. The distribution of crocodiles in the lowermost Bed II deposits demonstrates that the HWKE area did support wetland systems that could have accommodated the largest crocodiles in the basin (Figure 7.5).

Mary Leakey interpreted these sites to represent “living floors” due to their rich stone-bone materials concentrated in thin sedimentary layers. Despite the fact that aquatic environments are homes to crocodiles, the occurrence of crocodile body fossils in these Oldowan assemblages has been viewed as food refuse of stone tool-using hominins (e.g., West, 1995). This interpretation, however, is challenged due to the following reasons. First, teeth with complete or partially resorbed roots are lacking in the crocodile fossil assemblage, indicating that teeth were primarily shed during life. This is because the skeletal remains of dead crocodiles are usually predominated by functional and successional teeth that possess complete or partially resorbed roots. In addition, both cranial and postcranial specimens are present in the fossil crocodile samples. Second, crocodile skulls (which bear teeth) are large and heavy, and it is unlikely that hominins transported these massive non-meaty skulls back to the campsites for consumption.

Finally, the evidence of butchery of crocodile skeletal remains is lacking (e.g., West, 1995: 354, 374).

Table 8.1. Comparison between modern Grumeti’s pool and over-bank samples, and five Oldowan assemblages in terms of composition of large vertebrates. With the exception of crocodiles, reptiles are excluded from the sample. Carnivores, primates, and indeterminant mammals are also excluded. Olduvai data taken from Leakey (1971:257). Crocodile include cranial, teeth and post-cranial material. SZ5-6 = Mammal size 5-6.

	Pool/channel bed		Riverbank/ Over-bank		HWKE L2		HWKE L1		FLK22		FLKNN3		DK	
Species	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
Crocodile	113	29.4	4	0.4	70	13.6	0	0.0	14	2.4	14	4.5	5274	79.7
Hippo	31	8.1	1	0.1	7	1.4	2	0.6	0	0.0	0	0.0	34	0.5
Bovid	217	56.4	902	86.8	294	57.0	258	81.9	474	81.7	252	81.0	1046	15.8
Equid	22	5.7	128	12.3	14	2.7	25	7.9	40	6.9	10	3.2	42	0.6
Suid	1	0.3	1	0.1	33	6.4	16	5.1	50	8.6	35	11.3	167	2.5
SZ5-6	1	0.3	3	0.3	98	19.0	14	4.4	2	0.3	0	0.0	56	0.8
Total	385		1,039		516		315		580		311		6,619	

Figure 8.2. Frequency of species in modern Grumeti and Oldowan fossil assemblages. Croc=crocodile, Hip=hippopotamus, Bov=bovid, Equ=Equid, Sui=Suid, Sz5-6=Size 5-6 mammals. RB/OVB= riverbank/over-bank. Data from Table 8.1.

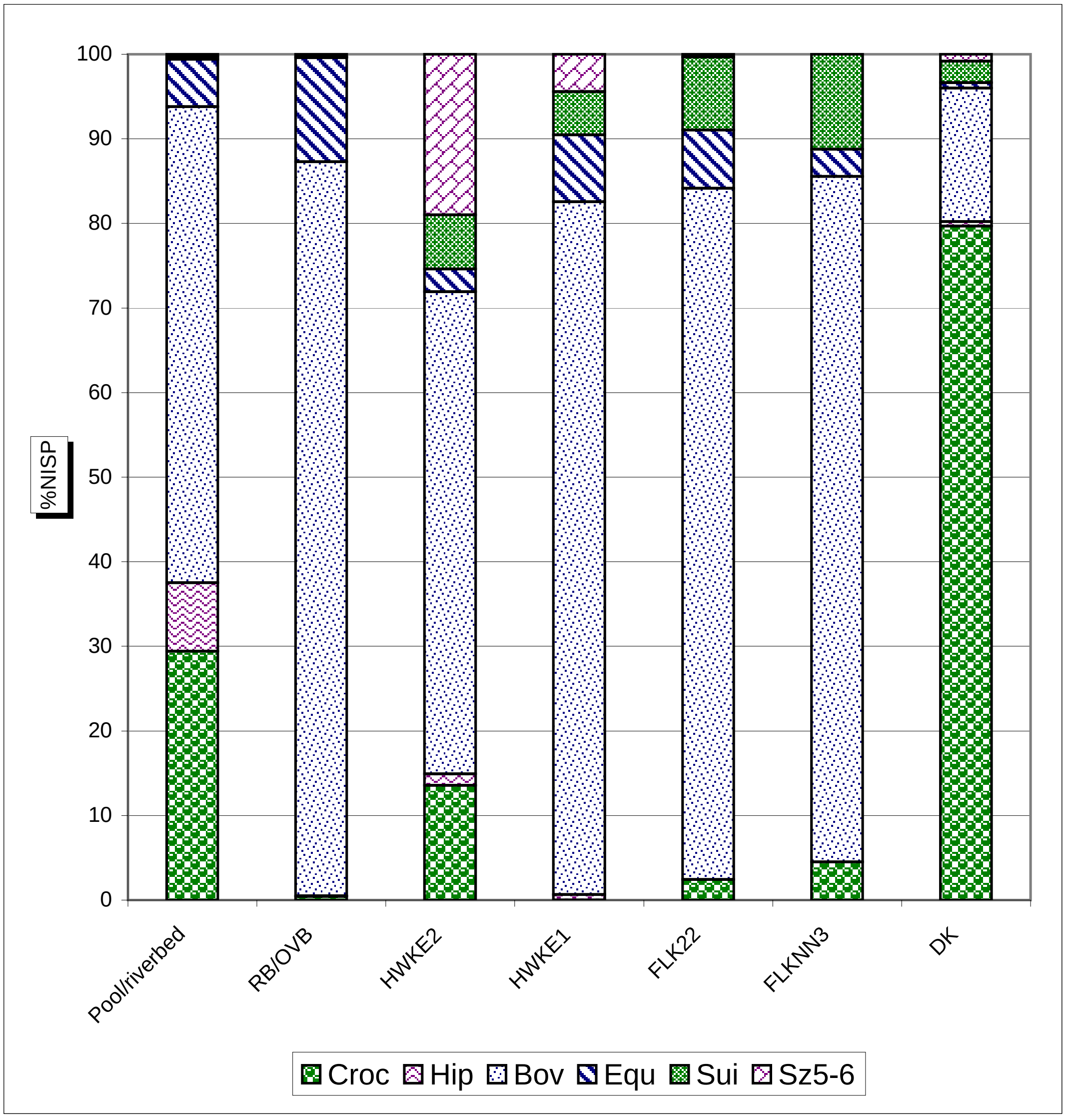
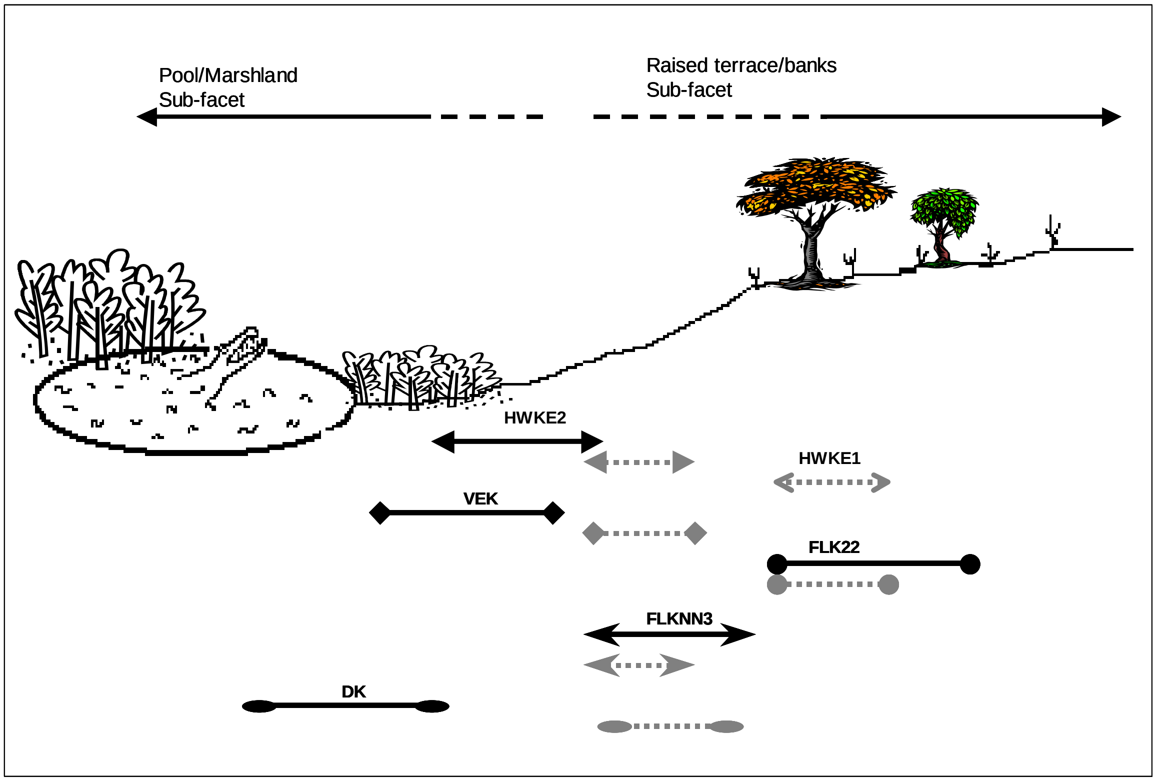


Figure 8.3. Two main landscape sub-facets modeled for Oldowan assemblages [HWKE level 1, HWKE level 2 and VEK (lowermost Bed II), FLK level 22, FLK NN level 3 and DK levels 2-3 (Bed I)] based on actualistic-derived model of crocodile taphonomy. The fossil assemblages are hypothetically located on landscape based on the abundance of crocodile body fossils (solid lines) and modified bones by crocodiles (dashed lines). The proximity of an assemblage to the crocodile-inhabited pool is determined by its composition of crocodilian material and bisected tooth-marked bone inferred from modern crocodile pools. Data obtained Figures 6.3 and 6.5 for modern, and Tables 7.8 and 8.1 for fossil samples. Species composition and crocodilian feeding traces data for HWKE 1, HWKE 2, FLK 22, FLKNN 3 and DK come from Leakey (1971), while VEK come from OLAPP. Arrows and landscape are not to scale.



ii) Crocodilian feeding traces

The incidence of tooth marks produced on long bones by crocodiles in the control sample is relatively high (68.8%) compared to the Grumeti and fossil samples (Tables 5.2, 6.12, 6.14b, 7.8). Because the control sample was created in the absence of physical biasing processes and inclusion of specimens modified by mammalian carnivores, the percentage of tooth-marked specimens was expected to decrease in modern landsurface bone samples, and fewer still in fossil assemblages, due to the conservative standards for recording bone modification by crocodiles, where only specimens containing bisected marks were attributed to crocodiles. This criterion underestimates the overall frequency of bone modification by crocodiles. This procedure however, ensures consistency in the recording of crocodile feeding traces in modern and fossil samples.

Observations from the modern landscape sample show that bone specimens modified by crocodiles occur more frequently in crocodile living and feeding sites such as pools (Table 6.14a). The frequency of long bone specimens bearing crocodile modification is relatively high in the pool/channel sample where crocodile specimens are also common, and very rare in banks where crocodile specimens are rare. In pools/channel beds, 43 out of 105, or 41% of long bone specimens (NISP) bear crocodile feeding traces, while only 3 out of 325, or 1% of long bone specimens in banks bear crocodile tooth marks. There is no evidence of crocodile specimens or bone modification in landscapes located farther away from the channel (i.e., distal floodplains).

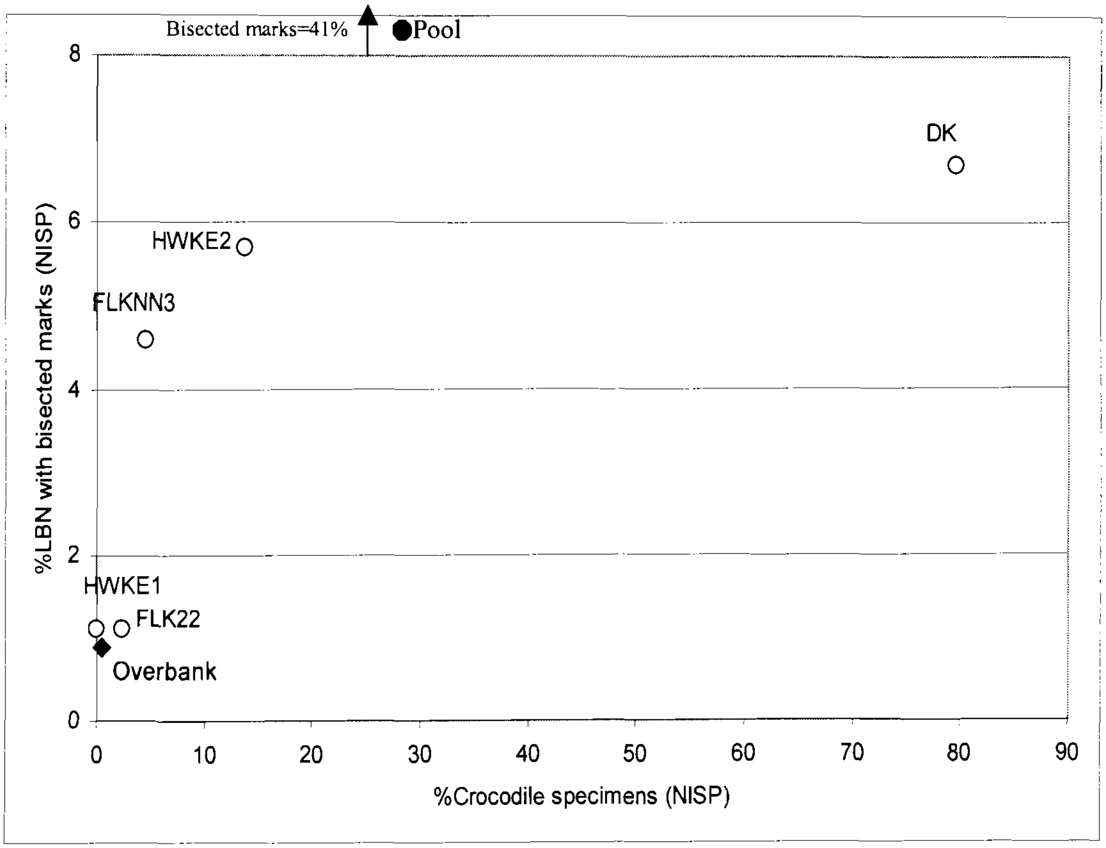
Occasional occurrences of crocodile feeding traces in bank sub-facets are likely to have resulted from one of two main processes. First, since crocodiles sometimes scavenge kills from lions on the riverbanks and over-banks, their feeding traces may remain on skeletal portions that were not dragged into water after dismemberment (e.g., Attwell, 1959). Second, when terrestrial carnivores scavenge from carcasses abandoned by crocodiles on the channel bed or near the riverbanks, they transport the carcasses to a safer place for consumption. Since crocodiles do not eat large meals at once due to their small stomachs (e.g., Grenard, 1991), they often abandon major unutilized portions of the large-bodied prey (> size 3-4 mammals), which may provide scavenging opportunities for terrestrial carnivores. Conversely, bone modification by mammalian carnivores is less frequent in crocodile-inhabited settings (i.e., pools/channel beds), but very high in adjacent bank settings where crocodile activities are not common (Table 6.14a, 6.14b).

Applying this actualistic model to the fossil record, fossil assemblages that contain crocodile modification are likely to have accumulated in or near active crocodile pools. The DK and HWKE level 2 samples, which have the highest proportion of crocodile skeletal remains (Table 8.2), contain high frequencies of bones modified by crocodiles (Figure 8.4). This observation suggests a pool or pool margin setting for DK and HWKE2 where carcasses were abandoned by crocodiles after consumption. The preponderance of shed crocodile teeth at DK may indicate continuous use of the pool or large and stable marshland system, while HWKE level 2 assemblage reflects a near pool margin or a small pool that is not as large as DK.

Although the proportion of crocodile specimens in the FLKNN3 assemblage is low compared to DK and HWKE level 2, crocodile tooth-marked bones are well represented, suggesting feeding activities by crocodiles (Figure 8.4). Based on the actualistic model, FLKNN level 3 probably accumulated on the outskirts of the marsh during the high water stand. During this time the edge of the marshes, where active feeding by crocodiles took place, extended close to the banks (Figure 8.3).

The incidence of specimens bearing crocodile tooth marks is rare in FLK 22 and HWKE level 1 samples as expected. Crocodile specimens are also rare in these assemblages, suggesting settings located farther away from the crocodile feeding zone (Table 8.1, Figures 8.3, 8.4).

Figure 8.4. Relationship between crocodile specimens and feeding traces in bone assemblages. Comparison is made between modern Grumeti pool/channel and bank sub-facet samples (solid symbols) and Oldowan fossil samples. Data from Tables 6.9b, 7.8, 8.1. LBN = Long bone.



3. Hypothetical hominin activities and trace fossils in wetland settings

Blumenschine and Peters' (1998) archaeological predictions for the lowermost Bed II landscapes suggests a paucity of hominin trace fossils, such as stone artifacts and butchered bones, in open settings with high terrestrial predator density, and lacking refuge trees. Hominin activities in these settings would be restricted to hasty production of knives (detached flakes) for dismembering carcasses. The stone tool kit was predicted to contain primarily tools for disarticulating scavengeable carcass parts for transport out of the danger zone, and rarely defense tools such as manuports and other large pieces. Butchery marked bone would be rare in this high-predation context, due to absence of defleshing and marrow processing.

A fuller range of hominin activities would be concentrated along the riparian corridors or tree-covered settings, where predation from mammalian carnivores was lower, and refuge trees were available (Peters & Blumenschine, 1995, 1996). The stone artifact assemblages in these wooded settings were predicted to contain a high density and wide variety of tools as lithic skills could be more safely practiced in these sheltered settings. Flaking debris (shatters) and other by-products of stone knapping would be abundant in the assemblage. The knives were useful for cutting and dismembering carcasses, while the flaked and pounding pieces were important for breaking up bones for marrow processing

The model developed in this thesis place predatory crocodiles in the wetlands hypothesized by Peters and Blumenschine. Presence of crocodiles in these wetlands increases the predation risk to foraging hominins, especially when they exploited resources located on the pastures near water's edge, or performed time-consuming tasks, such as marrow processing or other butchery activities. Since the crocodile hunting technique is mainly by ambushing from water, hominin activities such as production of cutting or detaching tools (flakes) and disarticulation of carcass parts, could be conducted on the banks away from the reach of lunging attack from crocodiles.

According to the Peters and Blumenschine (1995, 1996) land use model, the *Typha* marshlands formed on/or near lower stream mouths in the Eastern Lacustrine Plain would make available plant foods and scavengeable carcasses, when high lake waters receded. During this period scavenging hominins would have extended their foraging excursions from the Eastern Alluvial Fan to the upper and lower portions of the lacustrine plains to exploit *Typha* rootstocks. They could also procure carcasses killed by predators in the pastures, and obtain potable water in the fresh water portions of the marshlands and stream mouths. Trees along the drainages/stream and *Acacia* woodland belts on the lacustrine terrace and uppermost Eastern Lacustrine Plain would provide refuge trees (see Peters & Blumenschine, 1995, 1996: Figures 6A and 6B).

Predation from large mammalian carnivores is among the major negative affordances that would have been encountered by scavenging hominins, especially during the search for or dismembering of large carcasses in wetland areas. Presence of climbable trees nearby would provide escape routes, unless they were able to defend a small territory (Dead Hippo spring-like) against terrestrial carnivores by using defense stones.

Substantial predation hazard also came from crocodiles, particularly when hominins were dismembering or procuring a carcass on the water's edge, digging up *Typha* rootstocks, or kneeling down to drink from the fresher parts of the marsh. Such activities would have put hominins within range of attack by crocodiles submerged or concealed by reeds. Because crocodiles do not usually charge after their prey on land as do mammalian carnivores, activities conducted away from water's edge would have incurred substantially lower risk of crocodile attack.

i) Predicted archaeological signatures

The stone artifact assemblages deposited in wetlands utilized by hominins in response to hazards imposed by these habitat-specific predators are expected to be dominated primarily by manuports and other modified and unmodified large pieces (e.g., cobblestone, hammerstone, lava nodule) that could be used as probes thrown into pools to find out the location of concealed crocodiles. These 'stone probes' were probably thrown by hominins into the shallow parts or margins of the marshlands in anticipation of collecting rootstocks or procuring a scavengeable carcass. Therefore, the locally obtained stones and the low-quality material (for flake production), such as lava, would dominate the stone-probing assemblages.

Knife-like flakes and flaking debris are expected to be rarely represented in these contexts because the carcasses encountered on the pastures near the marshes would be dragged out of the range of crocodile attack to the banks for disarticulation prior to transport of carcass parts to refuge sites. Therefore, flaking debris and lost knives or flaked pieces (made out of quartzite or high quality stone material) are expected to occur more frequently in the butchery sites on the banks than at the water edges. Ideally, the manufacture of cutting/detaching tools would commence once a carcass was spotted on the marsh pastureland.

Depending on the size of the carcass encountered by hominins, however, hasty disarticulation, limited to detaching of limbs, may have been performed on the pastures. This activity may have led to production of few detached pieces and some flaking debris during tool sharpening or making of new cutting tools. These occasional butcheries near water zones however, would be performed after a careful investigation for a possible crocodile hiding nearby, by throwing stones into the water.

With the exception of butchery traces associated with the disarticulation of carcass parts, butchery marks are expected to be very low in the marshland areas occupied by crocodiles. Butchery marks are expected to be restricted to the pelvic area, where the hindlimbs are detached from the sockets.

The archaeological traces of crocodilian hazards predicted in this study are consistent with Blumenschine and Peters' (1998) archaeological predictions on landscape facets with high mammalian predator densities, with the exception of the heavier-duty probes. However, these heavy-duty defense tools are expected to concentrate on the adjacent dry part or banks of the marshlands.

Since the crocodile is a habitat-specific species, the archaeological signatures that would reflect their predation hazards would be related to the probing activities of scavenging hominins. In this respect, the presence of probing-stones is hypothesized as a unique archaeological indicator of crocodile hazard, and their abundance in archaeological record may indicate activities conducted at the edge of crocodile pools. What may distinguish this signature from those associated with defense against mammalian carnivore predation is that the probing stones would be deposited in water/subaqueous, while the defense-tools (against terrestrial predators) would be deposited on the adjacent dry land sub-facet. Given the extent of wetland fluctuations, however, it is uncertain if such sub-facet level can be distinguished sedimentologically.

ii) Trace fossils

The frequency of butchery marks in DK, HWKE2 and FLKNN3 assemblages, which are inferred to be located near crocodile habitats on the basis of crocodile specimens and feeding traces, are proportionately low comparing to the FLK22 assemblage (Table 8.2, Figures 8.5a and 8.5b). Since the FLK22 assemblage is inferred to be located on the banks farther away from the crocodile pool, probably in the distal part of the system (Figure 8.3), this observation is consistent with the general idea that intensity of butchery decreases with proximity to crocodile living sites.

The FLK22 bone assemblage contains a higher proportion of butchered long bone specimens than other assemblages, suggesting a full range of carcass processing (i.e., detaching carcass parts and breaking of whole bones) in a location that was relatively safe from crocodilian or terrestrial carnivore predation.

These data are supported by the stone artifact assemblage, which contains a full range of tools for processing carcasses, such as detached pieces, chopping and pounding tools (Table 8.3). The tool kit is dominated by detached pieces and flaking debris (91.5%) as predicted by Blumenschine and Peters (1998: Table 3) for this kind of low risk setting. The probing stones including manuports and utilized/modified cobblestones, hammerstones, and lava nodules (see Table 8.3) are proportionally less common in this low-risk setting, as predicted (Figure 8.6).

The frequency of cut-marked bones in FLKNN3 sample is two times lower than FLK22 but higher than DK (Table 8.2; Figure 8.5a) suggesting that butchery was not as complete as at FLK22. This behavior can be partly explained by the proximity of FLKNN3 to the marsh, where any prolonged butchery activity would expose hominins to crocodile predation, as demonstrated by hominin specimens (OH 8), which bear damage characteristic of crocodiles (Njau & Blumenschine, in prep.). This view is supported by preponderance of probing-stones (41.6%) in the stone artifact assemblage (Figure 8.6). The proportion of detached pieces is lower than that found at FLK22, suggesting a relatively low level of carcass processing at FLKNN3 compared to FLK22 (Table 8.3).

The HWKE level 1 assemblage, which, due to rarity of crocodile tooth-marked bones and lack of crocodile specimens (Figure 8.4), is inferred to be located relatively farther away from the marshes (Figure 8.3), lacks strong evidence of butchery contrary to my expectations (Figure 8.5a). Only two long bone specimens in the sample contain percussion marks, and none of the long bones is cut-marked (Table 8.2). While this result may reflect a sampling bias, as I sampled only a subset of the assemblage, Monahan (1996), who examined Leakey’s entire assemblage, also reported only two cut-marked long bones and two long bones with percussion marks, thus suggesting a low proportion of butchered bones at this level (ca. 1.5%). These data may indicate that complete carcass processing was not carried out by hominins during the accumulation of this level, possibly due to predation hazards from terrestrial carnivores.

However, the overrepresentation of manuports in the HWKE level 1 stone artifact assemblage may suggest hominins’ great need for defense tools before approaching the water edges (Table 8.3, Figure 8.6). These may have been probing stones, in part although the rarity of crocodilian trace fossils is not consistent with this prediction.

The HWKE level 2 assemblage lack cut-marks, as expected, due to proximity to crocodile pools as expressed by abundance of crocodile specimens (Figure 8.2) and crocodile feeding traces (Figure 8.5a). Contrastingly, detached and flaked pieces are well represented in the stone artifact assemblage, suggesting significant knapping of stone material at the site, probably conducted under a tree on the banks (Table 8.3). However, potential probing-stones are moderately represented in the assemblage (13.9%) indicating possible use of defense material against crocodiles the setting. The presence of probing-stones in the assemblage may support the idea that crocodiles hindered hominins efforts from butchering carcasses encountered on the marshland pastures.

The DK assemblage also contains a low proportion of cut-marked bones, as expected, due to proposed proximity to water. The butchery traces may reflect hasty disarticulation of carcasses procured by scavenging hominins on marshlands (Figure 8.5a). Leakey (1971) did not report manuports and other unmodified lava nodules and cobblestones (that were recorded in other Bed I and Bed II sites) from this site due to the abundance of these materials and proximity of the basalt stones to the floor/site. She recorded only the utilized cobblestone, hammerstone, nodules and anvils. Nonetheless, these pounding stones (cobblestone, hammerstone, nodule), which could as well used as probing-stones, are well represented (12.2%) in stone assemblage suggesting the use of defense tools by scavenging hominins (Table 8.3, Figure 8.6).

With the exception of FLK22, hammerstone bone-breaking activity is relative rare in crocodile contexts (Table 8.2, Figure 8.5b), as expected. Although marrow processing was predicted to be lacking in crocodile contexts, such as DK and HWKE 2, presence of percussion marks in these assemblages may indicate an occasional bone breaking restricted in the safer zones of the pastures, probably under climbable trees. In addition to defense, however, manuports and other large pounding pieces can be used to break-up bones for marrow processing.

Table 8.2. Long bone data from control, naturalistic and fossil samples indicating number of whole bones, MNE, NISP, NISP:MNE ratios, and occurrence of butchery marks in Olduvai assemblages.
PM= percussion marks, CM= cut marks.

Assemblage	Complete	MNE	NISP	NISP:MNE	PM	%PM	CM	%CM
Control - Carnivore	-	-	-	†4.72	-	‡28.6	-	-
Control - Crocodile	29	29	32	1.10	-	-	-	-
Pool/channel	59	92	105	1.14	-	-	-	-
Over-bank	75	173	325	1.88	-	-	-	-
HWKE level 2[1, 2]	7	25	42	1.68	1	2.4	0	0
HWKE level 1[1, 2]	16	60	87	1.45	2	2.3	0	0
FLK22[3]	15*	127*	731	5.76	200	27.4	137	18.7
FLKNN3[1, 4]	4	40	43	1.08	2	4.7	4	9.3
DK 2/3[1, 4]	35	210	282	1.34	12	4.3	5	1.8

†Control sample from Capaldo's (1997: Table 7) whole bone-to-mammalian carnivore scenario
‡Control sample from Blumenschine's (1995: Table 3) hammerstone-to-mammalian carnivore scenario
*Data taken from Bunn (1982) and Bunn & Kroll (1986)
[1] This study
[2] Monahan (1996), only butchery marks
[3] FLK22 data taken from Blumenschine (1995) with the exception of complete long bones and MNE
[4] Potts (1988) with exception of butchery data

Table 8.3. Proportion of stone artifacts in five Oldowan assemblages reported by Leakey (1971). MP= manuports; PP= pounding pieces (cobblestone, hammerstone, large nodules); DP= detached pieces (whole flakes only); FD= flaking debris (broken flakes and chips, by-products of detaching flakes, other fragments); FP= flaked pieces (chopping tools, scrapers, core-tools, etc.).

Assemblage	MP	PP	[†](MP + PP)	DP	[‡] (DP + FD)		FP		Total
	N	N	%	N	N	%	N	%	N
HWKE1	163	67	72.5	11	35	11.0	52	16.4	317
HWKE2	21	26	13.9	25	213	63.7	74	22.1	334
FLK22	96	57	5.9	258	2,348	91.5	60	2.3	2,566
FLKNN3	24	6	41.6	7	38	52.7	4	5.5	72
[¶]DK	-	147	12.2	242	894	74.6	154	12.8	1,198

[†] Proportion of presumed 'stone-missiles' used by scavenging hominins for defense against crocodiles near pool settings.

[‡] By-products of stone knapping most probably at the site of use. In various assemblages Mary Leakey does not separate "light-duty flakes" from "other fragments". I include these artifacts in this category.

[¶] Manuports are data is not presented by Leakey (1971: 39) owing to abundance and proximity of the basalt.

Figure 8.5a. Relationship between crocodile feeding traces (expressed as frequency of long bones bearing bisected marks) and incidence of long bones bearing cut marks in fossil assemblages. LBN= long bones. Data from Table 8.2.

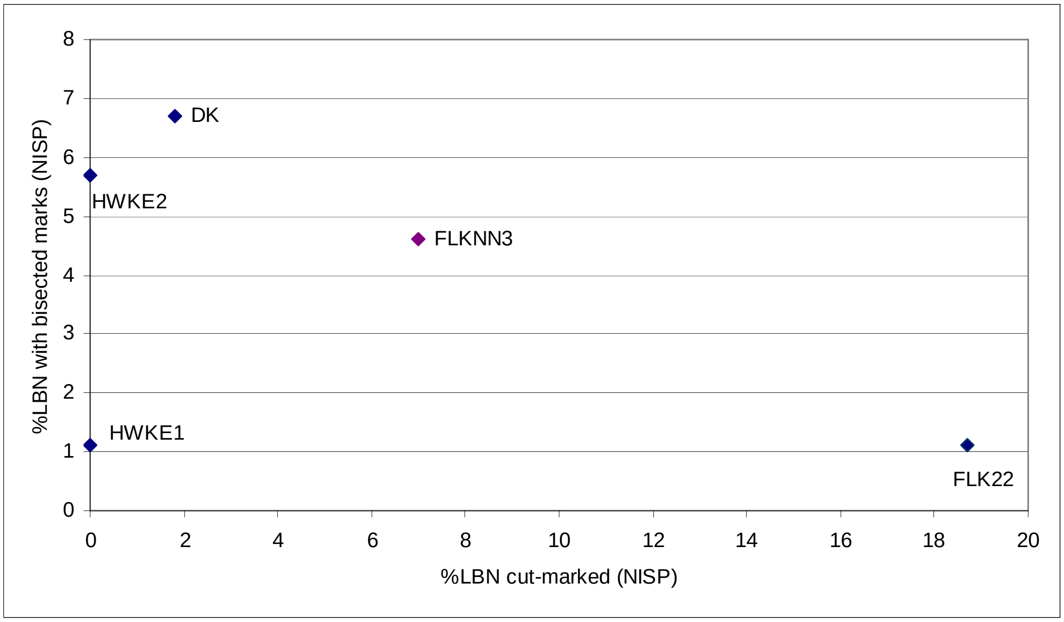


Figure 8.5b. Relationship between crocodile feeding traces (expressed as frequency of long bones bearing bisected marks) and incidence of long bones bearing percussion marks in fossil assemblages. LBN= long bones. Data from Table 8.2.

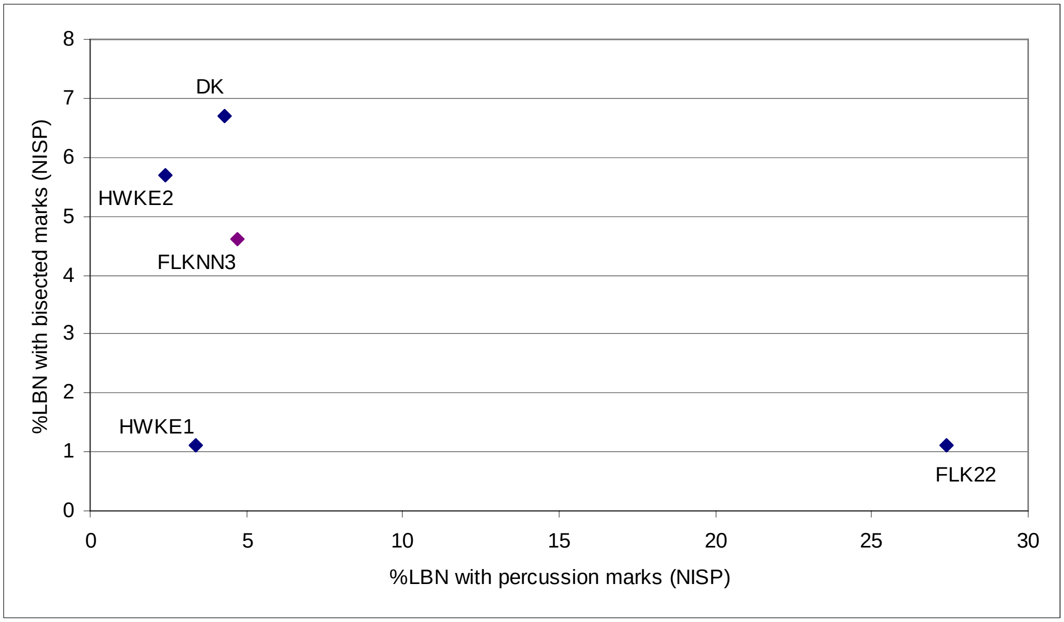
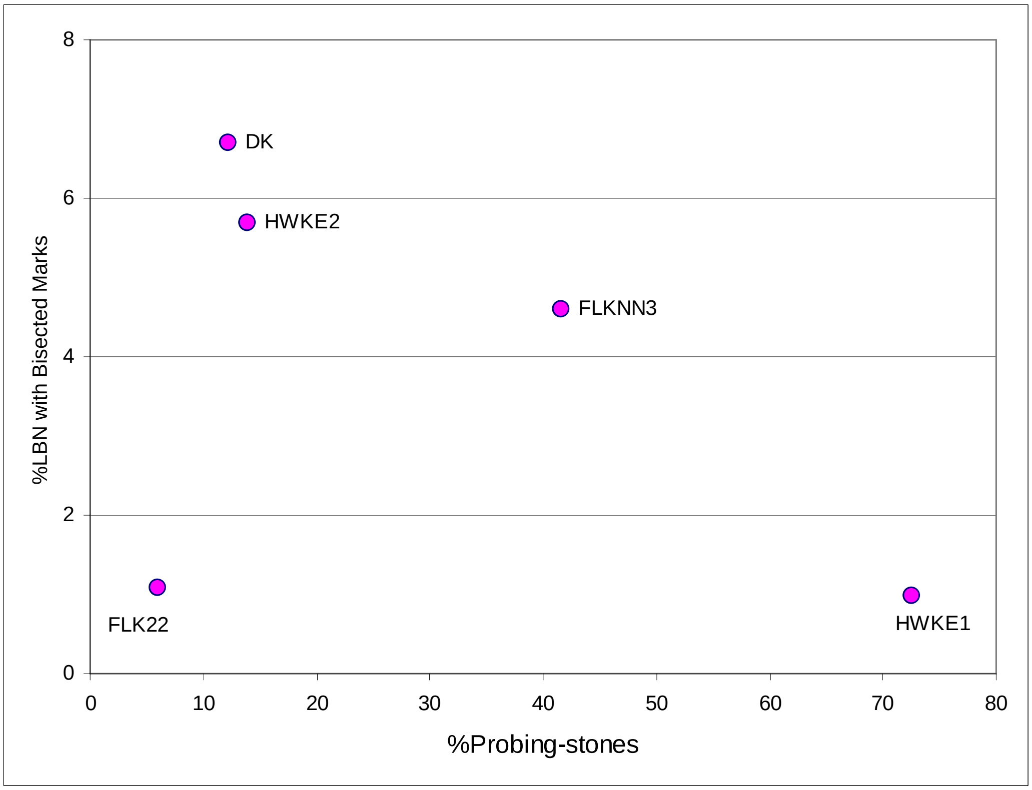


Figure 8.6. Archaeological signature of crocodile predation hazard expressed as percent of presumed defense tools against crocodiles (probing-stones) in stone artifact assemblages (data from Tables 7.8, 8.3).



ii) Degree of bone completeness

The degree of long bone fragmentation, measured as the ratio of long bone specimens to minimum number of long bones (NISP:MNE), is 1.14 and 1.88 for modern Grumeti River pools/channels and over-banks, respectively (Table 8.2). These actualistic results suggest that intact long bones are proportionately more common in crocodile pools where the degree of long bone fragmentation is low. The proportion of intact bones decreases in over-banks, where the degree of bone fragmentation increases due to an increase in ravaging by terrestrial carnivore.

Generally, the degree of bone fragmentation is relatively low in all fossil assemblages except FLK 22, while complete long bones are well represented in HWKE level 2 and DK, as expected (Table 8.2).

The abundance of butchered bones, high fragmentation of long bones, low frequency of complete long bones, and the low proportion of probing-stones and high proportion of detached pieces in the FLK22 stone and bone assemblages are consistence with my expectations that the assemblage was not accumulated near crocodile predation context (Figure 8.3). This archaeological evidence suggests that Oldowan hominins processed mammalian carcasses in relatively safe setting away from the water zone, probably near trees. The presence of escape trees and rarity of crocodiles in this kind of settings would permit relatively complete processing of stone tool products and carcasses, probably allow repeated visits by scavenging hominins to the marshland pastures.

Butchery and bone fragmentation data have been demonstrated to reflect the intensity of marrow processing by hominins and bone ravaging by hyenids in the FLK22 assemblage, thus indicating high hominin-carnivore competition (e.g., Blumenschine &

Marean, 1993; Blumenschine, 1995; Capaldo, 1997). High hominin and hyenid activity levels at FLK 22 coincide with low crocodile activities proposed for this setting (Figure 8.3, 8.4, 8.6). This famous archaeological level preserves one of the richest excavated paleoanthropological assemblages in Bed I.

The low frequency of butchered bones, low degree of fragmentation, and good representation of complete bones is consistent with the proposed wetland model, which place DK, HWKE2, and FLKNN3 in proximity to aquatic settings (Figure 8.3). Although the composition of these assemblages suggests crocodile contexts, it may also suggest low competition for marrow among hominins and hyenids. However, the current model suggests that the presence of crocodiles may have limited the efforts of hominins and hyenids to break-up bones near the marshes in order to obtain within-bone nutrients. This condition would prompt hominins to bring probing-stones with them to throw in the edge of the marshes before they get closer to obtain any prime resources presented by the aquatic setting.

Based on neotaphonomic observations, low fragmentation and good representation of complete bones indicates partial consumption of carcasses by crocodiles. Crocodiles are known to abandon nearly complete carcass parts of large prey due to their inability to chew bones (e.g., Davidson and Solomon, 1990; Njau & Blumenschine, 2006). Uningested carcasses are usually deposited in pools, or thrown on the surrounding margins or banks during dismemberment.

Bone abandonment or loss by crocodiles during feeding provides an alternative interpretation of low fragmentation of long bones in DK, HWKE level 2, and FLK NN3 assemblages, which has previously been inferred as the evidence of hasty and incomplete marrow extraction by hominins, resulting from high predation risk from terrestrial carnivores (e.g., Potts, 1984, 1988). Although still in its initial development, the analysis of crocodilian traces in combination with other archaeological bone signatures (e.g., butchery, degree of bone completeness and fragmentation) and stone artifact signatures (e.g., manuports or potential probing tools), may provide important ecologic information on the contexts of hominin trace fossils.

4. Landscape contexts of Oldowan trace fossils

The following model proposes landscape contexts in which fossil bones and archaeological materials were accumulated at HWKE levels 1 and 2, FLK 22, FLK NN3, and DK during Oldowan times. Based on the natural history and biology of crocodiles this species is a good indicator of aquatic habitats. The presence of shed teeth, crocodile feeding traces, and low degree of bone fragmentation in the bone assemblage suggests crocodile living areas. Leakey's interpretation of these assemblages as "living floors" is inconsistence with the evidence provided above, which suggests that the sites resemble modern crocodile living sites to various degree.

The Bed I sites of DK and FLKNN3 have been inferred to accumulate close to a marshland, due to presence of crocodile specimens (Leakey, 1971: 229) and abundance of manuports (Table 8.3). Although the nature of localized terrains is not known, DK taphonomically resembles modern crocodile pool settings, while FLKNN3 taphonomically resembles a bank or raised terrace setting near crocodile pool (Figure 8.3). The FLK22 bone assemblage suggests an over-bank setting, which may indicate a raised terrace setting near a vegetated ephemeral marshland occupied by crocodiles seasonally. Presumed probing tools are proportionately low in this assemblage (Table 8.3).

Recent geological and archaeological observations by OLAPP (e.g., Blumenschine *et al*., 2005b; Stanistreet *et al*., in prep.) suggest that HWKE1 assemblages were formed on a floodplain terrace adjacent to a braided stream. The taphonomic resemblance of the HWKE level 1 to modern over-bank settings, suggests a raised terrace located adjacent to a small marsh. However, the preponderance of probing-stones suggests large marsh probably inhabited seasonally by large crocodiles. The composition of HWKE level 2 assemblages suggests a near marshland setting inhabited by crocodiles.

The association of stone artifacts and butchered bones with crocodile body fossils and bones damaged by crocodiles suggest that scavenging hominins foraged under extremely dangerous conditions in wetland areas also occupied by crocodiles. The variability in hominin and crocodile trace fossils in bone assemblages may reflect in part the nature of wetland landscapes and proximity of hominin activities to marshes once inhabited by crocodiles.

CHAPTER 9. SUMMARY AND CONCLUSIONS

1. Introduction

In this chapter, I summarize some of the important findings of the naturalistic observations of crocodile feeding and the taphonomy of wetland vertebrates, and their significance for understanding the landscape contexts of Oldowan hominin trace fossils at Olduvai. Also the inferences made about the landscape settings of the fossil assemblages sampled in this study from Olduvai are summarized in this chapter. In the first chapter, I provided a general background on the nature of archaeological evidence at Bed I and lower Bed II with regard to the activities of early stone tool-using hominins and mammalian carnivores in wetland contexts composed of crocodilian body fossils. In order to understand the potential relevance of crocodile taphonomy to hominin paleoecology, I examined the life history and adaptations of this species in Chapter Three.

I have demonstrated and discussed the implications of the primitive dentition of crocodiles in producing distinctive tooth marks in recent and fossil assemblages, and how crocodilian feeding traces and skeletal remains are good indicators of specific wetland settings (see Chapters Five and Six). I provided examples of crocodile feeding traces in fossil record in Chapter Seven. In Chapter Eight I discussed the significance of crocodilian taphonomy in determining predation patterns of this species in wetlands at a fine landscape scale, and the impact of crocodiles on the distribution of scavenging hominin and terrestrial carnivore activities on landscapes. I will discuss some of the problems in the identification of crocodile feeding traces, and other questions, which require more investigation. I will also discuss how the methods of this study can be improved and developed in paleoanthropological and paleontological research.

2. The relevance of crocodile taphonomy

Crocodiles are more effective in killing large mammalian prey when they attain a larger body size (ca. 2 m). Although their techniques of capturing and feeding are different from mammalian carnivores, their methods of carcass consumption are patterned, and ensure production of diagnostic tooth marks and damage patterns to the skeletons of their prey. Crocodile predation occurs preferentially in pools, marshes or shallows located on lakesides, floodplains, deltas, or channel beds. These landscapes offer favorable settings such as calm water and vegetation (for concealment), which facilitate capture of land mammals, usually through ambushing. The victims are dragged into water, where they are disoriented and drowned, before the carcass is dismembered and consumed.

Large chunks of meat or articulated body parts, which are randomly torn from the carcass, are swallowed whole without chewing. Although adult crocodiles can swallow small size mammals (e.g., gazelle, impala) whole, quiet often they do not consume all of their large-bodied prey (e.g., size 4-5 mammals) because they possess a small gullet (e.g., Parsons & Cameron, 1977; Grenard, 1991). Also, bones that are too large or cumbersome to ingest, or too small to be picked off the ground by the snout of crocodiles are usually neglected.

This characteristic feeding behavior, which generates a predictable composition and characteristic of bone remains, is of great importance for interpreting bone assemblages formed under the influence of crocodiles. In this thesis, crocodiles are demonstrated actualistically to produce patterns of bone modification distinctive from that of mammalian carnivores, and this model is used to make inferences about the landscape contexts of some of the Olduvai paleoanthropological assemblages.

3. Inferring landscape contexts of hominin trace fossils

This thesis introduces a new taphonomic approach for refining our paleoanthropological methods of reconstructing environmental contexts of early hominin adaptation and evolution. The Oldowan samples from DK levels 2–3, FLKNN level 3, FLK level 22, and HWKE levels 1–2 provide examples of landscape reconstruction at a fine spatial scale that permits reliable interpretations of the contexts of the sites, and possible land use behaviors of hominins. The combination of data from modern wetland settings and feeding behaviors of crocodiles produces a framework for analyzing and interpreting large vertebrate bone assemblages in wetland contexts at a level of landscape sub-facet.

Since many paleoanthropological occurrences at Olduvai contain crocodile body fossils, the activities carried out at these sites by hominins are discussed in light of currently known crocodile taphonomy. Many of these deposits represent marshlands on fluvial, floodplain and associated lacustrine landsurfaces (Hay, 1976; Stanistreet *et al.*, in prep). However, the extensively transgressive nature of the paleolake makes it difficult to determine the actual landscape context (sub-facet) of hominin trace fossils and proximity of assemblages to the water bodies on the basis of geological evidence alone.

The presence of crocodile predation is documented in some of the Oldowan assemblages sampled in this study (e.g., DK, FLKNN3, FLK22, LOC 64, HWKE, and VEK) (see Chapter Seven). Tooth marks observed on some of the specimens are fully consistent with those produced by captive crocodiles. This diagnostic tooth-damage is attributed to *Crocodylus lloidi*, the only crocodilian that existed in the Olduvai Lake Basin during the Plio-Pleistocene. *C. lloidi* and their presumed descendants, the Nile crocodiles, possess more or less the same tooth structure and cusp morphology, thus expectedly producing similar traces on bone surfaces of their prey.

Traditionally, these assemblages have been interpreted to represent central foci of hominin land use (e.g., Leakey, 1971; Isaac, 1971, 1978, 1983; Potts, 1982, 1984), and the composition of crocodile body fossils in the assemblages was viewed as food refuse left by hominins (e.g., West, 1995:378-379). Paradoxically, the overwhelming majority of the crocodile remains are shed teeth (e.g., Leakey, 1971; Potts, 1988; West, 1995), and evidence of butchered crocodile skeletons is lacking in these assemblages (West, 1995: 354, 374). Large crocodile individuals are also represented in the assemblages, casting doubt as to why hominins would bother to carry these massive non-meaty skulls back to their base camps. If dead crocodiles were transported back to the campsites, the tooth assemblage would be expected to be dominated by specimens with complete or partial-resorbed roots. Instead Olduvai assemblages are dominated by shed teeth, which fall-off during life, particularly during feeding. These crocodile assemblages, therefore, suggest crocodile living sites/pools.

Since freshwater settings in semiarid lake basins are predictable for their availability of plant food resources and scavengeable carcasses, the need for hominins to obtain these resources from crocodile infested wetlands might have been one of the selective forces that shaped the land use of Oldowan hominins. Given that crocodiles rely on mammalian fauna for food, and in addition to presence of terrestrial carnivores in more open areas, hominin exploitation of resources in these locations would have been conducted under great predation hazard.

In lowermost Bed II, hominin activities were predicted to be concentrated in landscape settings with good tree cover, which typically afford low competition and predation risk from terrestrial carnivores (Blumenschine & Peters, 1998). Hypothetically, these kinds of settings would be expected in predation risk-free areas such as vegetated banks. The marshlands and stream mouths or drainages entering the paleo-lake (Peters & Blumenschine, 1995, 1996; Stanistreet *et al*., in prep) would support *Typha* rootstocks, scavengeable carcasses, potable water, as well as crocodile habitats. These food resources would attract hominins especially during the dry seasons. In order to access these prime resources hominins should have considered their safety by bringing potential throwing stones for defense against terrestrial predators and for probing in water. It is expected that the hominins would not forage in wetlands that are located a great distance from refuge trees.

The presence of trees would be advantageous to hominins by providing observation posts for terrestrial predators on the landscapes or partially submerged crocodiles in the wetland nearby. Various lines of evidence suggests that rich closed woodland environments were present in the Eastern Lake-Margins during the lower and middle Bed I times (e.g., Hay, 1976: 47, 53; Jaeger, 1976; Plummer & Bishop, 1994; Marean & Ehrhardt, 1995; Fernandez-Jalvo *et al*., 1998). Also, rich woodland settings have been suggested for the lowermost Bed II environments in the eastern part of the Lake-Margin (e.g., Sikes, 1994). The recovery of fossilized wood specimens (e.g., *Guibourtia coleosperma*) from archaeological sediments/OLAPP-trenches indicate that tall, shady trees existed at HWKE locale during the lowermost Bed II times (Bamford, 2005).

Observations from recent Grumeti River assemblages show a mixture of both crocodile and mammalian carnivore feeding traces, due to interactions of the two groups in this system. Crocodilian skeletal specimens combined with feeding traces are unique indicators of crocodile habitats, which are confined to freshwater settings, such as pools, where they usually live. Conversely, terrestrial carnivores predominate the over-bank landscapes. This observation can explain the occurrence of mammalian carnivore and crocodilian feeding traces in Oldowan assemblages.

Reports of crocodile attacks on humans are also common, particularly in villages when people go to fetch water, bathe, cross the watercourse, or forage along the water's edge (e.g., Guggisberg, 1972; Graham & Beard, 1973; Deeble & Stone, 1993). Although Oldowan hominins could have been killed in a similar manner (e.g., Davidson & Solomon, 1990), they could use stones for probing before exploiting the resources from the marsh area. Modern people use stones, wood or any material available on the banks or surrounding area for probing.

These observations suggests that the juxtaposition of stone artifacts and butchered mammalian bones in some of the Olduvai deposits that also contain evidence of crocodilian feeding and body fossils, probably reflects brief foraging excursions by hominins.

DK levels 2–3

The preponderance of crocodile teeth at DK suggests the proximity of the assemblage to crocodile occupied wetlands (Figures 8.2, 8.3). Observations made from recent Grumeti River landscapes indicate that crocodile-inhabited pools record a higher frequency of crocodile material than the adjacent sub-facets, such as riverbanks, over-banks, or distal floodplains. The presence of crocodile feeding traces in the DK assemblage (Figure 8.4) suggests crocodile predation.

The low proportion of butchered bones and the low degree of long bone fragmentation (Table 8.2) suggests low hominin and mammalian carnivore activities in this area. Also the occurrence of manuports (12.2%) in the stone artifact assemblage suggests possible use of probing tools by scavenging hominins during their brief excursions in the outskirts of the marshlands (Figure 8.6). This observation suggests that the DK assemblage was accumulated in a setting resembling crocodile pools, where hominin butchery activities were restricted to quick disarticulation of carcass parts that were transported to a safe place or a tree nearby for complete processing.

FLKNN level 3

According to the wetland model, this assemblage is consistent with a near-crocodile-pool setting (Figure 8.3). The assemblage from this hominin-bearing deposit contains a good proportion of crocodile shed teeth and specimens of large mammals and hominins bearing crocodile tooth marks (Figure 8.4). Leakey (1971: 229, 257) suggested that the overrepresentation of chelonia (79.5%) and the proliferation of kob materials in the bone assemblage indicate the proximity of the site to a marsh during the accumulation of level 3. Probably, the tooth-marked OH 8 foot represents remains of a hominin leg, which was vigorously shaken off its torso by crocodiles (Njau & Blumenschine, in prep.).

The relatively low frequency of butchered bones and the low degree of bone fragmentation suggests low levels of hominin and mammalian carnivore activities, probably due to threat of crocodile predation. The unusual abundance of potential probing stones (41.6%) in the stone artifact assemblage suggests the proximity of the assemblage to water occupied by predatory crocodiles.

FLK level 22

The FLK 22 assemblage contains low proportions of shed teeth and two long bone specimens in the analytical sample bearing bisected marks (Figure 8.4). On the basis of modern observations from Grumeti River, crocodile predation was very infrequent during the accumulation of this archaeological level. The frequency of butchered bones in association with stone artifacts (Figures 8.5a, 8.5b) is higher than in any other Oldowan assemblage at Olduvai (e.g., Bunn & Kroll, 1986; Blumenschine, 1995; Capaldo, 1997), indicating a high degree of hominin activities in this site.

The stone artifact assemblage is predominated by knives and flaking debris (91.5%) supporting the intensity of butchery in this site (Table 8.3). The low proportion of intact long bones and high fragmentation of long bones, indicative of hominin processing of marrow and carnivore ravaging of bones, appears to have occurred in the absence of immediate threats from crocodiles. The underrepresentation of crocodile signatures in this assemblage suggests that seasonal marshes probably occurred near this site (Figure 8.3). This observation is consistent with the infrequent occurrence of probing tools (Figure 8.6).

HWKE levels 1–2 (Lowermost Bed II)

Although all crocodile specimens reported by Leakey (1971:257) came from level 2, both levels contain crocodile feeding traces. The abundance of crocodile specimens and feeding traces in the level 2 assemblage suggests proximity to a crocodile pool (Figures 8.3, 8.4). Recent excavations extended in this area by OLAPP have yielded more shed teeth, although none of the long bone specimens showed evidence of bisected marks. Measurements taken from the OLAPP sample to determine size of crocodile teeth indicate that the largest teeth in Lowermost Bed II landscapes come from HWKE (Figure 7.5). This evidence suggests that the largest crocodiles were occupying large wetlands at HWKE.

The low frequency of butchered bones, low degree of fragmentation, and good representation of complete long bones may indicate low competition, due to absence of bone-cracking hyenas, or due to presence of crocodile living sites. However, the preponderance of manuports [which was described by Leakey (1971: 89) as unusual)] and other potential probing stones that account for about 72.5% of the total stone artifacts, indicates the proximity of these assemblages to waters inhabited by large crocodiles.

4. Contrasting crocodile and mammalian carnivore feeding traces

i) Tooth marks profile

Results from the controlled feeding sample show that the majority of uningested bone elements are not bitten during feeding by crocodiles. Only 21% of all bone specimens attended by crocodiles bear at least one tooth mark, contrary to assemblages produced by mammalian carnivores, in which the average of tooth marked specimens ranges from about 42% to 64% (Capaldo, 1995). Some tooth marks produced by crocodiles are distinctive morphologically. These are bisected pits and punctures, and hook scores (Njau & Blumenschine, 2006).

Depending on the size of the crocodile and the prey carcass, isolated to several dozens of pits and scores can be inflicted on an individual element. The size of pits and punctures produced on a single bone varies tremendously due to variation in tooth size in individual crocodiles (e.g., Kalin, 1933; Iordansky, 1973) and the possibility that multiple individuals may damage the same bone. The maximum diameters of pits range from about 0.1 mm to over 6 mm, while punctures range from ca. 1 mm to ca. 10 mm. Deep and large punctures also occur on cortical bone (see Appendix III).

On the other hand the typical size of mammalian carnivore pits reported by Dominguez-Rodrigo and Piqueras (2003) range from ca. 1.5 mm to 4 mm, while punctures range from 2.5 mm to 7.5 mm (Selvaggio & Wilder, 2001; Dominguez-Rodrigo & Piqueras, 2003). This suggests that tooth mark size data cannot reliably discriminate agents of bone modification particularly in assemblages attended by both crocodiles and terrestrial carnivores (*contra* Selvaggio & Wilder, 2001; Dominguez-Rodrigo & Piqueras, 2003; Pickering *et al*., 2004).

ii) Gross gnawing and bone fragmentation

Due to lack of precise occlusion between upper and lower teeth, chewing is absent in crocodiles. Thus, bones that are bitten during consumption lack gross gnawing or intensive breakage. Since feeding is accomplished by swallowing food items whole, uningested bones are abandoned as articulated units with minimal fragmentation. Typically, the assemblage created by crocodiles is minimally ravaged (NISP/MNE<2). In contrast, bone gnawing and fracturing is a common feature in mammalian carnivore bone utilization, specifically to access marrow, grease, brain tissue and micro-nutrients.

iii) Problems in identifying mammalian carnivore tooth marks

Recognition of species involved in the production of tooth marks in a bone assemblage is difficult, specifically for mammalian carnivores because all major extant families of this group are represented by several species with more or less similar tooth cusp morphologies. The internal morphology of mammalian carnivore tooth marks is more or less similar across species. While large terrestrial carnivores such as bone-cracking spotted hyenas can be distinguished by their ability to crush and produce tooth marks on bones of animals as large as size 3–4, lions can also produce significant amount of gnawing on the skeletons of large bodied herbivores without necessarily breaking open the bones. Therefore, bone utilization by lions on large prey may mimic hyenas bone modification in a low competition environment.

Similarly, smaller terrestrial carnivores such as jackals can produce tooth marks when scavenging from large bodied kills. Since the shapes of tooth marks are not practical in identifying taxa of gnawing carnivores, the size of tooth marks may only by used to indicate the basic tooth-size of the consumer that inflicted the mark.

The heterodont characteristic of mammalian carnivore also accounts for problems in recognizing the tooth marks of particular consumer. The dentition of mammals is divided into four types of teeth comprised of incisors, canine, premolars and molars, each type specialized for a specific function. Therefore, the variation of size and shape in tooth marks expresses the differences in the basic tooth or cusp of the bone consumer.

Since the anterior teeth of mammalian carnivores are initially used for defleshing, these may generate pits and scores, while the robust postcanine teeth, used primarily for gnawing, may produce punctures on cancellous bone. The carnassial blades, which are committed to slicing and shearing flesh, may produce punctures on cancellous margins of bones.

iv) Problems in identifying crocodile tooth marks

Unlike mammalian carnivores, whose different types of teeth on tooth rows allow different masticating tasks, crocodilians dentition is composed of uniform bicarinated teeth that are continuously replaced throughout life. This homodont ensures that crocodiles produce tooth marks that are much more uniform in shape than mammalian carnivores.

Since the tips of full-grown functional teeth are round and lack carina due to wear, the majority of individual tooth marks (ca. 90%) produced by crocodiles resemble mammalian carnivores in shape and internal morphology. The newly erupting teeth, which are bicarinated and small, are usually few in a tooth row compared to functional teeth. These bicarinated teeth are responsible for production of bisected marks. Since the majority of crocodile tooth marks may not be distinguished from those produced by mammalian carnivores, the majority of tooth marked specimens in fossil assemblages may be mistakenly attributed to mammalian carnivores.

Paleoanthropologists now need to consider another bone accumulator and modifier in addition to hominins and the suite of felids, hyenids and canids among larger mammalian carnivores. Together, the three sets of taphonomic agents provide for a complex range of potential interspecific interactions recorded in fossil assemblages.

5. Crocodilian fossil record

Information on crocodile bone utilization and modification is rare, even though this species is a notorious predator in tropical waters, and routinely preys on large land mammals (e.g., Schmidt, 1944; Cott, 1961; Neill, 1971; Guggisberg, 1972). Numerous late Tertiary and Quaternary deposits associated with fluvial, floodplains and lacustrine paleoenvironments in East Africa have yielded abundant crocodilian materials. Information on prehistoric bones tooth-marked by crocodilians, however, are rare. There are few reports inferring crocodile feeding traces in the fossil record (e.g., Dubois, 1927; Buffetaut, 1983; Pickford, 1996; Schwimmer, 2002).

Much of the body and trace fossil record for hominin evolution in the Pliocene and Pleistocene accumulated in ancient tropical wetland systems also inhabited by crocodilians. These include, Baringo and Rusinga (Tchernov & Van Couvering, 1978), Omo, Koobi Fora, Lothagam and Kanapoi in the lake Turkana Basin (Tchernov, 1976; Harris, 1978; Feibel, 1991; Leakey *et al.*, 1996, Storrs, 2003), Hadar (e.g., Aronson &

Taieb, 1981), Senga 5A site of lake Rutanzige (Harris *et al*., 1990), Olduvai Gorge (Leakey, 1951, 1971; Blumenschine *et al*., 2003), *et cetera*.

6. Inferring bone modification behavior of carnivorous dinosaurs

As the living representative of the large meat-eating archosaurians, crocodiles provide a unique opportunity to model the feeding behavior of carnivorous dinosaurs. Observations on the feeding behavior of modern crocodiles provide actualistic information on the feeding traces produced by predatory dinosaurs, such as *Tyrannosaurus rex*, on bone assemblages. The dental structure of crocodilians is more or less similar to that of *T. rex* making crocodiles a good living example for modeling feeding traces and behavior of this and other tyrannosaurids. Unlike the more blade-like, cross-sectionally lenticular teeth of non-tyrannosaurid theropods, those of *T. rex* have rounded cross sections (Farlow *et al*., 1991; Abler, 1999), more similar to the teeth of crocodilians (Poole, 1961; Pooley, 1989). The major dental difference between the two carnivorous archosaurians is the presence of well developed serrations on the carinae of tyrannosaur (Abler, 1992).

In addition to these morphological resemblances, feeding behavior and bone utilization of modern crocodiles is probably very similar to that of large meat eating tyrannosaurus, due to the inabilities of both groups to chew large bones (Fiorillo, 1991), and due to their habit of abandoning large portions of prey unutilized. *T. rex* have been inferred to kill and feed regularly on very large prey relative to their own body size (van Valkenburgh & Molnar, 2002), and quite often abandon major unutilized portions of the prey (Farlow, 1976a, 1976b). Similarly, adult crocodiles are capable of overpowering large-bodied prey ranging from buffalo size to rhinocerous, hippo and giraffe (e.g., Selous, 1908; Attwell, 1959; Pienaar, 1969), and typically abandon large parts of the carcasses they are unable to ingest (Njau & Blumenschine, 2006).

Evidence of tooth-marked bones in dinosaur assemblages

Reports of tooth-marked bones in dinosaur assemblages are far less common than what can be observed in mammal bone assemblages, and until recently the few reports made were anecdotal (Beasley, 1907; Mathew, 1908; Dodson, 1971). Traditionally, the association between the skeletal remains of presumed dinosaurian predator and prey was viewed as direct evidence of predator-prey interactions. Mode of carcass acquisition, such as hunting or scavenging, were directly interpreted from these assemblages (e.g., Cruickshank, 1986; Buffetaut & Suteethorm, 1989; Rogers, 1990; Currie & Jacobsen, 1995; Chin *et al*., 1998; Hungerbuhler, 1998; Frazzetta & Kardong, 2002; Sues *et al*., 2003). Biomechanical models have been advanced by paleontologists to establish criteria for determining dinosaurian physical capabilities influencing predatory behavior and bone utilization (e.g., Erickson *et al*., 1996; Erickson, 2001; Rayfield *et al*., 2001; Meers, 2002).

Tooth mark data from dinosaurian assemblages, however, have recently begun to be described in paleontological assemblages, often in an attempt to determine predator/scavenger-prey interactions (e.g., Fiorillo, 1991; Hunt *et al*., 1994; Erickson & Olson, 1996; Chure *et al*., 1998; Jacobsen, 1998; Tanke & Currie, 1998; Hurum & Currie, 2000; Rogers *et al*., 2003).

Tyrannosaurs and other carnivorous dinosaurs apparently produced a high density of tooth marks on fossil specimens (Chure *et al*., 1998; Jacobsen, 1998), although, Fiorillo (1991) reports very low proportions (≤ 4%) of tooth-marked specimens among six assemblages of dinosaur prey bones.

With the exception of the experiments conducted by Erickson *et al*. (2003) modeling the bite force of theropod dinosaurs (such as *T. rex*) using living alligators, neotaphonomic research that uses modern crocodilians to model dinosaurian carcass consumption is lacking. One possible reason may be that many paleontologists view theropod feeding behavior as more similar to that of Komodo dragons than crocodilians (Farlow, cited in Abler, 1999). It is only the report from Njau and Blumenschine (2006) that provides the first descriptions of tooth mark morphology produced by crocodiles, the only surviving relatives to this carnivorous archosaur.

Tooth mark morphology of predatory dinosaurs

Tooth marks, including punctures, grooves, and drag marks have been reported from dinosaur bone assemblages, but the descriptions are insufficiently detailed to determine whether the distinctive morphologies and anatomical patterning of marks, as produced by crocodiles, are present. Only Erickson (Erickson, 1999; Erickson & Olson, 1996) described punctures with eye-shaped cross sections, impressed by carinas as definitive bite marks from *T. rex*. Crocodiles produce similar types of tooth pits and punctures, which are distinctive feature of these thecodont archosaurians. These types of tooth marks are referred to here as “bisected marks” (Njau & Blumenschine, 2006).

7. Conclusions and future directions

This is the first systematic attempt to document crocodile tooth marks and bone modification in modern assemblages. This study concludes that crocodile bone modification is likely to be common but largely overlooked in fossil assemblages, and if such damage has been noted at all, it is likely to have been misattributed to mammalian carnivores. The results of this study permit identification of crocodilian habitats from taphonomic perspectives. Crocodilian taphonomy can be applied reliably to reconstruct hominin paleolandscapes in wetland contexts at a fine spatial scale.

Investigations of various archaeological assemblages at Olduvai, which contain potential signatures of crocodile predation, need to be completed. Assemblages deriving primarily from wetland associated deposits and containing crocodilian body fossils need to be examined, since some of them have been considered as living sites and contain hominin body fossils. These include MK, PDK, FLK NN level 4, and FLK N levels 1-2, 5 from Bed I, MNK Main, MNK Skull site, FC West Floor, and BK from Bed II, and Croc K from Beds III–IV.

Recognition of crocodilian trace fossils is of great importance for assigning bone assemblages to specific habitats, once depositional context is established. Also, the stability and size of the wetlands can be estimated based on the body size of the crocodiles. Further analysis will present a fuller picture of the evolution of brevirostrine crocodile adaptation from the lake margin environments of Bed I and lower Bed II to fluvial-lacustrine facies of upper Bed II and fluvial facies of Beds III–IV occupied sympatrically by *C. lloidi* and their descendants.

APPENDICES

APPENDIX I. Abbreviation and definition of some of the taphonomic attributes used the analysis following Blumenschine's convention for recording zooarchaeological and taphonomic data.

Attributes	Abbreviations and Definition	Examples
Taxonomic Groups:	MAM: Mammal (indeterminate) CAN: Canidae BOV: Bovidae EQU: Equidae HYA: Hyaenidae FEL: Felidae CRO: Crocodylia	
Mammalian Size Classes (Bunn, 1982)	1 10–50 lb. (5–25 kg)	- Thomson's gazelle
	2 50-250 lb. (ca. 25–100 kg)	- Grant's gazelle, impala
	3 250-750 lb. (ca. 100 kg–350 kg)	- Wildebeest, topi, zebra
	4 750-2,000 lb. (ca. 350–900 kg)	- Buffalo, eland
	5 > 2,000 lb. (> 900 kg)	- Hippo, rhino, giraffe
	6 > 6,000 lb. (> 2,700 kg)	- Elephant
Major Skeletal Regions/Groups:	CRA: Cranial AX: Axial GIR: Girdle LBN: Long bones CBN: Compact bones NID: Indeterminate bone	
Skeletal Part Element:	CRA: Cranial HCR: Horn core MND: Mandible HMND: Hemi-mandible TTH: Isolated tooth L: Lower U: Upper I: Incisor C: Canine P: Premolar (P1-P4) M: Molar (M1-M3) AX: Axial ATL: Atlas AXI: Axis CER: Cervical vertebrae THOR Thoracic vertebrae LUM: Lumbar vertebrae SAC: Sacrum CAU: Caudal vertebrae RIB: Rib STR: Sternum CLV: Clavicle VRT: Indeterminate vertebrae GIR: Girdle SCA: Scapula PEL: Pelvis (whole pelvis) INN: Half-pelvis LBN: Long bones HUM: Humerus	

	RAD: Radius ULN: Ulna FEM: Femur RADU: Radioulna (fused) TIB: Tibia FIB: Fibula MET: Metapodial MTC: Metacarpal MTM: Metatarsal CBN: Compact bones CAR: Miscellaneous Carpals TAR: Miscellaneous Tarsals AST: Astragalus (Talus) CAL: Calcaneum NVC: Naviculo-cuboid PHA1: First phalanx (manus or pes) PHA2: Second phalanx (manus or pes) PHA3: Third phalanx (manus or pes)	
Skeletal Part Portion	CO: Complete element FR: Indeterminate bone fragment FOR CRANIUM FRON: Frontal OCC: Occiput MAX: Maxilla NAS: Nasal PAL: Palate FOR MAND HRAM: Horizontal Ramus VRAM: Vertical Ramus COND: Mandibular condyle FOR VERTEBRAE BOD: Body and arch without spines SP: Spine LAT SP: Lateral/transverse spine NEU SP: Neural/dorsal Spine CEN: Centrum ZYG: Zygopophysis FOR RIBS PPX: Proximal head RSH: Rib Shaft fragment FOR LONG BONES EPI: Miscellaneous epiphysis NEF: Near epiphysis PX: Proximal end DS: Distal end MSH: Mid-shaft PSH: Proximal Shaft DSH: Distal shaft FOR INNOMINATES ILI: Ilium ISCH: Ischium PUB: Pubis ACET: Acetabulum FOR SCAPULA GLEN: Glenoid fossa SP: Spine	

	ACR: Acromium process BLADE: Blade (scapula)	
Skeletal Part Segment	CS: Long bone with complete shaft (cylinder) FR: Fragment of uncertain segmental location HF: Half of (LBN shaft) cylinder ANT: Anterior POST: Posterior MD: Medial LAT: Lateral DOR: Dorsal VEN: Ventral SUP: Superior INF: Inferior	

APPENDIX II. Observations and descriptions of each feeding episode in crocodile farms.

I. BAGAMOYO

1) Feeding Trial 1A

Medium size crocodiles (N=20) feeding on adult goat carcass (N=1)

A whole goat carcass with all limbs attached to the trunk was placed in the *banda* on the ground near the pool. The carcass has had its skin and visceral organs removed, but it retains all flesh. Twenty medium size crocodiles were released from the basking ground to the poolside. One crocodile approached the meat and grabbed the limb which was closest. Others followed and grabbed from the other side of the carcass. They held for a while and began pulling the carcass towards the pool. About four crocodiles held onto the rib cage, and some began to tear the loose meat off the ribs with their anterior teeth. The large individuals were vigorously rolling and forceful battering the whole carcass on the ground.

The forelimbs were the first limbs to come off the carcass. Within one hour both scapulae were disarticulated from the rest of the limb by death-rolling. The scapulae were swallowed immediately after disarticulation. The limbs were held for about 20 minutes in the mouths of other crocodiles, before maneuvering and swallowing the elements whole. The limbs were folded at the elbow joint and ingested from the elbow (distal humerus and proximal radioulna). This action took approximately 20 minutes (Table 1A). The animals would chase after each other trying to get hold of the carcass or trying to get help in breaking the bone. In the process the limb would be bitten all over. The hind limbs were swallowed whole by two of the medium size crocodiles without further reduction after being torn apart from the trunk. Swallowing took about 40 minutes, during which time the animals were maneuvered the limb by tossing it up in the air and mouthing back and forth until complete ingestion.

The rib cage took longer to be swallowed (2 hours). Unlike the limbs, the rib cage is not easy to swallow whole because it does not provide convenient sites for the crocodile's jaws to grasp or hold. Crocodiles were observed to use lateral teeth to rip meat off the ribs by twisting, shaking and death-rolling. Generally, the animals did not show any preferential selection of skeletal parts, rather smaller size of meat chunks were observed to attract the animals attention.

Trial 1A. Sequence of carcass disarticulation and ingestion by Nile crocodiles (N=20) feeding on fresh mature goat carcass (N=1). Skeletal regions are ranked according to sequence of consumption. The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Carcass parts collected	Time Min.
Head	1	Head – Neck	None	None	None	None	10
Forelimb	1	SCA-HUM	None	Scapula	Whole HUM-FOOT	None	20
Forelimb	1	SCA-HUM	None	Scapula	Whole HUM-FOOT	None	40
Hind limbs	2	Trunk-limb	None	Whole limb	None	None	40
Ribcage	1	1st–4th CERV	Random	Random	Random	Articulated rib cage & frags	120

2) Feeding Trial 1B

Medium and small size crocodiles (N=20) feeding on adult goat limbs (N=4)

Two pairs of articulated hind limbs from two adult goats were placed on the ground near the pool. Like Trial 1A, the carcasses retain all flesh. The limbs from each set were still attached to the pelvic girdles. Another set of crocodiles composed of small and medium size individuals were released from the basking ground to the poolside. One pair of hind limb was tossed first. Two crocodiles approached, grabbed and drag the carcass into water and submerged. The other set was tossed into the *banda* within 10 minutes in order to disperse the crocodiles from the first carcass.

In all occasions, femoral heads were pulled off from acetabelum by death-rolling and shaking, after the girdle having been split. The innominates were the first to be swallowed, within 20 minutes. After the femurs were torn apart from the girdle, the limbs were grabbed, by the knee joints, prior to complete ingestion. During this frenzy feeding the limbs were battered on the ground and shaken vigorously. It took almost 30 minutes before a pair of limb was swallowed by different sets of crocodiles.

Trial 1B. Sequence of carcass disarticulation and ingestion by Nile crocodiles. Two sets of fresh mature goat hind limbs (N=4) introduced to medium and small size crocodiles (N=20). Skeletal regions are ranked according to sequence of consumption. The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb	2	INNO-FEM	None	INNO	Whole FEM-FOOT	None	40
Hind limb	2	INNO-FEM	Knee joint	INNO	FEM-knee Lower limb	None None	80

3) Feeding Trial 1C

Medium and small size crocodiles (N= 10) feeding on immature cow limb (N=1)

An isolated femur of a large cow (size 3) was defleshed but left with significant quantity of meat. A set of medium and small size crocodiles were released from the basking ground to the poolside. Because the carcass was large and short it was not easy for crocodile to break or swallow, rather individual reptiles were mostly engaged in ripping meat off the bone, while others held the femur from both ends. The larger crocodiles tried persistently to break the bone by spinning and shaking. Frequently, the bone would be lost under water but later discovered other crocodiles. The bone was abandoned in water after most of the flesh was ripped off. After the initial hours of observations (3-7 p.m.), the bone was left in the pool and was collected on the following day at 3 p.m.

Trial 1C. Fresh isolated femur from immature cow (size 3-4) introduced to medium size crocodiles (N=10). The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Isolated femur	1	None	None	Flesh	None	Femur	24 Hrs

4) Feeding Trial 2A

Large crocodiles (N= 3) feeding on immature cow hind limb (N=1)

A hind limb of a large sub-adult cow (size 3) was bulk-defleshed but retains significant amount of meat and tendons. The limb consisted of innominate, femur, tibia and patella, calcaneum and astragalus embedded in the tendons attached to the limb. The sacrum and three caudal lumbar bones were fused to posterior side of the hipbone. The lower limb (metatarsal-foot) was disarticulated by the local butcher, and not was included in the feeding.

After the limb was tossed into the *banda* the largest reptile (female) grabbed the carcass and subdued it into the water. The male crocodile followed and held from the other end of the limb and submerged while pulling. The smaller female was watching this scramble from few feet away because it was chased away by the larger female. Nonetheless, the small female was able to get close and tear off pieces of flesh while the two crocodiles were holding the limb. At one time the male lifted the whole carcass up in the air by the iliac blade and bounce it on the floor with fast and powerful force. The femoral head was detached from the hip joint, while some of the torso vertebrae were detached and flown off.

The two large reptiles rolled, twisted and battered the limbs without being able to break the limb. The animals avoided to ingest the pelvic girdle whole but they actively tearing chunks of meat off the bone, mainly by using anterior teeth. The pelvis was abandoned in water after 70 minutes of feeding, and all animals turned their attention to the limb. Most damage occurred on the vertebrae processes because of battering the carcass hard on the floor and wall. After 2 hours the animal stop fighting and occasionally each animal will try to pick up the limb from water and hold in its mouth, effortless trying to break it. The loose flesh, scraps and tendons were moderately ripped off the bone. Both the isolated pelvis and articulated limb bones were left in the pool overnight (24 hours), and there were no further action on the bones.

Trial 2A. Sequence of carcass disarticulation and ingestion by Nile crocodiles (N=20) feeding on fresh hind limb from immature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb	1	INNO-FEM	VRT, SACRUM	VRT	None	INNO, LUM, SAC ***Isolated*** FEM-TIB-TAR ***articulated***	30

5) Feeding Trial 2B

Large crocodiles (N=3) feeding on adult goat (N=1)

A complete carcass of an adult male goat was place in the *banda* after the skin and internal organs were removed. The large crocodile approached and pulled the carcass by the lower limb into the water. The other reptiles joined and start pulling, twisting and shaking the carcass. The male hold on the frontal skull by its jaws and twist and pull off the head probably with couple of cervical bones attached. The skull was held in the mouth for a while and submerged in water. The remaining trunk was bounced off grounds and shaken hard and was broken off probably near caudal lumbar region.

The hind limbs still attached to the pelvis were pulled apart by the two large reptiles each swallowing the complete element after battering several times on the wall and ground. One of the forelimb was eaten by the small female after detaching the scapulae with the help of the male. The male swallow the scapula. Later the cranial side of the ribcage was squeezed easily in the mouth of the large female while the other where tearing off meat and scrap from the lateral and caudal sides and all submerged in water, spinning and tossing the carcass up in the air. The other forelimb and skull were lost in water and were not observed eaten. However, after cessation of the experiment 24 hours later both elements were not found in the pool. Probably, the cranial was crushed and swallowed.

Trial 2B. Sequence of carcass disarticulation and ingestion by large Nile crocodiles (N=3) feeding on fresh mature goat carcass (N=1). Skeletal regions are ranked according to sequence of consumption. The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Head	1	Head - Neck	Broken?	Not observed	None	None	24 hrs
Forelimb	1	Trunk-SCA	SCA-HUM	SCA	HUM-FOOT	None	20
Forelimb	1	Trunk-SCA	Not observed	Not observed	Not observed	None	24 hrs
Trunk	1	Trunk-LUM	SAC-PEL	Not observed	Not observed	None	24 hrs
Hind limb	1	PEL (separated)	None	INNO-FOOT	None	None	60
Hind limb	1	as above	None	INNO-FOOT	None	None	80

6) Feeding Trial 3A

Medium and small size crocodiles (N=20) feeding on adult cow forelimb (N=1)

A complete forelimb of an adult cow (size 3) with moderate amount of flesh was provisioned to medium and small size crocodiles. The scapula was detached from the limb after 2 hours of scrambling. The animals ripped off meat from bone by spinning. Since the animal could not further process the limb, one or two animals at one time would be seen holding the limb in the mouth, often submerging with the bone. In several occasion the limb was lost in the water but picked up again. The limb was left in the pool for 24 hours. Radioulna was still articulated to carpals, metacarpals and phalanges when retrieved from the pool. Tendons on elbow joints were torn off resulting into the snap of proximal ulna. Only scraps left on the bone after cessation of the experiment.

Trial 3A. Sequence of carcass disarticulation and ingestion by Nile crocodiles (N=20) feeding on fresh mature cow forelimb (N=1). Skeletal regions are ranked according to sequence of consumption. The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Forelimb (whole)	1	SCA-HUM	None	Flesh on SCA & HUM	None	Isolate SCA Articulated HUM-RADU-FOOT	120 24 hrs

7) Feeding Trial 3B

Medium size crocodiles (N=10) feeding on mature cow lower limbs (N=4)

Two pairs of front and hind lower limbs (metapodial articulated to foot) were given to medium size crocodiles. Two of the bones were skinned while the rest were left with skin. After fierce scrambling one of the largest crocodile get hold of defleshed metacarpal and positioned it perpendicular to the long axis, opened its jaws wide and closed with force-full bite. The bone crushed but held together by the tendons and flesh. The bone rested in the mouth for about 20 minutes before the animal began to mouth the bone while swallowing slowly from proximal side of the bone (e.g., Carpenter, 1928). It took 16 minutes to swallow the complete limb. With exception of one lower limb with skin, which was lost in the pool and the animal's failure to eat, the rest were swallowed by the largest reptiles in the group.

Trial 3B. Two pairs of front and rear lower limbs (N=4) from cow attended by Nile crocodiles (N=10). One limb from each set has skin and others have no skin.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
MTC-Skin	1	None	None	None	None	MTC-FOOT	24 hrs
MTC-no skin	1	None	None	Proximal	None	None	36
MTT-Skin	1	None	None	Proximal	None	None	50
MTT-no skin	1	None	None	Proximal	None	None	45

8) Feeding Trial 4A

Large crocodiles (N=3) feeding on mature cow forelimb (N=1)

A complete forelimb of an adult cow (size 3) was provisioned to three large crocodiles. Only the bulk muscles were defleshed but tendons were left intact. The male approached the limb and grabbed it from the radioulna. The large female joined and grabbed the limb from the blade of the scapula and fight began immediately with the bone taken into water. The submerged several times delivering powerful bites while rolling and pulling. While the two large animals were trying to break up the limb, the small female was busy nibbling flesh and scraps off the scapula, shoulder and elbow joints, and along the length of the limb. The scapula was detached off the limb after 16 minutes. The large crocodile kept the blade in its mouth for a while, holding from cranial side trying to swallow without success and abandoned after about 25 minutes. It joined the other two reptiles and grabbed the limb from them by pulling it from humerus and tried to swallow. It threw the limb up several times and delivers severe bite blows, while shook and hit the limb against the ground and wall. Occasionally the other crocodiles held the bone from the other side and continue to nibble the scraps. Each animal was seen to hold each piece (scapula and limb) at different times and this practice continued for three hours when both bones where abandoned in the pool and no effort was made by crocodiles to retrieve them. The humerus was still articulated to radioulna and carpals after cessation of the experiment.

Trial 4A. Sequence of carcass disarticulation and ingestion by large Nile crocodiles (N=3) feeding on a fresh and complete forelimb from mature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Forelimb (whole)	1	SCA-HUM joint	None	Flesh on SCA-HUM	Attempt whole bone	SCA ***Isolated***	16
						HUM-RADU-CARPALS ***articulated***	180

9) Feeding Trial 5B

Medium and small size crocodiles (N=20) feeding on immature cow forelimb (N=1)

A complete forelimb (missing lower part) of sub-adult cow (size 3) with moderate flesh was provisioned to medium and small size crocodiles. Only the bulk muscles were defleshed but tendons left intact. The scapula was detached from the limb after 12 minutes of fierce scrambling. Several animals roll and twist to tear off meat from the limb while others hold firm the limb with their anterior and cheek teeth. In several occasion the limb was lost in the water but picked up again. The limb was left in the pool for 24 hours. The humerus was still articulated to radioulna and carpals after cessation of the experiment.

Trial 5B. Sequence of carcass disarticulation and ingestion by medium and small Nile crocodiles (N=20) feeding on a fresh and complete forelimb from immature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Forelimb (whole)	1	SCA-HUM joint	None	Flesh on SCA-HUM	Flesh & tendons on SCA, HUM, RADU	SCA ***Isolated*** HUM-RADU-CARPALS ***articulated***	12 24 hrs

10) Feeding Trial 6C

Large crocodiles (N=3) feeding on mature cow hind limb (N=1)

A complete hind limb (missing lower limb) of an adult cow (size 4) was detached from the pelvis and provisioned to the large crocodiles without much defleshing. The crocodiles kept holding the carcass under water from both ends without much effort to break the large bone. Because the limb was large with abundant meat the animal engaged in tearing the flesh off the bone by rolling, while using cheek and anterior teeth to hold and pull. This practice continued for three hours often with breaks in between of up to 20 minutes. When the limb collected after 24 hours, a large quantity of meat was still present on the bone without significant damage to bones. The crocodiles were also not hungry as usual.

Trial 6C. Sequence of carcass disarticulation and ingestion by large Nile crocodiles (N=3) feeding on a fresh and complete hind limb from mature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb (missing pelvis)	1	None	None	Flesh on FEM & TIB	None	FEM-TIB-TAR ***articulated***	24 hours

II. ENGOSHERATON FARM

11) Feeding Trial 7

Medium and small size crocodiles (N=5) feeding on immature cow forelimb (N=1)

A defleshed forelimb (but with substantial quantity of meat and tendons) of sub-adult cow (size 3) was provisioned to five crocodiles. The scapula was detached from the limb after 25 minutes of rolling, twisting and pulling. In several occasion the limb was lost in the water but picked up again. The largest crocodile hold the limb by radioulna for about 40 minutes trying break the bone by hitting and rolling. The limb was left in the pool for 24 hours.

Trial 7. Sequence of carcass disarticulation and ingestion by medium and small Nile crocodiles (N=5) feeding on a fresh and complete forelimb from immature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column. See coding for skeletal elements in Appendix I

Skeletal Region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Forelimb (whole)	1	SCA-HUM joint	None	Flesh on SCA-HUM	Flesh on SCA-HUM	SCA ***Isolated*** HUM-FOOT ***articulated***	25 12 hrs

12) Feeding Trial 11

Medium and small size crocodiles (N=5) feeding on immature goat (N=1)

A whole goat carcass (missing head) was defleshed but leaving substantial amount of meat. The internal organs were removed. The largest reptile was very aggressive and grabbed the carcass by the lumbar-sacrum region and submerged into water. It rolled and bounced the carcass hard on the ground and break the pelvic girdle from the trunk after 20 minutes. Since the pool is small the two small animals did not get close to the actions. One crocodile hold the thigh of one leg and rolled. The pelvis was separated and each animal submerged with their pieces in mouth and start hitting and delivering hard jaw blows on the meat, while swallowing from the pelvis side. The limb swallowed halfway and crocodile rest for quite a while before start ingesting again. The two other crocodiles got hold of the trunk, and one forelimb was pulled off the body, followed by the second limb within 40 minutes apart. The small crocodile get the limb and run away into the small pool. One crocodile got hold the neck region and hit the carcass hard several times on the ground and the skull flew-off the body. Generally the ribcage was not grossly damaged. The right side left intact, while the 4 caudal ribs the left side were snapped.

Trial 11. Sequence of carcass disarticulation and ingestion by medium and small size Nile crocodiles (N=5) feeding on fresh young goat carcass (N=1). Skeletal regions are ranked according to sequence of consumption. The maximum duration/ time taken for complete ingestion or abandonment of skeletal region is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb	1	Trunk-PEL	None	Hind limb	None	None	20
Hind limb	1	Trunk-PEL	Not observed	Not observed	Not observed	Not observed	24 hrs
Forelimb	1	Trunk-forelimb	SCA-HUM	Scapula	HUM-FOOT	None	70
Forelimb	1	Trunk-forelimb	SCA-HUM	Scapula	None	HUM-FOOT	90
Trunk	1	Random	Random	Flesh	None	Axial	24 hrs

13) Feeding Trial 13

Medium and small size crocodiles (N=5) feeding on immature cow hind limb (N=1)

A complete hind limb comprised of upper and lower parts was provisioned to Nile crocodiles. The femur was pulled off acetabelum within 30 minutes of feeding by two crocodiles each holding from other end, while the rest were ripping meat off the bone. The innominate was grabbed by one individual and later abandoned in water after failure to break or swallow the element. In several occasions the rest of articulated limb was abandoned in the water but picked up again by one of the largest individuals. At one occasion the largest crocodile held the limb by the tibia for about 40 minutes trying break the bone by battering and rolling. The limb was abandoned and left in the pool for 24 hours without further dismembering.

Trial 13. Sequence of carcass disarticulation and ingestion by medium and small size Nile crocodiles (N=5) feeding on a fresh and complete hind limb from an immature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column. See coding for skeletal elements in Appendix I.

Skeletal region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb (whole)	1	Pelvic- femoral head	None	Flesh on pelvic girdle, femur & proximal tibia	None	Isolated innominate Articulated Femur - foot	25 24 hrs

14) Feeding Trial 14

Medium and small size crocodiles (N=5) feeding on mature cow hind limb (N=3)

A hind limb (but missing pelvis) of an adult cow (size 3) was provisioned to five crocodiles. The largest crocodile hold the limb by tibia trying break the bone by battering and rolling, while another crocodile was holding on the other side. Often the two small crocodiles were pushed out of the battle and not observed to approach the limb food when the largest individual was present. The animals were not observed to pick up the bones from the pool after about five hours of experiment. The limb bones were left in the pool for 24 hours.

Trial 14. Sequence of carcass disarticulation and ingestion by medium and small size Nile crocodiles (N=5) feeding on a fresh hind limb from mature cow (N=1). The maximum duration/ time taken for complete ingestion or abandonment of skeletal part is indicated on the last column.

Skeletal region	N	First disarticulation/ breakage	Second disarticulated/ breakage	First ingestion	Second ingestion	Remains	Time Min.
Hind limb (whole)	1	None	None	Flesh on femur & proximal tibia	None	Articulated Femur -foot	24 hrs

III. Preliminary Feeding Trials

These initial feeding trials were carried out in 2000 in order to gather basic taphonomic information on crocodile’s ability in modifying large mammalian bones the way mammalian carnivores do. The only information available then with regard to crocodilian feeding traces were based on anecdotal observations (e.g., Davidson & Solomon, 1990) and inferences made from paleontological record (e.g., Avilla et al., 2004; Buffetaut, 1983; Davidson & Solomon, 1990; Pickford, 1996). I began my observations by testing whether the crocodiles preferentially select skeletal parts and portions for consumption the way mammalian do (e.g., Blumenschine, 1986a).

15. Trial 1

Small size crocodiles (N=5) feeding on isolated cow elements (N=19)

Nineteen complete elements from immature cows were placed on the sandy basking ground outside of the pool. Five crocodiles were first released from the poolside to the basking area in order to feed on the fresh bones. Three of the reptiles had a maximum length of 1.87 m and two were 1.1 – 1.56 m long. The reptiles did not discover the food immediately after release because they are accustomed to small chunks of meat tossed from the wall of the *banda* to the pool side. This behavior may suggest that crocodiles are slow in discovering food on the ground. Only three elements (1 metacarpal and 2 scapula) were removed from the site by three crocodiles.

Initially, one of the largest crocodile (ca. 1.5 m) recognized the food and approached the bones. It grabbed the scapula from the glenoid end and held it for a while before moving away with the bone. The other large crocodile sensed this discovery and approached the assemblage. One grabbed the defleshed metacarpal and carried it away from the scene. A small crocodile recognized the food and selected the small scapula, which laid closest to her.

Upon grabbing a bone specimen, the first reaction of each crocodile was to run towards the pool. But since the door was locked, they stayed in the basking area. At different times the five crocodiles were found to scramble and exchange on the same three specimens by pulling the bones from each other. This exercise went on for almost 4 hour until either they lost interest in the bones after failure to swallow or lost them in the sandy ground. The remainder of the bone specimens were ignored and left on site untouched. It seems that the basic instinct of crocodiles is to follow the individuals that hold a pieces of food in their mouths.

Trial 1. Carcass utilization by small size Nile crocodiles (N=5) on I solated but complete fresh elements (N=19) from immature cows. Only three elements were attended by crocodiles. The observation was ceased after four hours.

Skeletal element	N	Condition	Feeding
Metacarpal-foot	1	No skin	Attended
Metacarpal-foot	1	With skin	Ignored
Metatarsal-foot	1	No skin	Ignored
Metatarsal-foot	1	With skin	Ignored
Scapula	1	Defleshed	Attended
Scapula	1	Defleshed	Ignored
Scapula	2	Defleshed	Attended
Scapula	2	Defleshed	Ignored
Scapula	3	Defleshed	Ignored
Mandible	1	Defleshed	Ignored
Mandible	2	Defleshed	Ignored
Hemi-mandible	3	Defleshed	Ignored

16. Trial 2

Small and Medium size crocodiles (N=20) feeding on isolated cow elements (N=19)

Additional fifteen small to medium size crocodiles were released to attend the same assemblage. The first ten individuals released from the pool, which did not participate in the first experiment (Trio 1) attacked the assemblage and carried all the bones away from the site to the pool. Once a crocodile with food dived into water, other crocodiles would follow into water and try to grab the food. Scrambling for the bones went on for almost two hours until some of the large crocodiles were able to swallow some of the specimens.

After the disappearance of all the specimens from the basking area and making sure that there was no individuals holding a bone, the pool was drained the following morning to recover any remains left on the bottom of the pool.

Trial 2. Carcass utilization by small to medium size Nile crocodiles (N=20) on isolated but complete fresh elements (N=19) from immature cows.

Skeletal element	Specimens recovered
Metacarpal-foot	1 (with no skin)
Scapula	5
Mandible (split into 2 halves)	3

17. Trial 3

Large crocodiles (N=3) feeding on isolated cow elements (N=3)

Two complete crania of young cows with flesh, skin and brains and a complete pelvis (defleshed but with substantial amount of flesh) were placed on the ground for the large crocodiles to feed. The crocodiles did not eat the carcasses probably because they had large meal within the previous week. The carcasses were removed from the *banda* after three days.

18. Trial 4

Medium size crocodiles (N=40) feeding on mature goat (N=1)

A whole goat carcass with all limbs attached to the trunk was placed in the *banda* on the ground near pool. The carcass has had its skin and visceral organs removed but retain all flesh. About 40 medium size reptiles were released from the basking ground to attend the carcass on the poolside. After the carcass grabbed and pulled into water a big explosion of scrambling over the carcass occurred and the carcass was torn apart randomly into large parts and was completed without with 1 hour of recording.

19. Trial 5

Medium size crocodiles (N=30) feeding on mature goat (N=1)

This time the number of medium size crocodiles were reduced to 30 individuals to feed on a whole goat carcass (similar to Trio 4). Like Trio 4 above, only few small fragments flown-off during feeding were recovered but no skeletal remains of significant size or damage was recovered after feeding was completed.

APPENDIX III. Contrasts between the feeding traces produced by large mammalian carnivores (MC), including larger hyaenids, felids and canids, and Nile crocodiles (CROC) on larger mammal bones and bone assemblages. Assemblage characteristics assume *in situ* deposition and no contributions from other taphonomic agencies. NISP, number of identified specimens; MNE, minimum number of elements; MNI, minimum number of individuals (From Njau & Blumenschine, 2006).

Feeding Trace		Observed Characteristics
Tooth Mark		
Morphology		
- Interior morphology		
	Similarities	Interior surface of pits, scores and furrows show crushing. Micro-striations within or emanating from a pit, or within a score occur occasionally.
	Differences	Possible microscopic (> 10x magnification) differences not measured in this study.
- Pits	Similarities	Shallow to deep with bowl-shaped to irregular cross-section. Pit may have a score emanating from one margin.
	Differences	**MC**: Circular to angular in plan. Typical diameter of pits generated by jackals, hyenas, lions and dogs from ca. 1.5 - 4 mm (jackals= smallest, dogs= largest)[1]. Bisected pits not observed. **CROC**: Circular to oval in plan. Some pits are partly or wholly bisected by a sharp linear depression that can exceed the diameter of the pit, showing a V-shaped cross-section across the bisector (= “bisected pit”). Pit diameters range from 0.1 mm (pin-prick-like) to over 6 mm.
- Scores	Similarities	Usually linear, less commonly curved or angulated in plan, sometimes emanating from a well-defined pit. Superficial to deep with usually U-shaped cross-section.
	Differences	**MC**: Average lengths for jackals, hyenas, lions and dogs, ca. 3 - 13 mm. Average breadth, ca. 0.4 - 2.2 mm[1]. “Hook scores” not observed. **CROC**: Presence of “hook scores” (partially to fully parabolic in plan). Score lengths, ca. 3.5 - 55 mm; breadths, ca. 0.1 - 2.5 mm.
- Punctures & furrows		
	Similarities	Circular to oval in plan.
	Differences	**MC**: Semicircular tooth notches (half punctures) commonly occur at

	fracture edges. Punctures through the thick cortices of large, complete long bones are not observed. Bisected punctures are not observed. Average diameter of punctures is ca. 2.5 - 7.5 mm for canids, felids and hyenas[1, 2]. Furrows are linear in plan with average length from ca. 13 - 24 mm, and average breadth from ca. 1.8 - 5.0 mm for dogs, hyenas and lions[1]. **CROC**: Punctures sometimes bisected as in pits. Punctures through thick cortical bone may be associated with chipping and shallow to deep cracks emanating from opposite sides of puncture, and running along the long axis of the bone. Serial puncturing observed occasionally. Diameters, ca. 1.0 - 11 mm, though one puncture of 21 mm was inferred to have been produced by a Serengeti crocodile. Furrows and notches not observed.
<u>Pattern of Tooth Marking</u>	
- Orientation of scores	
Similarities	Variable, but usually tending to transverse to the longitudinal axis of long bones.
Differences	Possible fine differences not recorded in this study.
- Location and density	
Similarities	Marks can occur on any part of a bone as isolated occurrences or in clusters.
Differences	**MC**: Clusters with typically 2 – 5 marks. Denser concentrations possible along gnawed margins or fracture edges, especially on robust portions, or in the case of “boredom gnawing.” Tooth marks can occur on the thickness and internal surface of fragmented bone. **CROC**: Clusters with generally higher mark densities. Extremely high densities (tens) of pits and sub-parallel scores occur on major grasping areas from attempted disarticulation. Isolated to multiple pits and scores occur on portions of elements lacking narrow grasping points, including at snapped edges. The tooth-marked control specimens bear an average of about 50 marks (Table 3). Serial marking involving pits, punctures or

		scores made by as many as three adjacent teeth occurs rarely.
- Incidence of tooth-marked specimens		
	Differences	**MC**: High frequency of fragmentary tooth-marked specimens, typically > 50% of NISP (e.g., Table 4). Frequent tooth-marking of more or less complete specimens from defleshing and associated marginal gnawing of soft portions. **CROC**: Lower proportion of tooth-marked specimens (ca. 21% of NISP from the control sample; Table 4), most of which are complete.
Gross Gnawing		
	Differences	**MC**: Very marginal gnawing to complete destruction of soft, cancellous bone (e.g. proximal humerus, distal femur, iliac crest and blade; ischial tuberosities, scapular blade, vertebral processes), often producing a crenulated edge. **CROC**: None.
Disarticulation		
	Similarities	Dependent on joint strength. Whole forelimb typically dismembered first.
	Differences	**MC**: Typically through gross gnawing. Partial or complete destruction of skeletal elements plus dispersal of bones can leave few associated articulating specimens. **CROC**: Through death-roll, pulling, shaking or battering of the bone. Abandonment of complete skeletal units plus lack of bone transport can leave many associated articulating specimens.
Fragmentation		
	Similarities	Common snapping of thin, flat bone portions (e.g., vertebral processes, distal rib shafts). Common ingestion of smaller bone pieces.
	Differences	**MC**: Fragmentation of bones with interior cavity (e.g. long bone shafts, cranial case, mandibular horizontal ramus), typically producing spiral breaks, occasionally notches and crenulated margins, and relatively high

	NISP/MNE values (about 5 for long bones[3]). Destruction preferentially of lower density elements or element portions by gnawing and ingestion. Ingestion of complete bones usually limited to podial elements. High ravaging and dispersal by consumers can produce low MNE/MNI values. Regurgitated pieces with acid etching, polishing and/or tooth-marking. Some small fragments defecated. **CROC**: Uningested fragments uncommon and limited mainly to snapping of thin, flat bone portions. Snapping rarely associated with crenulation. Retention of many complete specimens, producing NISP/MNE value close to 1 (1.06 for the control collections). Destruction by ingestion of whole bones or skeletal units, dependent on bone size, not structural density. If carcass is large relative to crocodile size, MNE/MNI will be relatively high. Regurgitation of bones not observed; defecated bones are completely demineralized[4].

[1] Dominguez-Rodrigo & Piqueras (2003).
[2] Selvaggio & Wilder (2001).
[3] Capaldo (1995).
[4] Fisher (1981a).

APPENDIX IV. Extinct large mammalian fauna that lived in Serengeti plains during the Plio-Pleistocene times, and their preserved fossils are exposed in the Olduvai Beds I–IV (Leakey, 1971; Leakey, Savage & Coryndon, 1973; Gentry & Gentry, 1978a, 1978b; Leakey & Harris, 1987).

Extinct species	Closest extant species	Tribe	Family	Order	Bed
Ceratotherium simum	Primitive white rhino		Rhinocerotidae	Perissodactyla	**I – IV**
Stylohipparion sp.	3-toed spp		Rhinocerotidae		
Sivertherium maurusium	Gigantic giraffid		Giraffidae	Artiodactyla	
Giraffa stillei	Pygmy giraffe		Giraffidae		
Antidorcas recki	Springbok (*A.marsupialis*)	Antilopini	Bovidae		
Megalotragus kattwinkeli	Large kongoni/ or wildebeest	Alcelaphini	Bovidae		
Hippopotamus gorgops	Highly amphibious hippo		Hippopotamidae Tetraprotodont		
Kolpochoerus olduvaiensis	K. limnetes		Suidae		
Elephas recki	Hypsodont teeth		Gomphotheriidae	Proboscidea	
Anancus kenyaensis	No tusk		Gomphotheriidae	Proboscidea	
					I – Lower II
Ancylotherium hennigi	Chalicothere-related to horse		Chalicotheriidae	Perissodactyla	
Hipparion ethiopicum/ Hipparion lybicum	Smaller zebra, highly cursorial		Equidae		
Equus oldowayensis	Massive grevy's zebra		Equidae		
Connochaetes taurinus Olduvaiensis	Wildebeest	Alcelaphini	Bovidae	Artiodactyla	
Connochaetes africanus	Black wildebeest/		Bovidae		
Parmularius altidens	Topi/ hartebeest or (*Damaliscus lunatus)*		Bovidae		
Beatragus antiquus			Bovidae		
Tragelaphus strepsiceros maryanus	Greater kudu	Tragelaphini	Bovidae		
Kobus sigmoidalis Arambourg	Kob, waterbuck	Reduncini	Bovidae		
Giraffa gracilis	Small giraffe		Giraffidae		
Kolpochoerus limnetes	Giant forest hog, bush pig		Suidae		
Metridiochoerus andrewsi			Suidae		
Phacochoerus modestus	Primitive warthog		Suidae		
Hippopotamus kaisensis	Large H. amphibius		Hippopotamidae Tetraprotodont		
Deinotherium bozasi	Lower tusked		Deinotheriidae	Deinotherioidea	
Dinofelis sp (sabertooth)	False sabertooth		Felidae	Carnivora	
Megantereon sp.			Felidae		
Megantereon eurynodon			Felidae		
Machairodus sp.			Felidae		
Crocuta aff. ultra			Hyaenidae		
Canis africanis	Wolf (C. lupus)		Canidae		
Theropithecus oswaldi	Large Gelada baboon		Cercopithicinidae	Primate	
Cercocebus sp.			Cercopithicinidae		
					Mid II – IV
Hippotragus gigas	Sable antelope	Hippotragini	Bovidae	Artiodactyla	
Tragelaphus strepsiceros grandis	Larger Greater kudu	Tragelaphini	Bovidae		
Pelorovis oldowayensis	Buffalo	Bovini	Bovidae		
Syncerus acaelotus			Bovidae		
Damaliscus angusticornis	Kongoni/ Hartebeest	Alcelaphini	Bovidae		
Damaliscus agelaeus	Blesbok?		Bovidae		
Metridiochoerus compactus	Giant pig		Suidae		
Giraffa jumae			Giraffidae		

Photo I. Lateral view of complete scapula of an adult cow disarticulated from the forelimb by small and medium-sized captive Nile crocodiles. The specimen bears a dense concentration of tooth marks on the blade and neck (white arrow), but lacks gnawing on the dorsal margin of the blade, a portion frequently gnawed by mammalian carnivores. Bottom picture is a close-up of the caudal margin of the scapular blade (inset box) displaying a classic bisected mark (black arrow) and a series of small pits (white arrow), some of which are bisected (from Njau & Blumenschine, 2006).

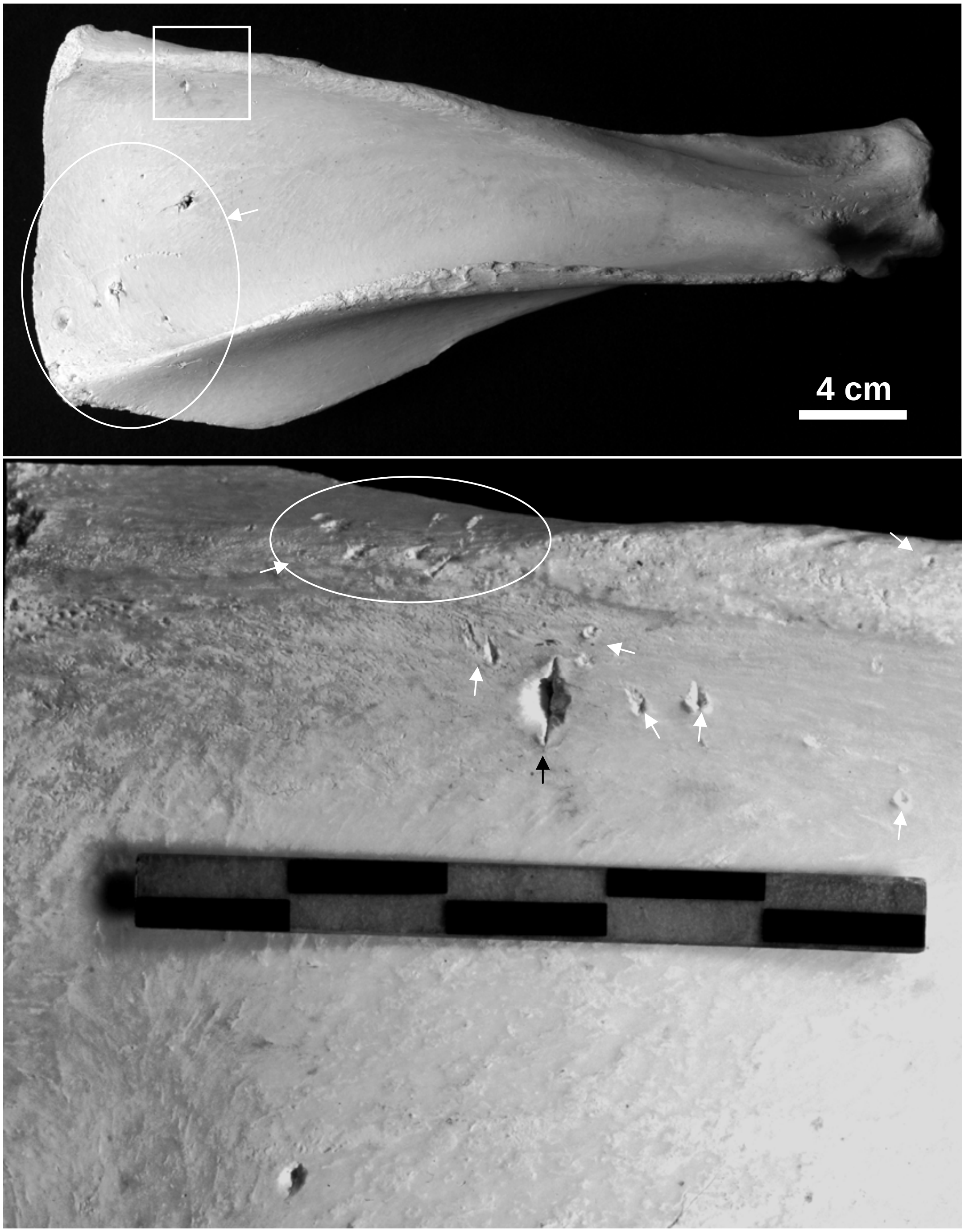


Photo II. Medial aspect of the same scapula as in Photo I (Top), exhibiting an array of pitting, scoring and puncturing on the blade and neck. Close-up of blade and neck (inset boxes) at bottom, showing numerous small pin-prick-like pits, some of which are bisected (black arrows), and a larger bisected pit (black arrow). A set of three parallel (possibly serial) scores emanating from pits (white arrow) were probably inflicted in one bite by a small captive crocodile.

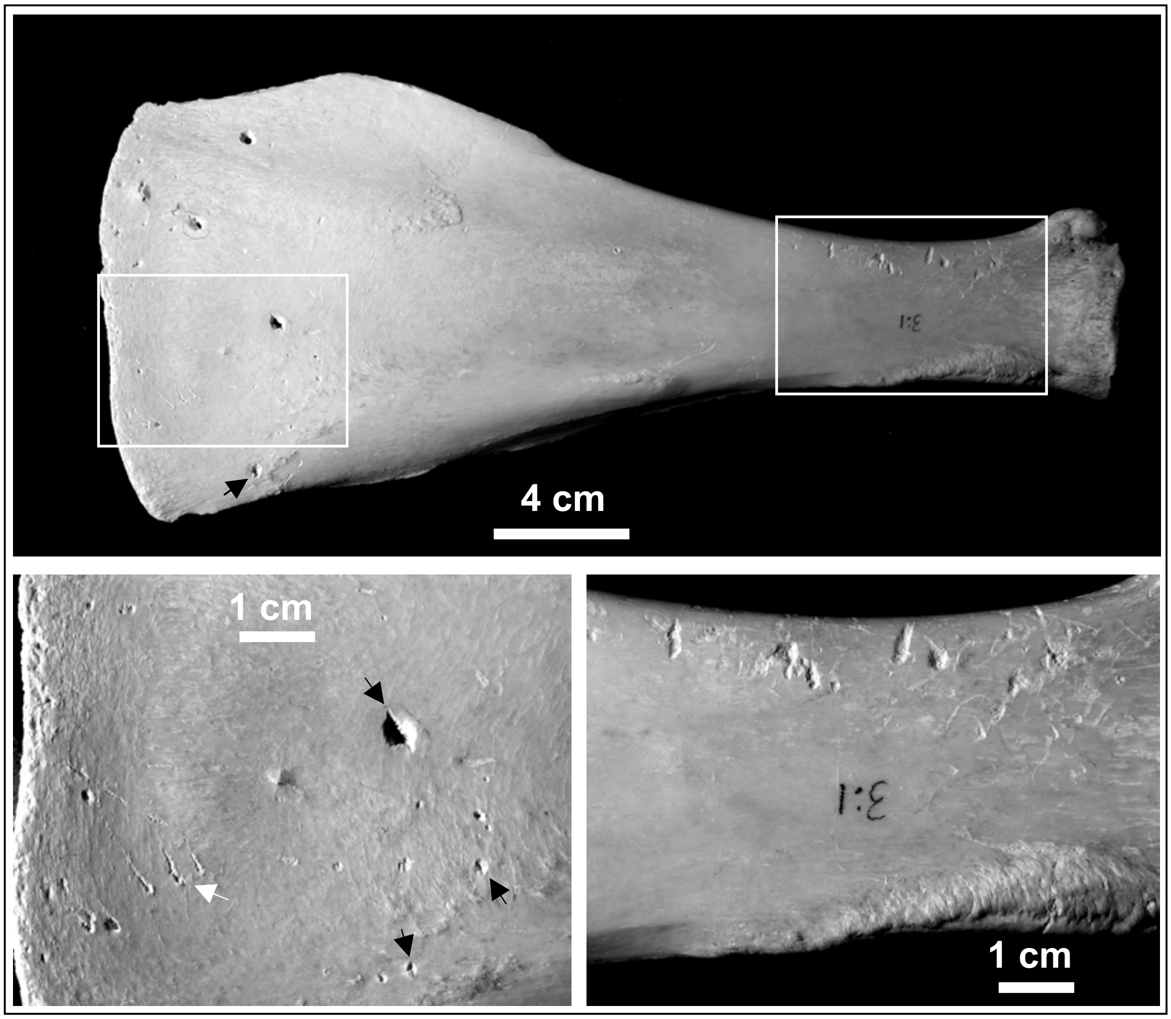


Photo III. A lateral view of the caudal portion of the innominate of a sub-adult cow with two pairs of serial bisected punctures on the ischium. The ilium had been sawn off prior to feeding. Medium-sized captive crocodiles inflicted the punctures when they detached the whole hindlimb from the innominate. The ishcial tuberosities are ungnawed, unlike the often severe reduction of this bone portion by mammalian carnivore gnawing. Below is the close-up of serial punctures, showing the internal bisection in each puncture. The bisection extends slightly from one side of one puncture, forming a triangular projection (arrow).

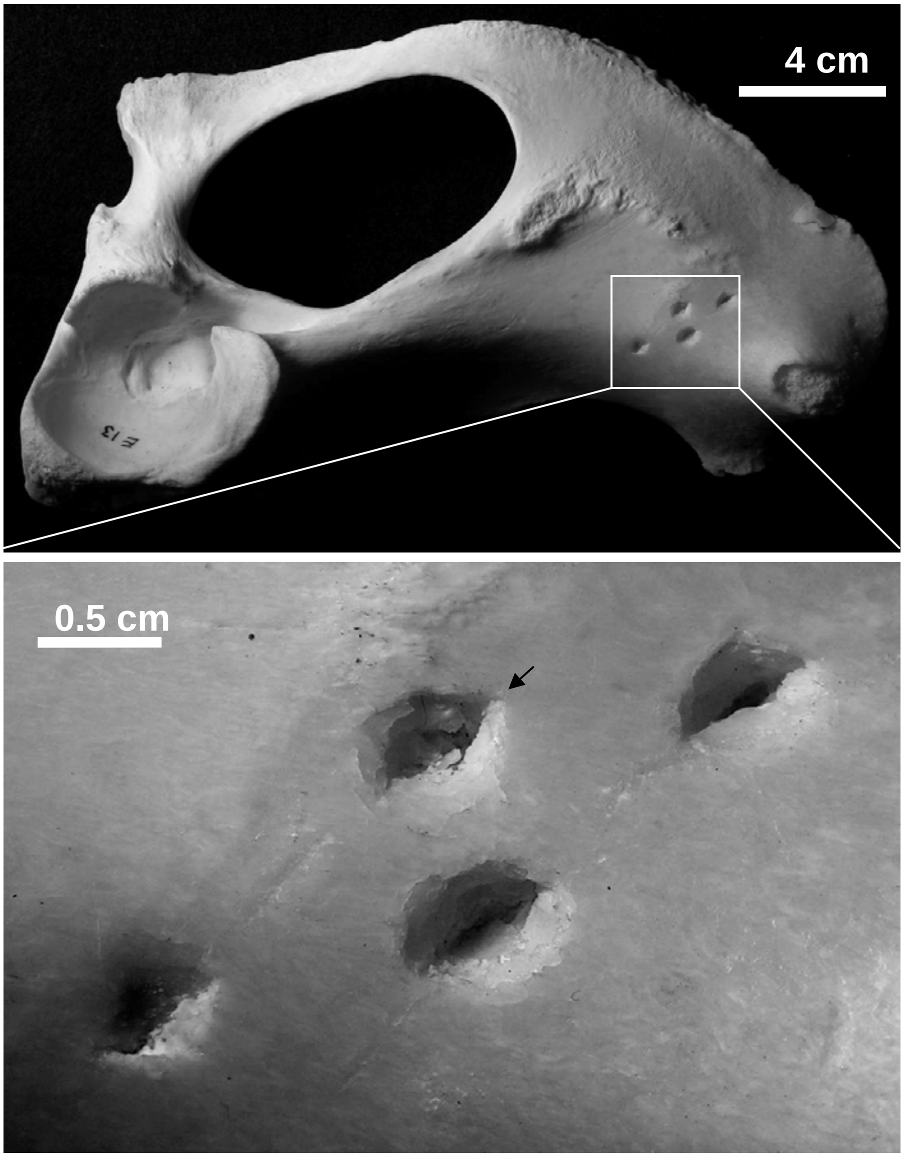


Photo IV. Medial and lateral views of the distal end of a complete tibia of a sub-adult cow displaying tooth marking inflicted by large captive Nile crocodiles. The tibia lacks gnawing on portions typically gnawed by mammalian carnivores, particularly on the tibial crest (not shown). The marks include faint to large pits and scores, including many bisected pits (only some of which are indicated by arrows), which tend to be oriented transversely to the bone's long axis. The animals grasped this region firmly with their jaws during a frenzied but unsuccessful attempt at disarticulating it from the femur and foot bones (from Njau & Blumenschine, 2006).

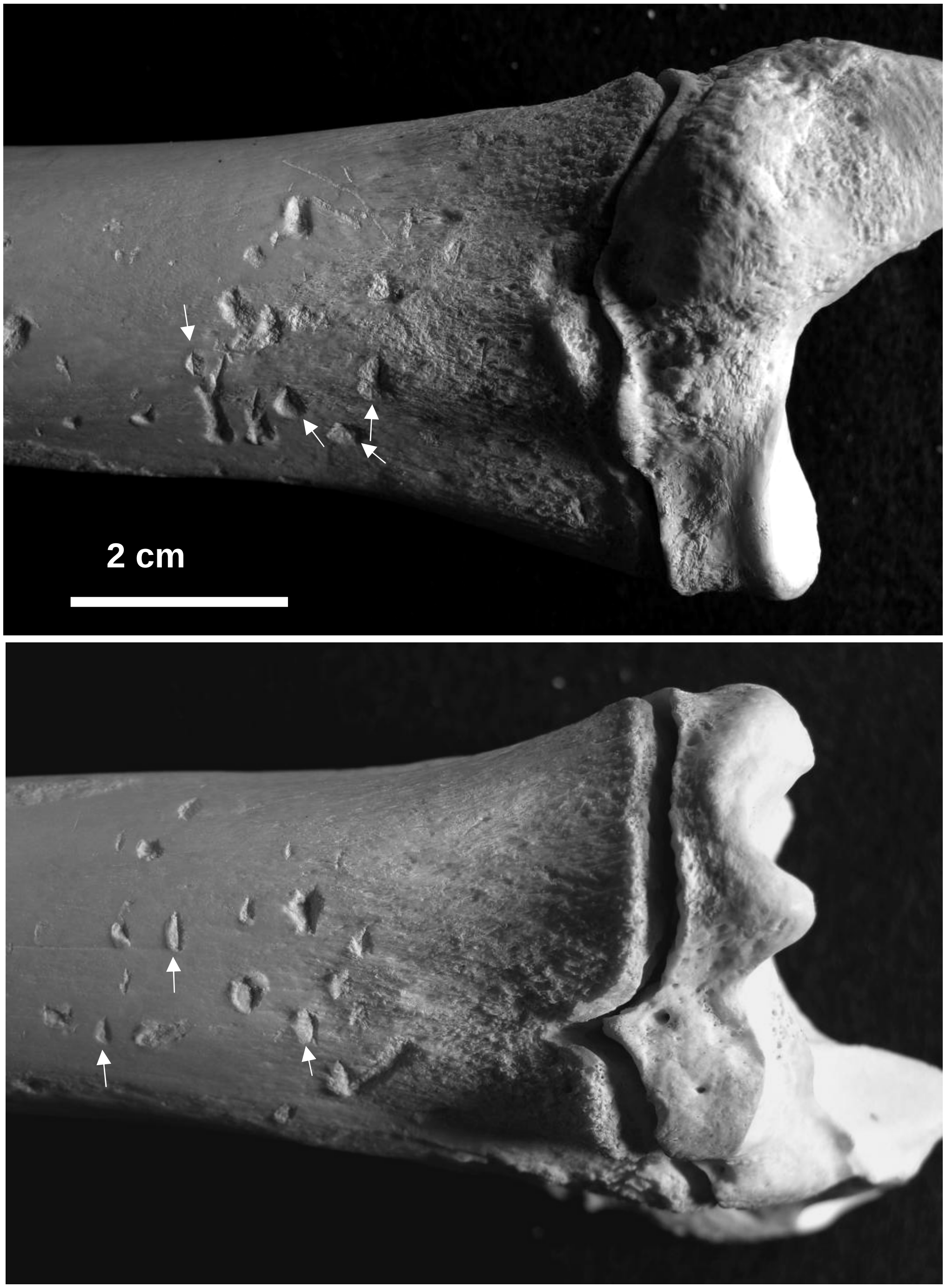


Photo V. (A) Lateral view of the proximal portion of a complete humerus of an adult cow heavily tooth-marked by large captive Nile crocodiles. The humerus was detached from the scapula during feeding, but remained articulated to the lower limb on abandonment. Small and shallow to large and deep tooth pits, a bisected pit (arrow), scores, and serial punctures (penetrating thick cortical bone) occur on the shaft and end. Despite the heavy tooth-marking, the head and tuberosities of the proximal end are ungnawed, unlike the common, marginal to complete destruction of these bone portions by mammalian carnivores. (B) Close-up of the punctured area, showing chipping of the margin of all punctures, and a longitudinal crack emanating from the distal end of the area with three superimposed punctures (on right). Another puncture exhibits a triangular projection on one side (arrow), aligned with the teeth that produced the serial puncturing (from Njau & Blumenschine, 2006).

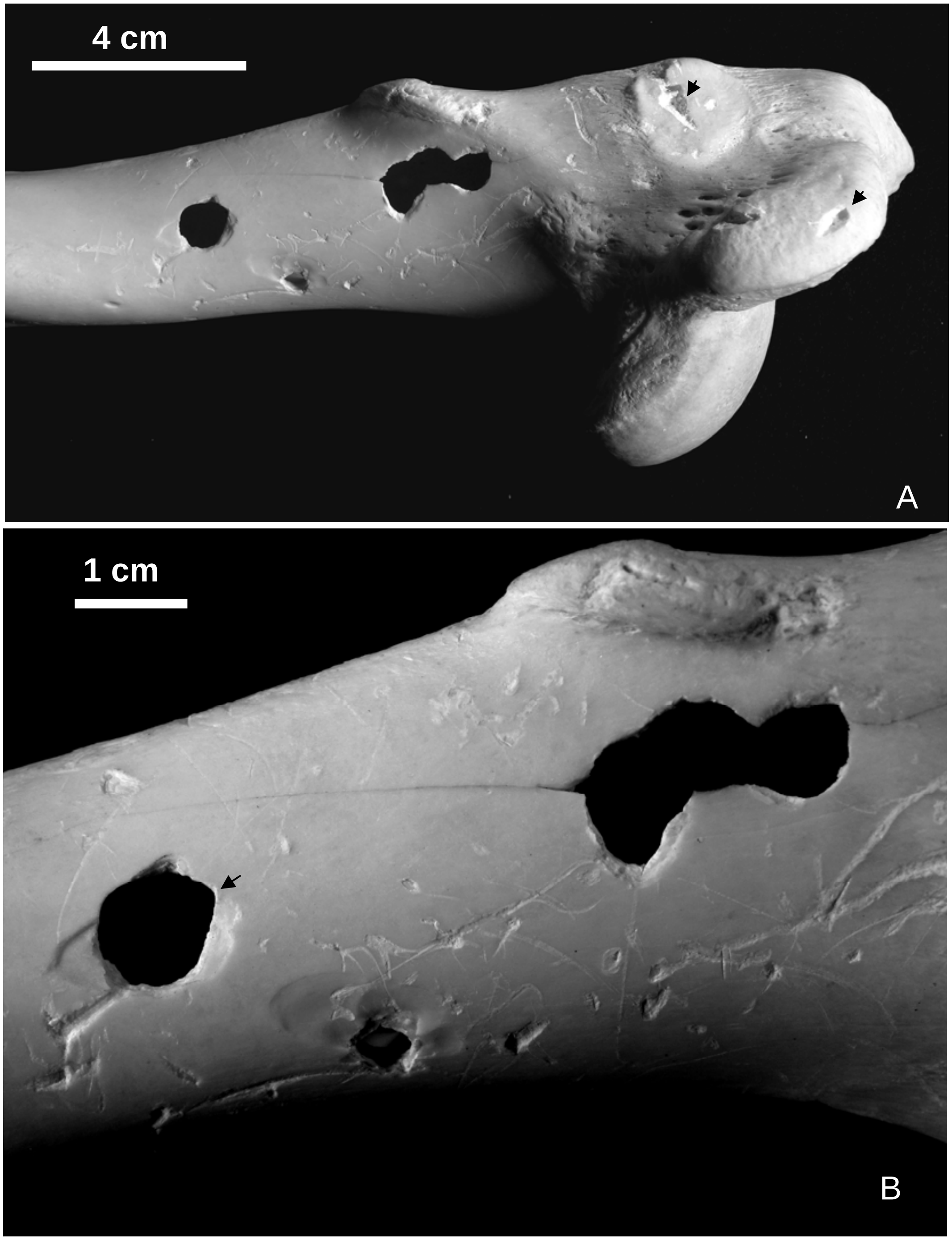


Photo VI. Heavily tooth-marked femur (Top) of a sub-adult cow consumed by captive Nile crocodiles. The enlarged part of the shaft shows variety of marks on both medial (Middle) and lateral (Bottom) faces, including parallel scores (black arrow). The white arrow indicates a ‘hook score’. The unfused epiphyses are ungnawed despite high-density tooth marking (from Njau & Blumenschine, 2006).

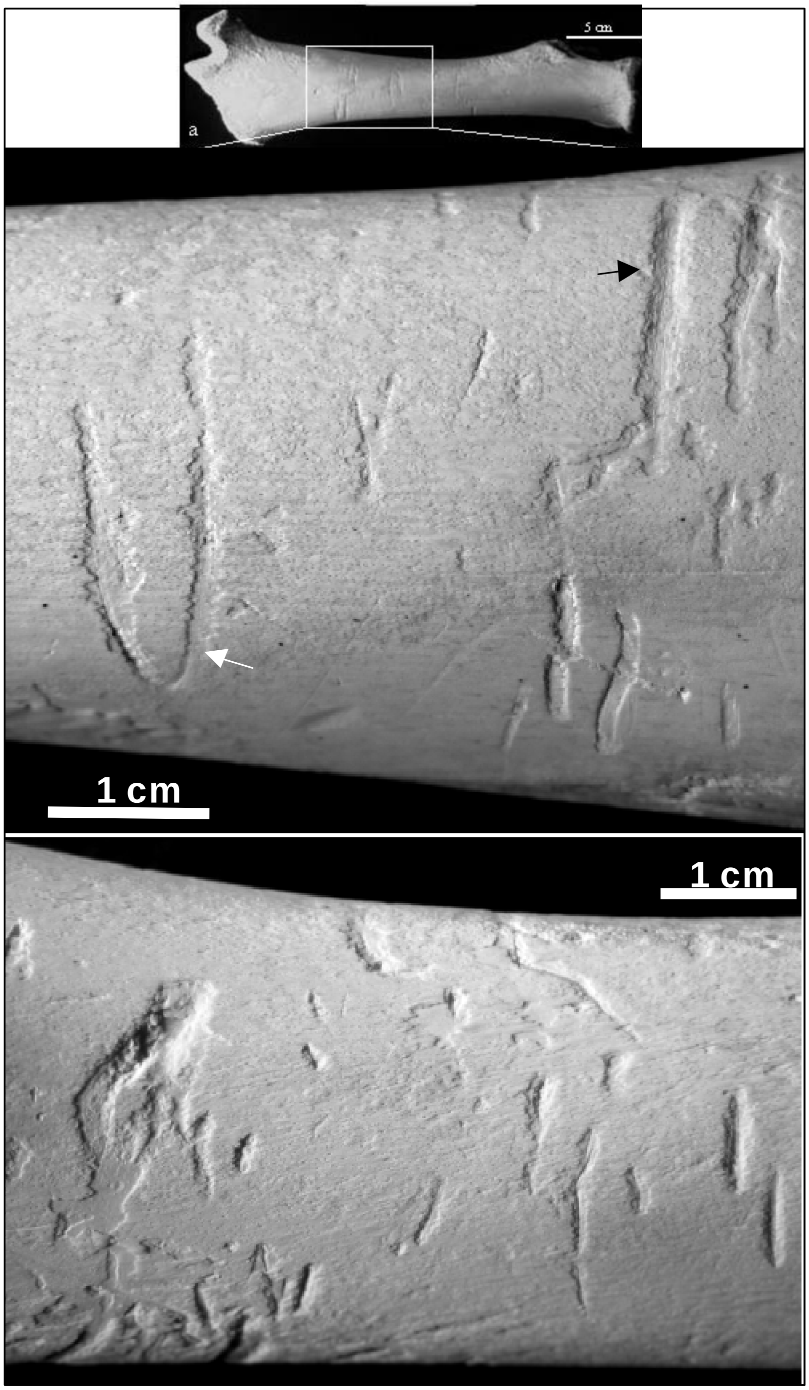


Photo VII. Anterior and posterior views of complete metacarpal of a sub-adult cow modified by small-sized captive Nile crocodiles. The bone is heavily tooth-marked with pits ranging from small pinprick-like to large pits but no punctures. Scores are transversely-to-oblique in orientation. Despite the heavy tooth marking the epiphyses are not gnawed.

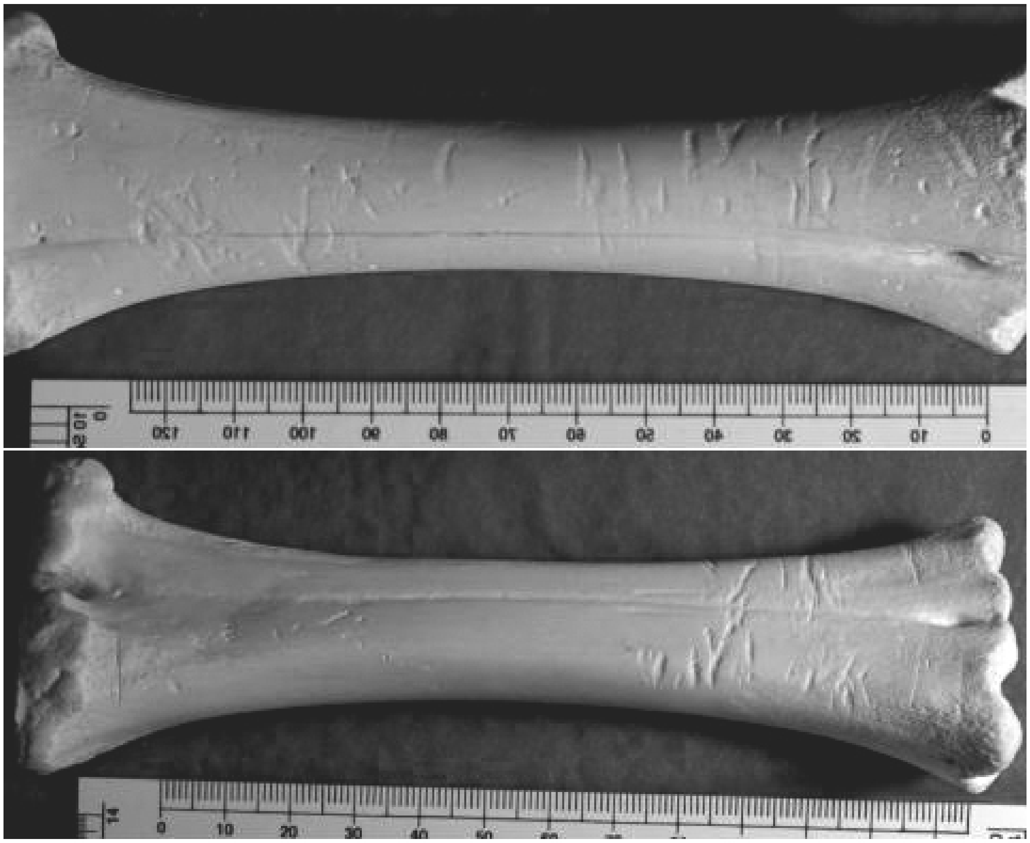


Photo VIII. A tooth-marked complete rib of an adult buffalo from a drying pool on the channel, previously utilized by crocodiles, in lower Grumeti River. Some of the tooth marks are bisected (black arrows).

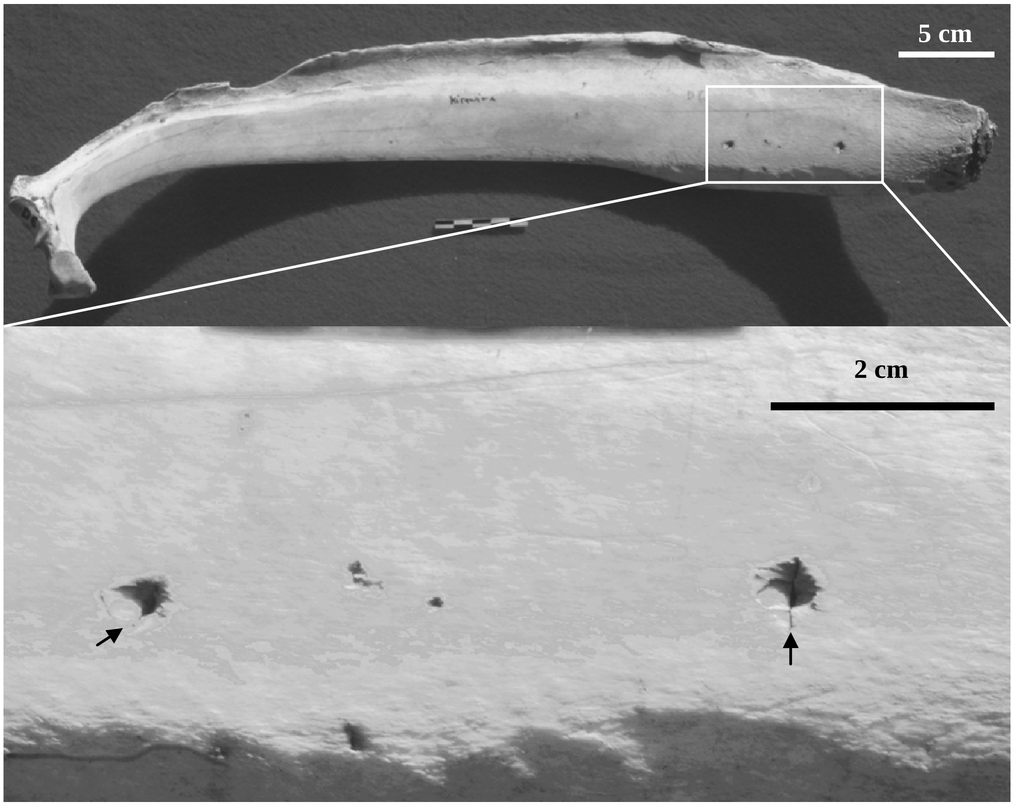


Photo IX. (A) Lateral view of a degreased, lightly weathered and tooth-marked wildebeest hemi-mandible from a channel bed of the lower Grumeti River, Serengeti. The ascending ramus and symphyseal region are missing, both on a snap of uncertain origin. (B) Close-up of the anterior portion of the hemi-mandible, showing one puncture and a number of pits, three of which are bisected (arrows). A natural foramen with an embedded small pebble lies immediately above the puncture. (C) Bisected pit (black arrow) and a puncture with a triangular projection on two sides (white arrows). Bisected pits and one puncture with triangular projections occur on the medial side of the hemi-mandible. The bisected pits and punctures with triangular projections indicate modification by crocodiles. Mammalian carnivores are not implicated in consumption, because the gonial angle is ungnawed, and the bone adjacent to the missing portions is not tooth-marked (from Njau and Blumenschine, 2006).

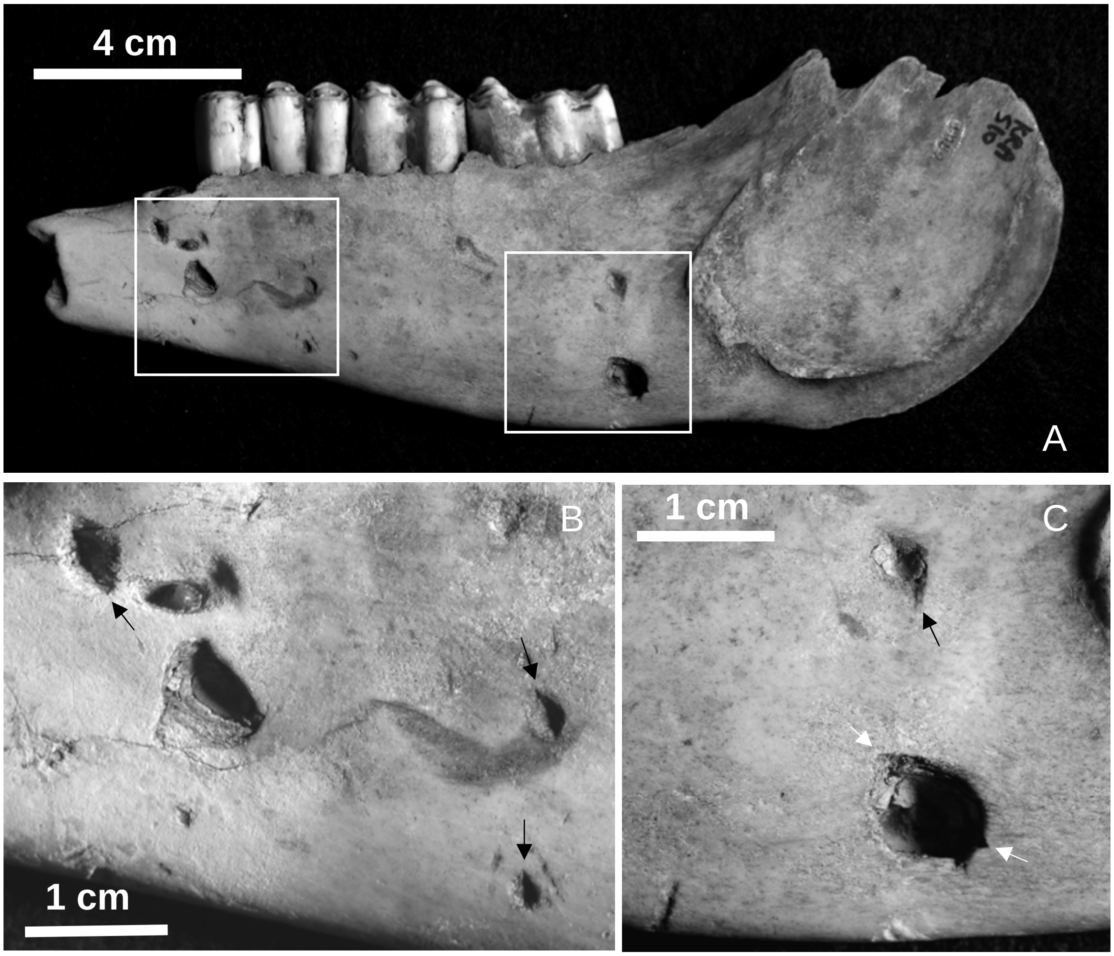


Photo X. Superior and posterior views of a subaerially weathered cranial case of an adult male wildebeest found near a crocodile pool in the lower Grumeti River, Serengeti. (A) The frontal bears five single and one superimposed set of large punctures (smaller holes are natural foramen), some of which bear triangular projections (arrows). (B) Two large punctures on the occipital region, one of which bears a clear triangular projection (arrow). The face was not found, and may have been destroyed by mammalian carnivores. However, the triangular projections on some of the punctures are indicative of crocodile modification.

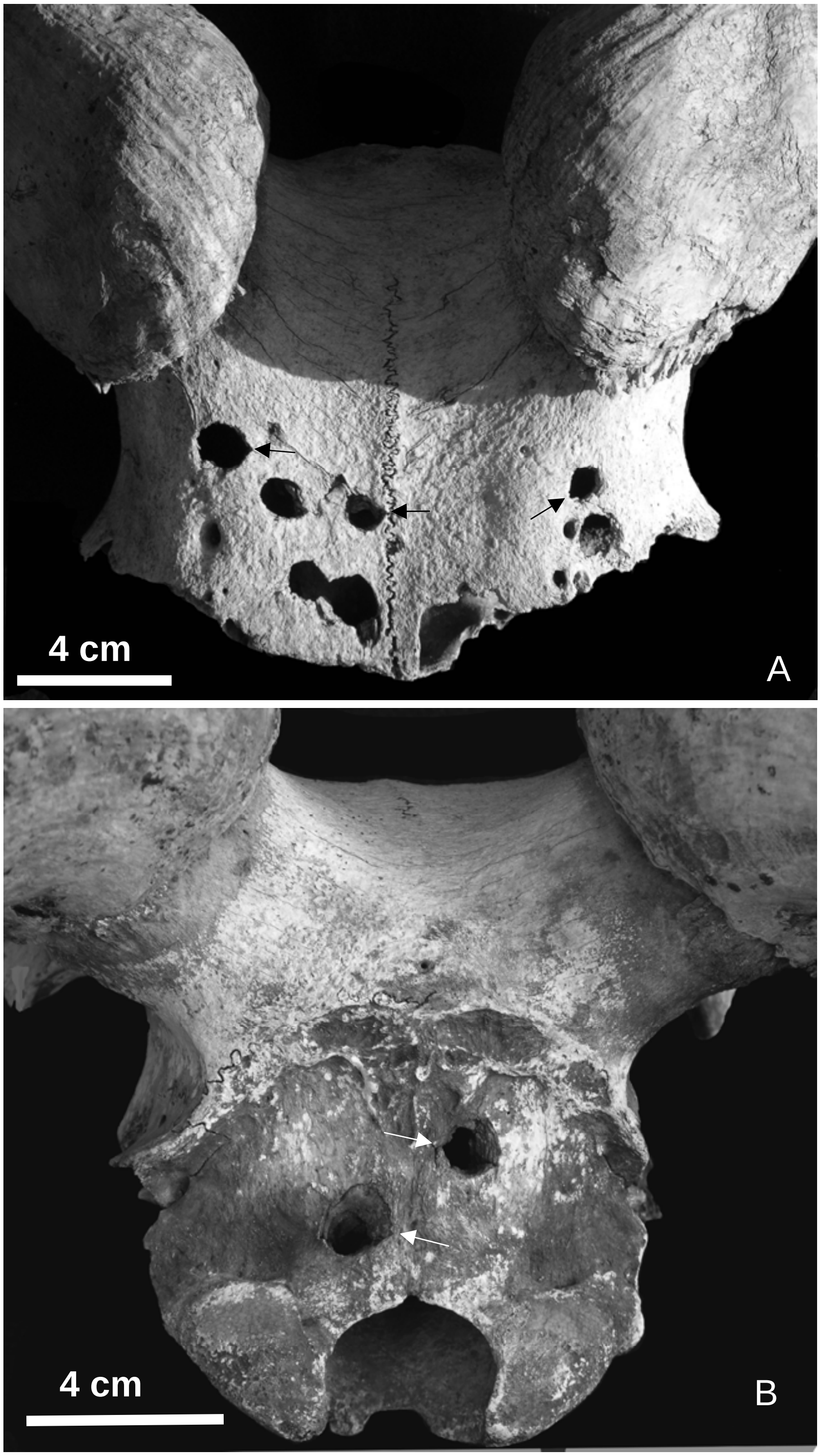


Photo XI. Anterior (A) and posterior (B) views of the distal portion of post-depositionally broken complete tibia (other portions recovered but not shown) of a juvenile eland-sized bovid from OLAPP Trench 21, Lowermost Bed II, Olduvai Gorge. Surfaces are densely and deeply tooth-marked with pits and transversely-oriented scores. Some elongated pits are bisected (close-ups in B). The heavy pitting and scoring, bisected marks, bone completeness, and lack of gnawing on the proximal end are indicative of modification by large crocodiles, not mammalian carnivores (from Njau & Blumenschine, 2006).

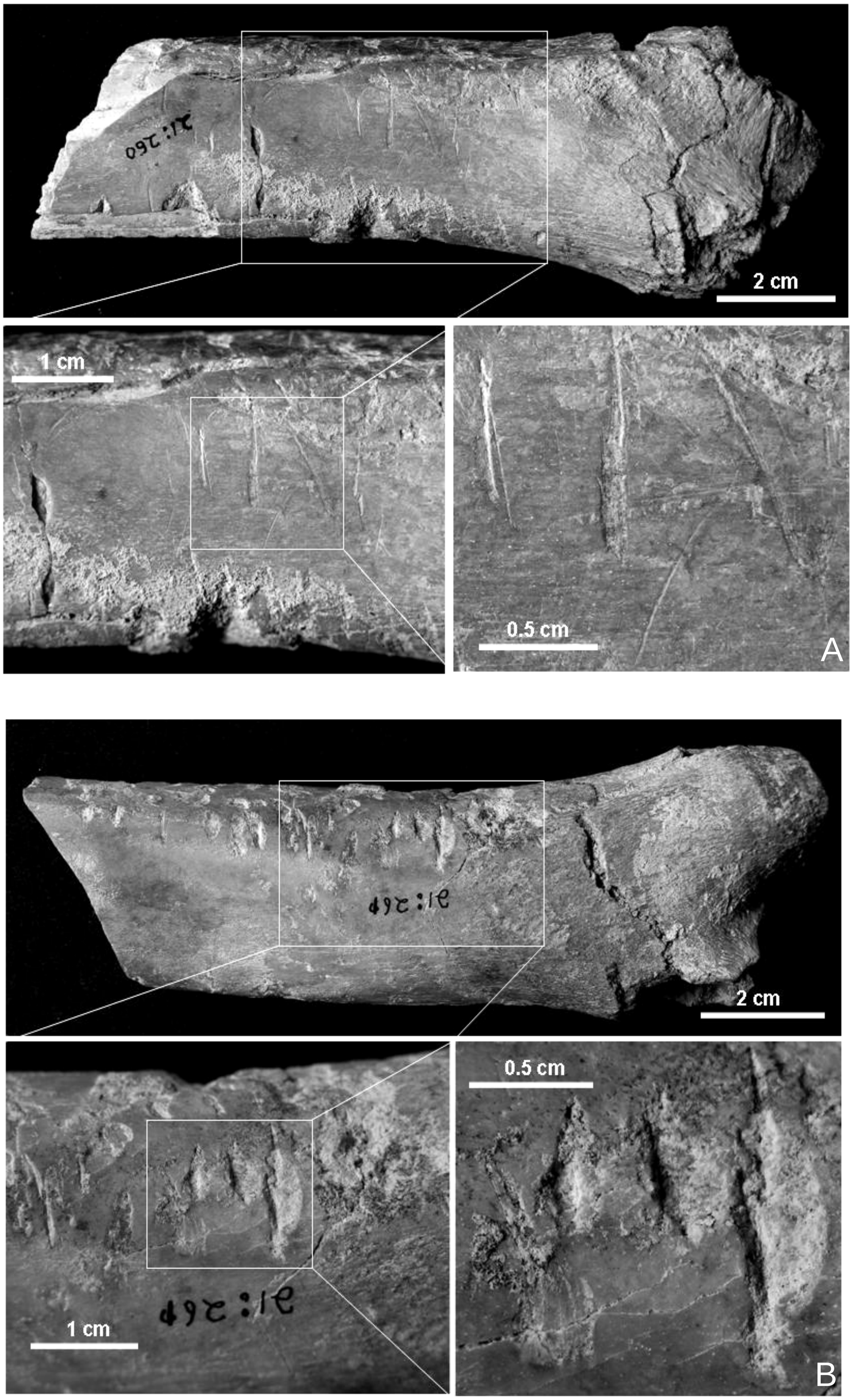


Photo XII. (A) Posterior view of the proximal portion of a post-depositionally broken complete femur (distal end recovered but not shown) of an adult zebra-sized equid from OLAPP Trench 21, Lowermost Bed II, Olduvai Gorge. Some of the large punctures bear triangular projections (arrows in B). These, the extensive tooth-marking over the whole bone, the bone’s completeness, and the lack of gnawing are indicative of modification by large crocodiles, not mammalian carnivores (from Njau & Blumenschine, 2006).

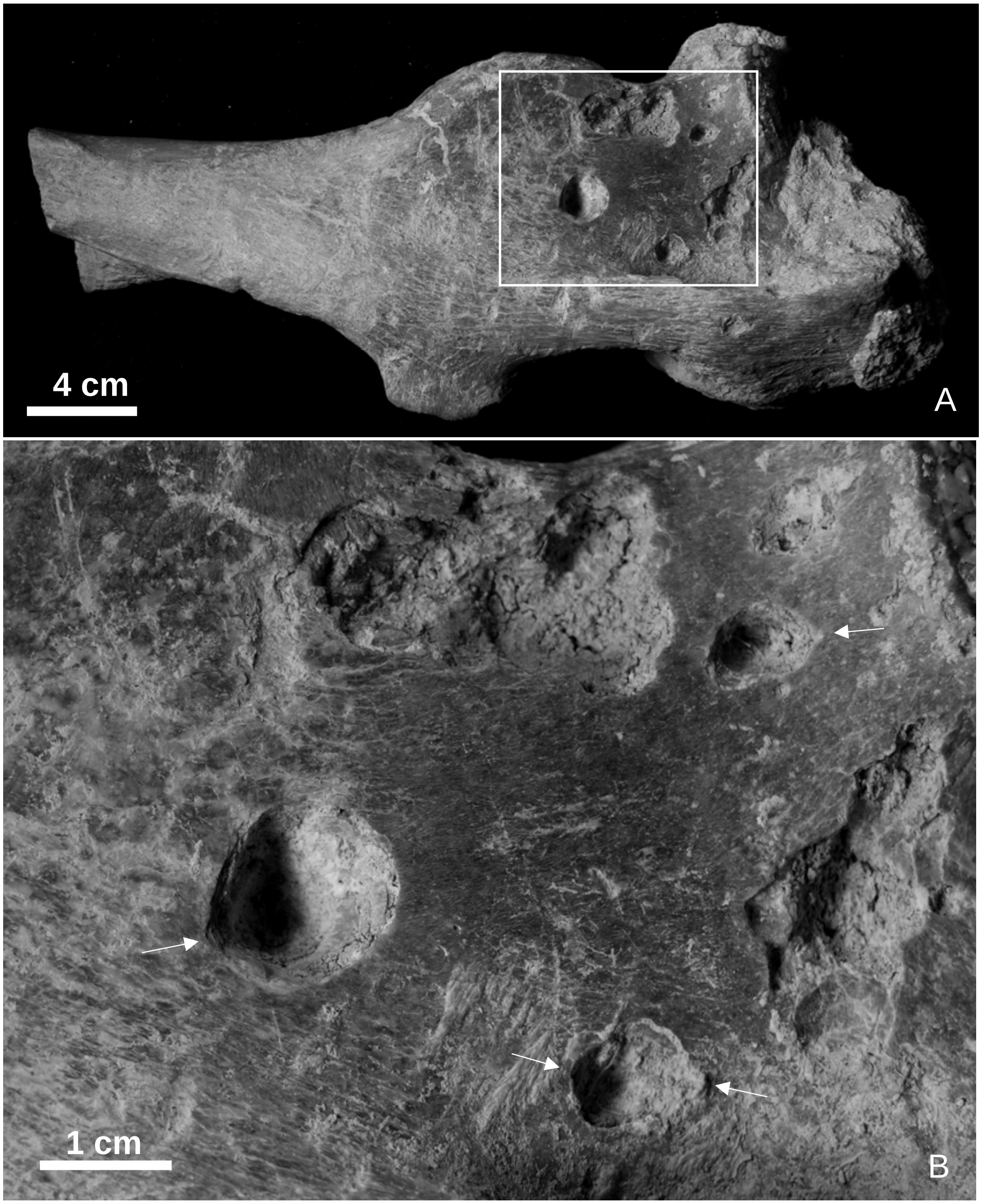


Photo XIII. Anterior view (Top) of a complete radius of an adult Grant's gazelle-sized bovid from OLAPP Trench 57, Bed I, Olduvai Gorge, bearing tooth marks over the whole surface. Close-up of the antero-medial shaft (Bottom), showing deep transversely-oriented scores along with other tooth marks. The chipping of the cortical surface occurred post-depositionally. The intense tooth-marking along with the completeness of the bone is indicative of modification by medium-sized crocodiles, not mammalian carnivores.

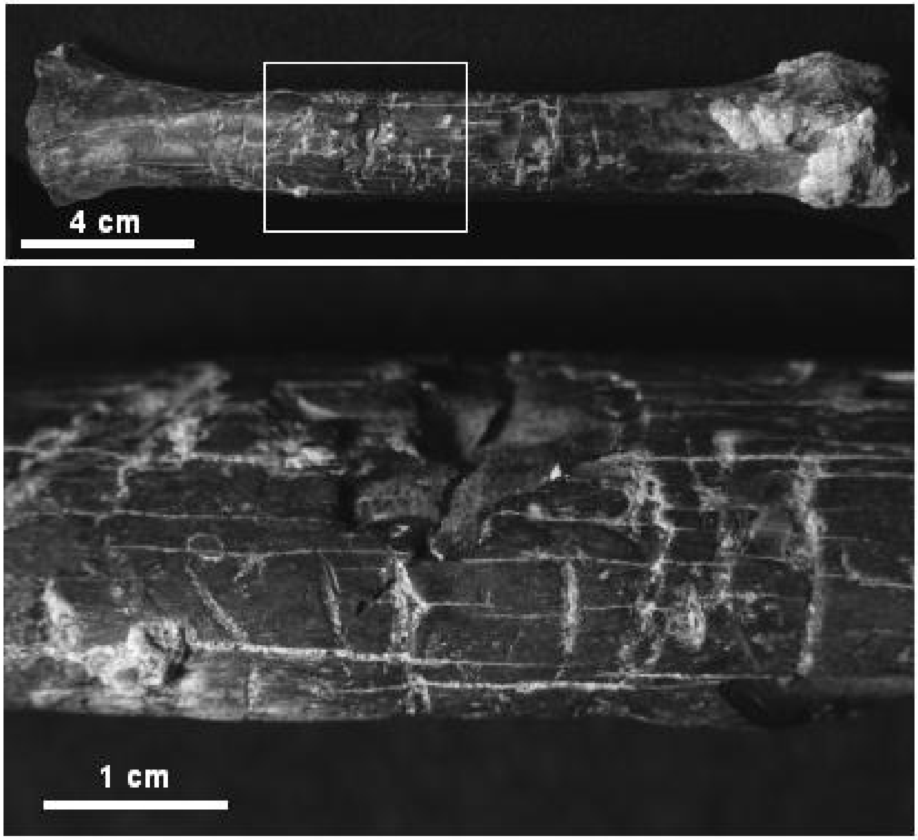


Photo XIV. Cow quarters (Top) provisioned to captive crocodiles at Bagamoyo crocodile farm. Small crocodiles in one of the *bandas* (Bottom).

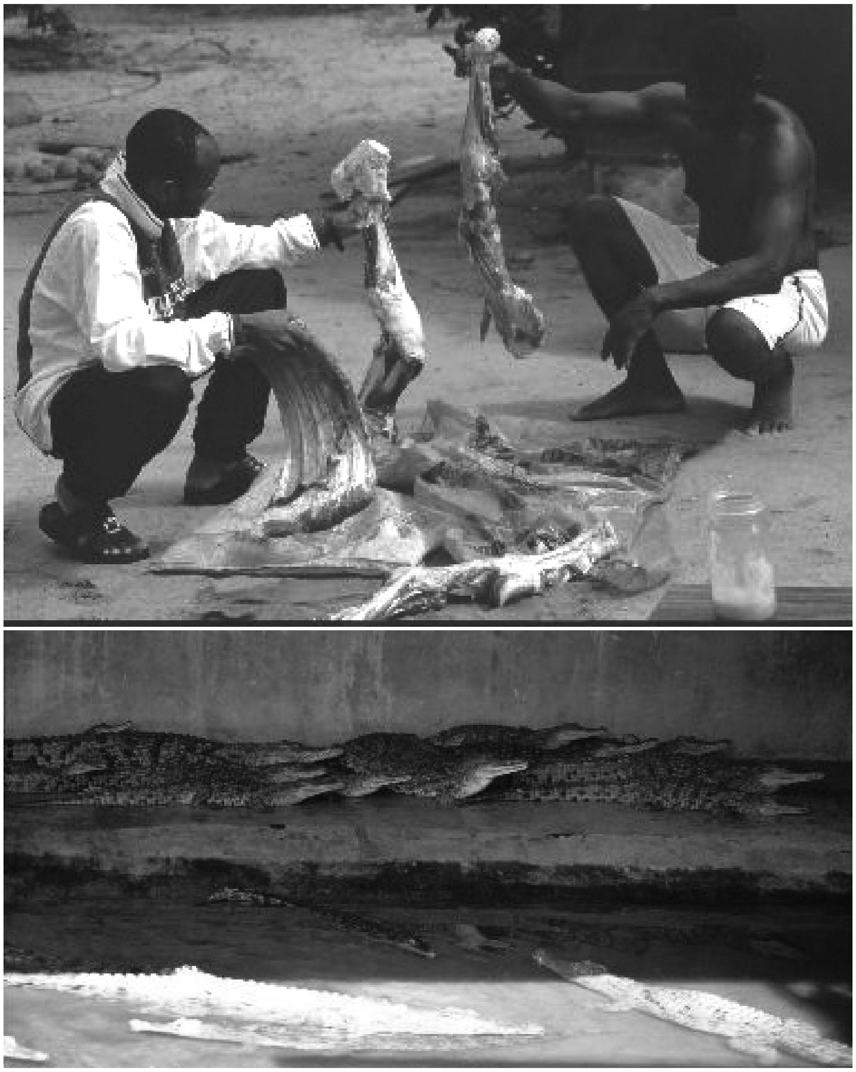


Photo XV. A medium-sized crocodile grab an articulated limb of a cow (Top) before is joined by another crocodile (Bottom) with the intention of reducing the carcass into small pieces prior to ingestion.

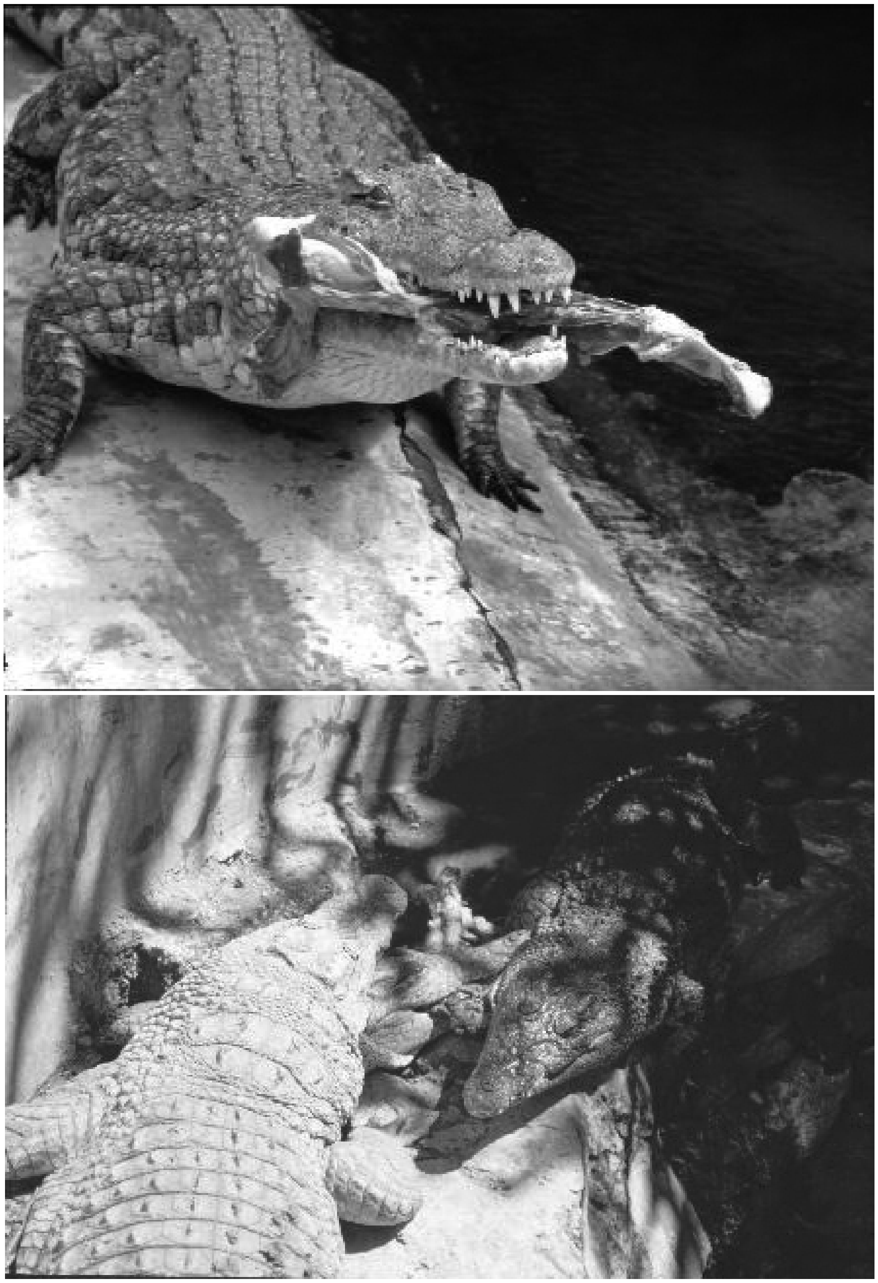


Photo XVI. The same individuals in Photo XV holding the limb firmly from each end by their jaws before spinning (Top) in order to break or disarticulate the carcass. Each crocodile holding its carcass part (Bottom) after disarticulation.

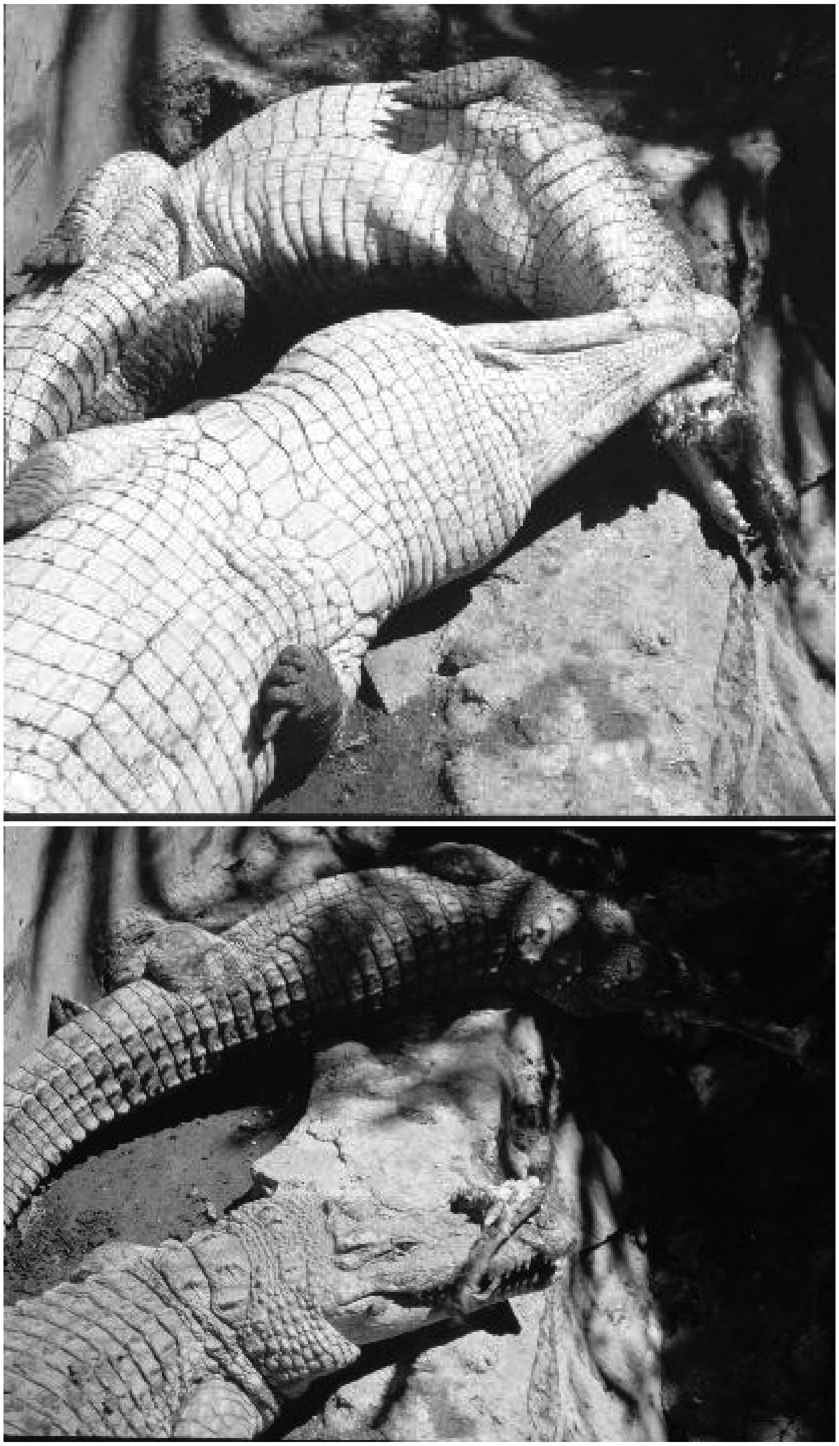
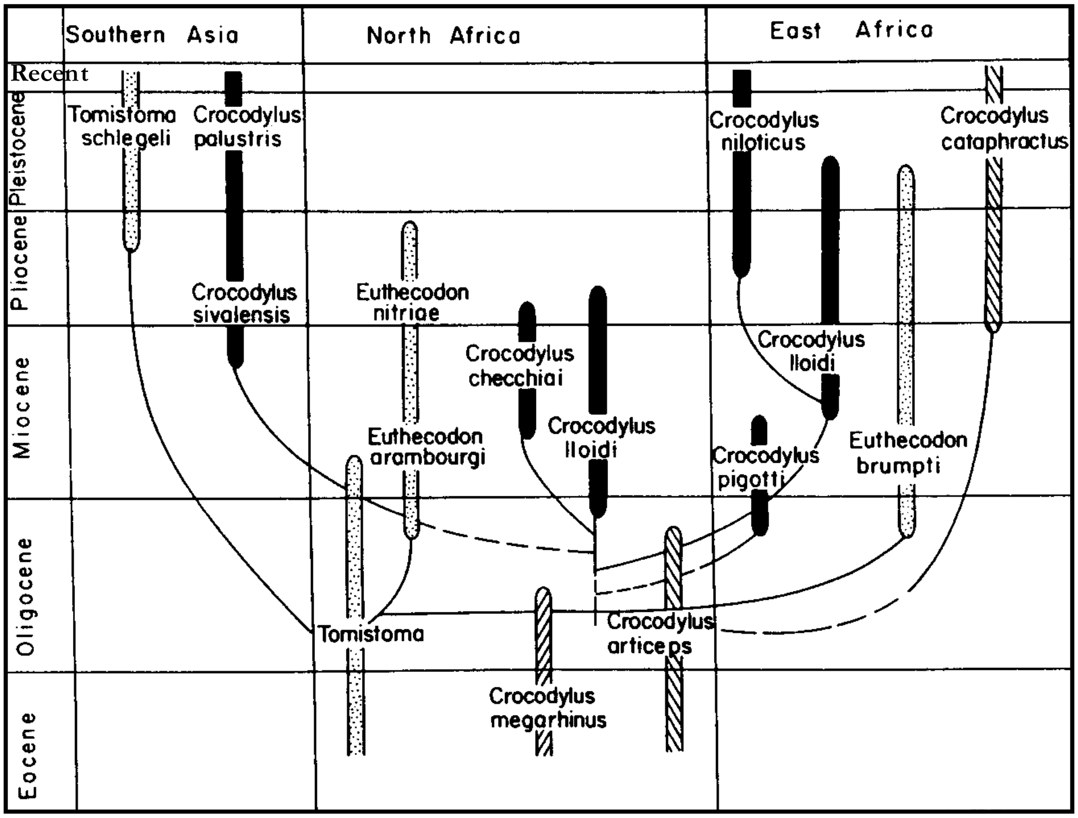


Photo XVII. A large crocodile (ca. 5 m long) died under a tree on the riverbank (Top) near one of the study sites in Lower Grumeti River. A crocodile skull collected from the margin of one of the crocodile pools (Bottom).

PLATE I. Phylogenetic relationships between the Crocodylidae and Tomistomidae in North and East Africa, and their descendants in the Oriental region reconstructed by Tchernov (1986: 53).



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Academic and Employment Positions

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Publications

2006 Njau, J. K. & Blumenschine, R. J. A diagnosis of crocodile damage to large vertebrate bones, with fossil examples from Olduvai Gorge, Tanzania. *Journal of Human Evolution*, 50: 142-162.

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