NEBRASKA
PUBLICATIONS
CLEARINGHOUSE

JUL 2 5 '00

NEBRASKA LIBRARY COMMISSION
LINCOLN, NE 68508

Taphonomic Evidence of Bone Processing from the Oligocene of Northwestern Nebraska

Hannan E. LaGarry
Conservation and Survey Division
of the School of Natural Resources

School of Natural Resources
Institute of Agriculture and Natural Resources
University of Nebraska-Lincoln
Professional Paper No. 2

University of Nebraska-Lincoln

Administration
Harvey S. Perlman, J.D., Chancellor, University of Nebraska-Lincoln
John C. Owens, Ph.D., Vice Chancellor for Agriculture and Natural Resources
Mark S. Kuzila, Ph.D., Director, School of Natural Resources/Conservation and Survey Division

The Conservation and Survey Division of the School of Natural Resources at the University of Nebraska-Lincoln is the agency designated by statute to investigate and interpret the geologically related natural resources of the state, to make available to the public the results of these investigations, and to assist in the development and conservation of these resources. It consists of informal program areas in geology, water, soils and remote sensing/geographic information systems.

The division is authorized to enter into agreements with federal, state and local agencies to engage in cooperative surveys and investigations in the state. Publications of the division and cooperating agencies are available from the Conservation and Survey Division, 102 Nebraska Hall, University of Nebraska-Lincoln, Lincoln, Nebraska 68588-0517; by phone at: (402) 472-7523; or e-mail: jotteman1@unl.edu. More information and a list of publications can be found on the Conservation and Survey Web site: http://csd.unl.edu.

The School of Natural Resources applies an integrated systems approach built upon disciplinary strengths in the physical, biological and social sciences to provide quality higher education, to address complex natural resource and environmental issues, to provide relevant scientific information to stakeholders and to encourage the stewardship of natural resources.

It is the policy of the University of Nebraska-Lincoln not to discriminate on the basis of and to provide information and educational programs to all regardless of sex, age, handicap, race, color, religion, marital status, veteran's status, national or ethnic origin or sexual orientation.

Contents

Abstract / iv
Introduction / 1
Geologic Setting / 1
The Brule Formation of Northwestern Nebraska / 2
Stratigraphy / 2
Depositional Environment / 2
"Old Floyd Hall Place" / 4
Materials and Methods / 4
Sampling Locality / 4
Sampling Method / 5
Assessment of Bone Processing / 5
Coprolites / 5
Postcranial Fragments / 5
Recognition of Non-carnivore Modifications / 5
Recognition of Bone Processing / 6
Body Size Delineation / 6
Processing Distribution Delineation / 7
Results and Discussion / 7
Bone Processing Within the Coprolites / 7
Breakage / 7
Articulation / 8
Corrosion / 8
Skeletal Representation / 8
Faunal Composition / 8
Identity of the Processing Carnivore / 12
Discussion / 13
Bone Processing of the Postcranial Fragments / 13
Non-processing Features / 14
Bone Processing Features / 14
Rodent Gnawing / 20
Breakage / 20
Processing of Skeletal Elements / 21
Description of Size Categories / 21
Distribution of Processing on Size Groups / 26
Discussion / 27
Summary and Conclusions / 29
Acknowledgments / 30
References / 30

Illustrations

1. Stratigraphy and geology of the "Old Floyd Hall Place," showing the locations of measured section, sampled areas and the sampled interval / 3
2. Sample collected from UNSM Sx-6 and Sx-7 / 4
3. Method for assessing bone processing in the Orellan sample / 8
4. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7 / 9
5. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7 / 10
6. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7 / 11
7. Histograms showing the frequency of diameters measured in the coprolite sample collected from UNSM Sx-6 and Sx-7 / 12
8. Postcranial bone fragments from UNSM Sx-6 and Sx-7 showing bone processing / 17
9. Photographs of postcranial bone fragments from UNSM Sx-6 and Sx-7 showing bone processing / 18
10. Bone fragments from UNSM Sx-6 and Sx-7 showing bone processing / 19
11. Histograms derived from measurements (table 1) of bone fragments / 22
12. Histograms derived from measurements (table 1) of bone fragments / 23
13. Composite "skeletons" showing taxon-free groups / 24-26

Tables

1. List of mammalian taxa within 1989-1991 samples from UNSM Sx-6 and Sx-7 / 6
2. Measurements of postcranial bones used in this study / 7
3. Frequency of processing of individual skeletal elements / 14
4. Distribution and character of preburial damage to skeletal elements from UNSM Sx-6 and Sx-7 / 15
5. Size groups (I-V) assigned to taxa from UNSM Sx-6 and Sx-7 / 16

Abstract

I examine bone processing in autochthonous assemblages of coprolites and fossil bone, representing about 80,000 years of early Oligocene deposition and bone accumulation, from volcaniclastic floodplain sediments of the Orella Member of the Brule Formation (White River Group) in northern Sioux County, Nebraska. The samples were collected using brooms to sweep fossiliferous surface litter from small areas within University of Nebraska State Museum (UNSM) localities Sx-6 (0.08 km^2) and Sx-7 (0.05 km^2) during 1989-1991. The coprolites (n = 1,250) contained teeth and bones of didelphid marsupials, lagomorphs, camels, oreodonts, leptomerycids, hypertragulids, and canids. Based on their size, degree of fragmentation, types of breakage, corrosion by stomach acids, bone articulation, skeletal part representation, and prey fauna composition of their contained bone, the coprolites were likely produced by a carnivore having a body size and feeding habits similar to the coyote, *Canis latrans*. Based on body sizes and dentitions of Orellan carnivores, the large amphicyonid *Daphoenus vetus* likely produced most of the coprolites.

Processing of the postcranial bone sample (n=1,706) consisted of gouging, pitting, spalling, and transverse scratching by mammalian carnivores and rodent gnawing. Based on the frequency, style, and distribution of bone processing observed on five size groups of postcranial bone fragments, the bone assemblage was moderately processed by carnivores of several body sizes having canid-like dentitions and exhibiting "wolf-like" processing behaviors. Based on the body sizes and dentitions within Orellan carnivores, the canids *Hesperocyon* and *Mesocyon*, and the amphicyonids *Daphoenus hartshornianus* and *D. vetus* likely produced most of the bone processing.

Introduction

The volcaniclastic rocks of the White River Group of western Nebraska, southwestern South Dakota, eastern Wyoming, and northeastern Colorado have yielded one of the world's most abundant and diverse late Eocene and Oligocene mammalian faunas (see Savage and Russell, 1983; Emry and others, 1987). Since fossils were discovered in these rocks more than 100 years ago (Meek and Hayden, 1857, 1861), studies have focused on the systematic paleontology of the mammalian faunas, lithostratigraphy, and biostratigraphy (Matthew, 1899, 1909; Sinclair, 1921; Wanless, 1922, 1923; Osborn, 1929; Scott and Jepsen, 1936; Clark, 1937, 1954; Wood, 1937, 1940; Scott, 1940, 1941; Schultz and Stout, 1955; Clark and others, 1967; Schultz and Falkenbach, 1968). Few taphonomic studies, which generally attempt to identify the processes involved in an organism's death, decay, destruction, burial, and fossilization (Olson, 1980; Marshall, 1989), have dealt with White River Group faunas despite the availability of many unexamined and important samples. Taphonomic studies can provide data on paleoclimates, survivorship and mortality trends, community composition and turnover, and modes of bone modification and accumulation in the geologic past (summarized in Behrensmeyer and Kidwell, 1985).

In the mid-1920s, Johannes Weigelt, the German taphonomist, was impressed by certain parallels between bone modification and accumulation in northwestern Nebraska's Oligocene faunas and recent carcass and bone assemblages of East Africa:

> *In the oreodont beds of Nebraska, it is evident that predators found and devoured an abundant prey. The carcasses of oreodonts have been torn apart and the parts carried off . . . a curious sort of sorting takes place. The bones have been bitten into and then gnawed by rodents. . . . Where the remains of prey pile up, the predators' droppings are scattered everywhere. Carnivores had the habit, shared by living hyenas, of forming bone depositories. We could not otherwise explain why we find skulls and lower jaw fragments of* Hoplophoneus, Hyaenodon, *oreodonts,* Leptomeryx, Perchoerus, *and* Mesohippus *all mixed together in one place* (Weigelt, 1989, p. 93, in translation).

In Weigelt's day there were no established procedures for the recording and analysis of taphonomic data, although he made major contributions in this regard. Since then, taphonomic studies have described how carnivorous animals modify and accumulate the bones of their prey, addressing such diverse topics as tooth marks, patterns of disarticulation, prey preferences, selective consumption of skeletal elements, introduction or removal of preferred orientation, caching of bone at den sites, and selective consumption of prey age classes (Sutcliffe, 1970; Hill, 1976, 1979, 1980, 1989; Haynes, 1980a, 1980b, 1982, 1983, 1985, 1988; Klein, 1982, 1983; Andrews and Nesbit-Evans, 1983; Klein and Cruz-Uribe, 1984; Hill and Behrensmeyer, 1984)

Alterations in size, structure, and texture of bone by a carnivorous mammal's teeth are termed *bone processing*. These alterations may be distinct from bone modifications made by the teeth of noncarnivorous animals, physical processes such as weathering, abrasion by fluvial sediments, and trampling, and hominid tool use (summarized in Marshall, 1989). Bone processing has been recognized in the Neogene fossil record of the Great Plains (Haynes, 1980a; Fiorillo, 1988; Hunt, 1978, 1988, 1990; Thomasson and others, 1990), and some authors have used a uniformitarian approach (see Gifford-Gonzalez, 1989) to qualitatively compare modifications produced by extant and fossil taxa (for example, Haynes, 1980a, 1983). Haynes (1985, 1988) and Behrensmeyer and others (1979) have commented on the (as yet unrealized) potential for ecological reconstruction of extant and fossil predator kill sites. This work has shown that most forms of bone processing can have analogs within the fossil record, although much more research is needed to define their character and extent.

Weigelt's observations indicated the potential for taphonomic study of White River Group faunas. Both field-collected and museum samples of the White River fauna contain abundant evidence of bone processing. In this paper, I use current taphonomic methods to describe bone processing in a large sample of fossil material from the White River Group of northwestern Nebraska. The goals of this study are to: 1) survey, characterize, and quantify carnivore-induced bone modifications within an Oligocene fauna of the White River Group; 2) using a uniformitarian approach, qualitatively describe the observed features interpreted as bone processing and compare them to bone processed by extant mammalian carnivores; 3) examine the distribution of bone processing between and within various size groups of mammals in the fauna, and 4) discuss the implications of the types and distributions of bone processing for the paleoecology and behavior of Oligocene carnivores.

Geologic Setting

The late Eocene-Oligocene White River Group of northwestern Nebraska, composed of the Chamberlain Pass, Chadron, and Brule formations, consists of a large volume of volcaniclastic claystones and siltstones, limestones, and epiclastic sandstones deposited by fluvial, lacustrine, and eolian processes (LaGarry, 1998; Terry, 1998; Terry and LaGarry, 1998). These deposits are well known for their fossil vertebrates, which formed the basis for early geological research in this region (Meek and Hayden, 1857, 1861;

Hatcher, 1893; Darton, 1899; Wanless, 1922, 1923; Ward, 1922; Osborn, 1929; Clark, 1937, 1954; Schultz and Stout, 1938, 1955; Clark and others, 1967; Schultz and Falkenbach, 1968). These rocks and their abundant fossils have provided a detailed record of late Eocene and Oligocene mammalian evolution and climatic change (Evanoff and others, 1992; Prothero and Swisher, 1992; Prothero, 1994; Retallack, 1983, 1997). In northwestern Nebraska, these rocks are exposed as steep cliffs and discontinuous badlands north of the Pine Ridge escarpment (see LaGarry and LaGarry, 1997d).

The Brule Formation of Northwestern Nebraska

The sample of vertebrate fossils used in this study was collected from the Orella Member of the Brule Formation at University of Nebraska State Museum (UNSM) localities Sx-6 and Sx-7 (fig. 1), which are collectively known as "the Old Floyd Hall Place" (Bodarc, Nebraska, 7.5' USGS quadrangle: LaGarry and LaGarry, 1997b). The Brule Formation in western Nebraska was first described by Darton (1899), but the stratigraphic classification of Schultz and Stout (1938, 1955) has formed the basis for the majority of White River Group research in northwestern Nebraska. Schultz and Stout (1938, 1955) divided the Brule Formation into the Orella and Whitney members, and Swinehart and others (1985) later added the "brown siltstone" member (for discussion, see LaGarry, 1998).

Stratigraphy

Schultz and Stout's (1938, 1955) Orella Member consisted of 56-85 m of interbedded massive silty clays, laminated silty clays, nodular sandstone, siltstone, claystone, gypsum, gypsiferous paleosols, and channel sandstones. Their Orella Member was subdivided into the Orella "A," "B," "C," and "D," based on the inferred presence of regional marker paleosols, unconformities, and valley incision and backfilling. The upper boundary was the "white bed," a thin, discontinuous siltstone, and the lower boundary was the "upper purplish-white layer," a volcanic ash. Schultz and Stout's (1938, 1955) Orella Member was used to define the Orellan North American land mammal age, or NALMA (Wood and others, 1941), and was divided into biostratigraphic zones based on oreodont phylogeny (Falkenbach and Schultz, 1951; Schultz and Falkenbach, 1968).

Based on their geologic mapping, LaGarry and LaGarry (1997d) concluded that the marker beds previously used to define the stratigraphic boundaries of the Brule Formation were not mappable outside Schultz and Stout's (1955) type area for the Orella and Whitney members.

Subsequently, LaGarry (1998) proposed lithologically defined units for the Brule Formation. Based on LaGarry's (1998) lithologic reinterpretation, the Orella Member consists of thinly interbedded sheet sandstones, laminated and massive volcaniclastic clayey siltstones and silty claystones, and channel sandstones occurring throughout the unit. LaGarry (1998) recognized two lithotopes within the Orella Member: one consisting of thinly interbedded overbank deposits, primarily sheet sandstones, laminated volcaniclastic clayey siltstones, and laminated volcaniclastic silty claystones, and a second consisting of channel sandstones. LaGarry's redefined Orella Member is similar to Clark and others' (1967) Scenic Member of the Brule Formation in the Big Badlands of South Dakota, except that the Scenic Member contains abundant nodules (Retallack, 1983) and the Orella Member does not (see Terry and others, 1995; Wells and others, 1995). In LaGarry's (1998) redescription, Schultz and Stout's (1955) "Orella D," which consists of massive, nodular volcaniclastic siltstone, is included in the basal part of the overlying Whitney Member. Terry and LaGarry (1998) redefined Schultz and Stout's (1955) "Orella A," which consists of 8-10 m of volcaniclastic silty claystones, as the uppermost part of the underlying Chadron Formation.

Following these revisions, the stratigraphic boundaries of the Orella Member are no longer coincident with those of Schultz and Stout's (1955) Orella Member and Wood and others' (1941) Orellan NALMA, which is a geochron (see Emry and others, 1987). Also, Stevens and Stevens' (1996) revision of the oreodonts has eliminated or redefined most taxa on which Schultz and Falkenbach's (1968) biostratigraphic zones were based. However, the faunal sample used in this study was collected from rocks that Schultz and Stout (1955) would likely have classified as "Orella B" and "Orella C," and it is within the biochronologically defined Orellan NALMA (early Oligocene) as characterized by Emry and others (1987).

Depositional Environment

Harvey (1960) and Terry and others (1995) interpreted the Orella Member to be a sequence of stacked "couplets" of thin overbank sheet sandstones and volcaniclastic silty claystones that filled and overtopped cut-and-fill paleochannel sequences during two or more separate and alternating periods of incision and backfilling. Harvey's (1960) interpretation was of cyclic deposition within nested paleovalleys. However, Terry and others (1995) suggested that the Orella Member was deposited during a period of complex overlapping and episodic cutting and filling.

Schultz and Stout (1955) and Schultz and others (1955) subdivided the Orella based on the stratigraphic positions of what they interpreted to be paleosols. In contrast, Clark and others (1967) argued that there were no paleosols within the Orella Member, and that the Orella Member was dominated by overbank sheet deposition rather than pedogenesis. More recently,

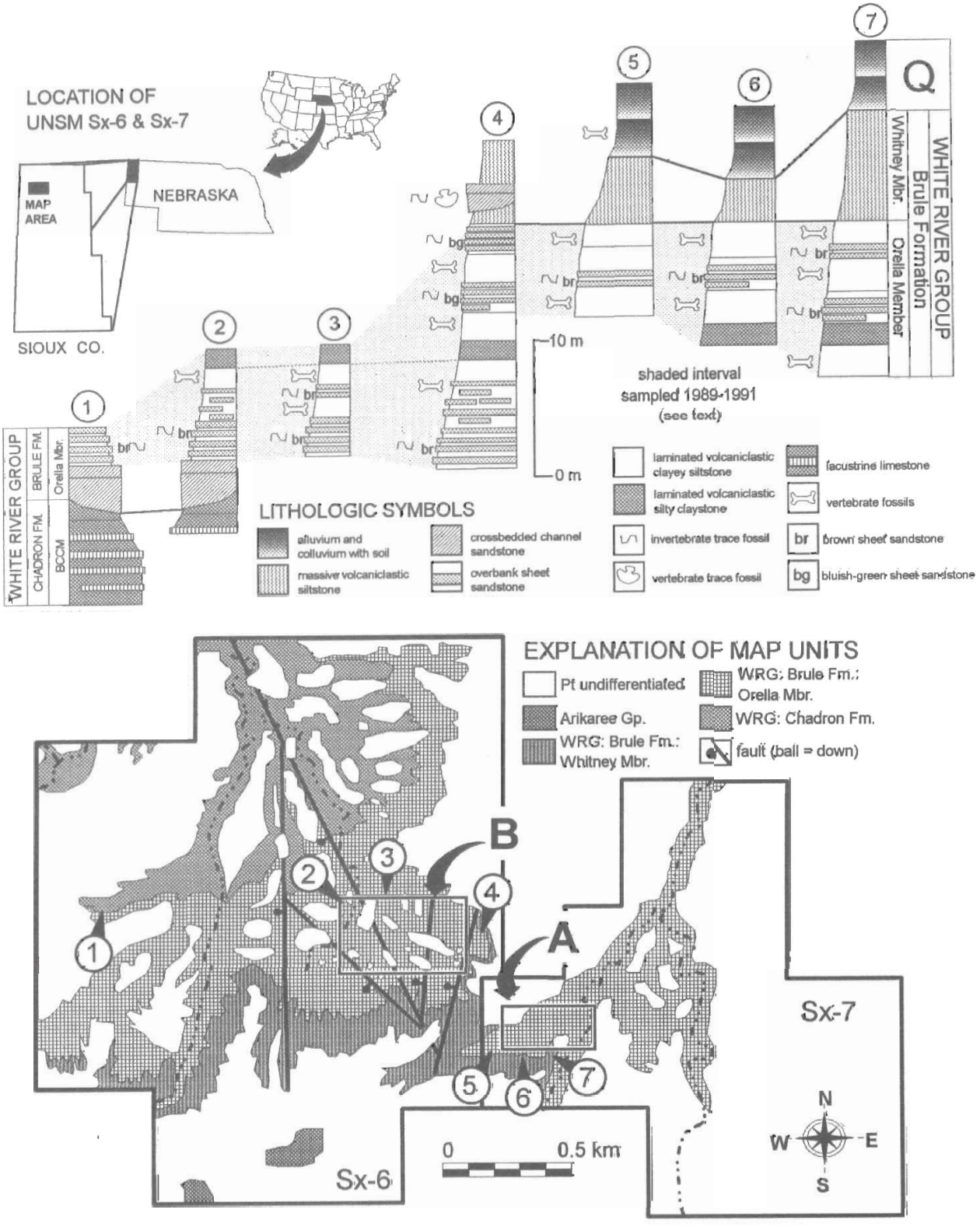


Fig. 1. Stratigraphy and geology of the "Old Floyd Hall Place" (UNSM Sx-6 and Sx-7), showing the locations of measured section, sampled areas (A, B) and the sampled interval (shaded). Modified from LaGarry (1998).

Terry and others (1995) described "entisols" within the overbank clayey siltstones and silty claystones based on the presence of root traces and very limited soil structure and horizonation. They interpreted the Orella Member to contain many poorly developed paleosols, rather than a few major paleosols below regional unconformities, as interpreted by Schultz and others (1955).

"Old Floyd Hall Place"

The Orella Member is 26-29 m thick at Schultz and Stout's (1955) type area at Toadstool Geologic Park in northeastern Sioux County, but it pinches out at the Wyoming state line to the west and the base of the Pine Ridge escarpment near Chadron, Nebraska, to the east (LaGarry and LaGarry, 1997a, 1997c). The "Old Floyd Hall Place" is located 42 km west of Toadstool Park, where the Orella Member is 20 m thick (fig. 1) and the second Orella lithotope, which consists of channel sandstones, is restricted to the base of the unit (LaGarry, 1998). In addition to being thinner overall, the Orella Member at the "Old Floyd Hall Place" is more thinly bedded, has fewer sheet sandstones, and fewer volcaniclastic silty claystones than at the type area at Toadstool Park. The over- and underlying strata are also less thick, so the Orella Member at the "Old Floyd Hall Place" likely represents a condensed section with respect to the type area.

Materials and Methods

Sites sampled for the analysis of bone processing should: 1) represent a limited range of habitats present during the faunal interval being studied, with a single depositional environment being the preferred case; 2) contain abundant fossil bone, so that the widest possible range of bone modifications might be recovered; 3) if taphonomically biased, contain clear indications of the character and extent of the biases; and 4) be completely collected, such that no significant amount of processed or potentially processed material is excluded from the analysis (see Voorhies, 1969b; Binford, 1981; Shipman, 1981; Marshall, 1989). These criteria are easily met by samples obtained by quarrying a concentration of fossil bone (for example, Voorhies, 1969a; Fiorillo, 1988; LaGarry, 1988). However, LaGarry and Hunt (1992, 1993) reported that concentrations of bone are very rare within the White River Group of northwestern Nebraska, and vertebrate fossils within the Orella Member commonly occur as isolated partial skeletons and fragmentary skeletal elements that, on exposure, form a surface litter of fragmented postcranial bones, coprolites, and pieces of tortoise shell.

Sampling Locality

Exposures at the "Old Floyd Hall Place" (fig. 1) were sampled because (see criteria 1-3 above): 1) the exposed sequence consists entirely of the overbank lithotope (see LaGarry, 1998), with the exception of the basal sandstones, which were not sampled; 2) vertebrate fossils are abundant there; 3) unlike other, more prominent localities (for example, tourist-accessible Toadstool Park), this site (according to the landowner) is rarely visited and collected, providing some assurance that samples obtained from there were not significantly biased by prior collecting; 4) 5-18 m of the Orella Member is exposed, an exposure that could serve as a potential source of fossils; and 5) broad, flat

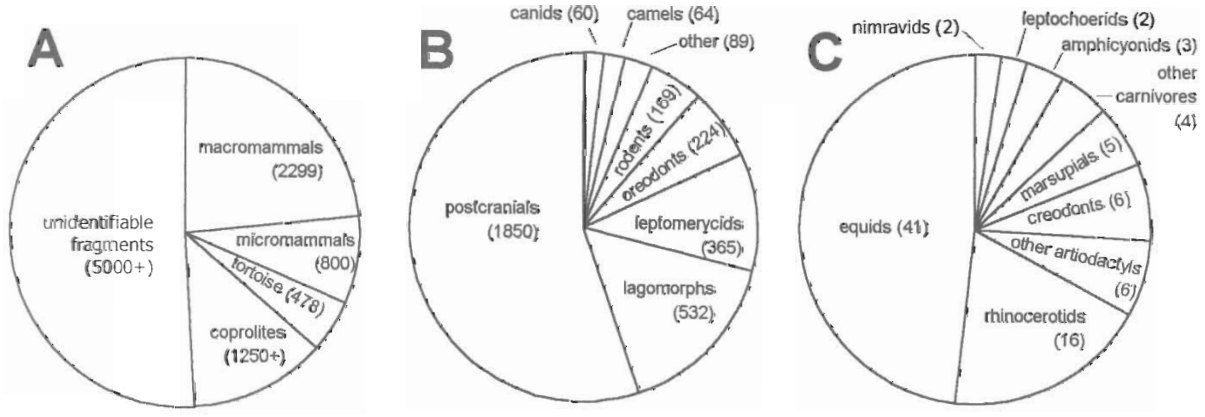


Fig. 2. Sample of fossil material collected from UNSM Sx-6 and Sx-7: A) composition of total sample; B) composition of combined micro- and macromammals in A; and C) composition of "other" category in B.

expanses are present between exposures, greatly facilitating the use of the sampling method (see below). The two small areas selected for sampling (A, B: fig. 1) contained the greatest concentration of fossiliferous surface litter. Quaternary sediments that could serve as a source of reworked fossils were present within the sampled areas, but examination of these sediments indicated that little, if any, bone was present within these sediments at this locality.

Sampling Method

Traditionally, fossils are collected from the White River Group by picking up surface litter one piece at a time or collecting *in situ* specimens in plaster jackets. These practices bias samples towards larger, more easily seen fragments and complete elements. In order to avoid this bias, the sample used in this study was collected by using paintbrushes and whisk brooms to thoroughly sweep up *all* fossiliferous surface litter, including unidentifiable shards and pieces (satisfying criteria 2 and 4), within small areas of 0.08 km^2 and 0.05 km^2 of UNSM Sx-6 and Sx-7, respectively (fig. 2). These areas were sampled in 1989, 1990, and 1991. The resulting samples were combined for study, and consisted of a mixture of fossilized jaws, teeth, fragmentary postcranial bones of mammals and tortoise, tortoise shell fragments, coprolites, animal scats and bits of modern vegetation (fig. 2). Fossil material was placed in a 0.495 mm screen while adhering clay residues were rinsed off. This was not "screen washing," in that no sediment was processed with the fossil material. The sweeping process provided a virtually sediment-free sample, as if it had been recovered from a paved surface. The fossil material was judged to have been eroded from the clayey siltstones because sandstones within the Orella Member are well-cemented, as are bones within the sandstones. Preliminary inspection of the sample showed that none of the postcranial fragments had adhering remnants of sandstone or cement, which is more resistant to weathering than the fossilized bones or coprolites.

Assessment of Bone Processing

Preliminary inspection of the sample revealed that evidence of bone processing is preserved within the coprolites and on the fragmentary postcranial bones. Recognizable cranial material, except for isolated teeth, maxillary fragments, and partial rami, is poorly represented in the sample, as are identifiable rib fragments. If originally present within the rock, this material was likely reduced to tiny fragments after weathering from the rock. The teeth of larger mammals are rarely processed or eaten by extant carnivores because they have little nutritional value and are indigestible (Behrensmeyer and others, 1979; Hill, 1980; Haynes, 1982, 1988). Consequently, teeth were not used in the study of bone processing, but were used to compile a faunal list (table 1).

Coprolites

Coprolites, or fossilized feces, of carnivorous mammals have been recognized from the White River Group since the 1920s (Sinclair, 1921; Wanless, 1923). These coprolites are cylindrical, unsegmented masses that often contain bones and teeth (Edwards and Yatkola, 1974). The excellent and abundant preservation of coprolites within the Orella Member is likely due to the fine-grained volcaniclastic sediments in which they were buried, their apatite composition, rapid burial by overbank deposition, and a seasonally dry climate during the early Oligocene (Edwards, 1973a, 1973b; Edwards and Yatkola, 1974; Retallack, 1983, 1997; Prothero, 1994). Few studies have addressed the processing of prey bone during ingestion, digestion, and excretion by extant mammalian carnivores (Mellett, 1974; Andrews and Nesbit-Evans, 1983). In order to make comparisons with existing studies, the coprolites were prepared by mechanically excavating their encased bone. Once this bone was exposed, I examined it for types and amounts of breakage, the degree of articulation of skeletal elements, corrosion by stomach acids, skeletal part representation, and where possible, the identity of the prey species. I estimated the general body size of the carnivore(s) that excreted the coprolites by measuring the maximum diameters of complete coprolites and partial coprolites in which the maximum diameter was preserved, and I then compared these data to the extant scatological record.

Postcranial Fragments

Preliminary examination revealed about 60% of the total postcranial bone sample had been damaged while weathering from the bedrock. About 30% of the total sample showed evidence of breakage prior to burial during the Oligocene. In general, weathering from the bedrock and subsequent subaerial exposure produced sharp breaks that expose cleavage faces of calcite that had accumulated within the marrow cavity and other voids within the bone. This recent breakage also interrupts the pattern of diagenetic staining by iron and manganese on the surface of the bone, whereas this staining uniformly covers surfaces that were broken prior to burial or diagenetic alteration within the sediment. Oligocene bone processing has produced characteristic patterns of breakage that vary from element to element, and these patterns were identified and described.

Recognition of Non-carnivore Modifications

Prior to an analysis of bone processing, non-carnivore bone modifications must be identified. Bone accumulating naturally on the land surface can be modified by fluvial rounding, weathering, rodent gnawing,

Table 1. List of mammalian taxa within 1989-1991 samples from UNSM Sx-6 and Sx-7.

MARSUPALIA	
	Herpetotherium sp.
LAGOMORPHA	
	Paleolagus sp. (small)
	Paleolagus sp. (large)
CREODONTA	
	Hyaenodon sp. (small)
CARNIVORA	
	Daphoenus sp. (large)
	Hesperocyon sp.
	Hoplophoneus sp. (small)
	Parictis sp.
	Paleogale sp.
INSECTIVORA	
	Leptictis sp.
ARTIODACTYLA	
	Miniocherus sp.
	Merycoidodon sp.
	Poebrotherium sp.
	Hypertragalus sp.
	Hypisodus sp.
	Leptomeryx sp.
	Agriochoerus sp.
	indeterminant entelodont
PERISSODACTYLA	
	Mesohipus sp.
	Hyracodon sp.
	Subhyracodon sp.
RODENTIA	
	Ischyromys sp. (small)
	Ischyromys sp (large)
	Cedromys sp. (large)
	Eumys sp.
	Paradjidaumo sp.
	Helioscomys sp.

root etching, burrowing by insect larvae, and scratching and breakage by trampling (Miller, 1969, 1975; Hill, 1976, 1980; Behrensmeyer, 1978; Binford, 1981; Haynes, 1985, 1988; Fiorillo, 1988, 1989; Behrensmeyer and others, 1989; Irving and others, 1989; Marshall, 1989). These modifications, where present, were described as the sample was inspected for bone processing.

Recognition of Bone Processing

Many studies have specifically addressed bone processing in the extant and fossil records, but no standard terminology for bone processing is available. Terms in current use include "fractures," "spiral fractures," "flakes," "comminutions," "chop marks," "cutmarks," "grooves," "scratches," "slices," "designs," "cracks," "splintered," "pitted," "scoured," "punctured," "perforated," "shredded," and "exfoliated," among others (summarized in Marshall, 1989). In this study I use the simplified terminology of Haynes (1980a, 1983) and LaGarry (1988), which divides carnivore processing into *gouging*, *pitting*, *spalling*, and *transverse scratching* and excludes bone breakage not unambiguously resulting from the application of a carnivore's teeth. *Gouging* consists of broad, shallow grooves or furrows. *Pitting* consists of holes or punctures that may or may not completely penetrate the outer compact bone and enter the underlying cancellous bone. *Spalling* consists of the breaking off of a "spall," or a large chunk of bone. *Transverse scratching* consists of individual or sets of small scratches oriented approximately perpendicular to the long axis of the bone. These features were recognized through visual inspection of the sample, and the character and potential origins of those features present in the sample will be discussed below.

Body Size Delineation

Extant mammalian carnivores select a particular range of prey body sizes (Kruuk and Turner, 1967; Mech, 1970; Kruuk, 1972; Schaller, 1972; Kingdon, 1977; Peterson, 1977; Miller, 1979; Haynes, 1982). For example, lions in the Serengeti Plains of eastern Africa most frequently prey on zebra and wildebeest having body sizes from 100-350 kg, whereas leopards most frequently prey on Thompson's gazelles, impala, and reedbuck having body sizes from 10-100 kg (Kruuk and Turner, 1967). Extant carnivores are also opportunistic and will pursue other, typically smaller, prey when it is available (Kruuk and Turner, 1967; Kingdon, 1977). However, body size and availability, rather than membership in a particular taxonomic group, determine the preferred prey of extant carnivores. In order to investigate this in Oligocene faunas, I divided the Orellan fossil sample, which represents the "pool" of potential prey, into size groups for further analysis. This approach is justified when there is direct evidence, in the form of bone processing, that a carnivore interacted with a "prey" item (see Gifford-Gonzalez, 1989). However, heavily processed assemblages are a "residue" of the original sample of prey carcasses and may consist of only a few scraps or unrecognizable shards (see Haynes, 1982, 1985, 1988).

Therefore, assigning processed bones to groups of any kind is problematic. Nevertheless, the composition of the Orellan bone sample demonstrates that body size estimates can be derived from postcranial debris, simply by taking note of the relative size of durable elements in the sample. Several methods for estimating body size are available, such as measuring the diameter of the femoral shaft (Gingerich, 1989) or (for carnivores) the length of the lower carnassial (Legendre, 1986; Legendre and Roth, 1988). Ratios of various dental, cranial, body length, and postcranial bone measurements have also been used (Damuth, 1990; Janis, 1990; Scott, 1990; Van Valkenburgh, 1990). These techniques require securely identified or well-preserved skeletal material for the most accurate results, neither of which is generally available in the sample used here. However, for the purposes of this paper, a series of size divisions can be identified and

used to construct size groups for comparison. I used a single, very simple measurement that could be taken on the most frequently surviving parts of each skeletal element (table 2).

Processing Distribution Delineation

Shipman (1981) advocated that when analyzing patterns of bone breakage to identify their most probable cause, "like should be compared to like," or when describing breakage of the distal end of a humerus in a sample of fossil or modern bone, all distal ends of humeri in the sample should be considered. This method is based on the premise that the structure of a bone determines how it will break and bones of similar structure will break in similar ways. I apply this concept to bone processing as defined by Haynes (1980a, 1983) and LaGarry (1988). For example, when analyzing the processing of distal ends of humeri of a given size group, all humeri within that size group were compared and used in the analysis (fig. 3). This produces an "average" state of processing for each element within a size group. Thus, the average state of processing of the distal end of the humerus within one size group can be compared to the average state of processing of the distal end of the humerus in other size groups. Shipman (1981) also advocated that taphonomic studies of bone breakage "consider the pattern, not the individual bone," because few types of breakage, by themselves, clearly identify their cause. However, patterns of differential breakage may indicate a cause of breakage for the whole assemblage. I have also applied this method to bone processing identified within the Orellan sample. In order to identify differences in how prey of different sizes were processed, I examined the distribution of bone processing on a composite prey "skeleton" for each size group and compared the distributions of processing among size groups.

Results and Discussion

Data from this study consist of the results of the examination of the coprolites and the results of the examination of the postcranial fragments. These data are described and interpreted individually; they are then interpreted as a whole in order to make broader statements about the paleoecology and behavior of Oligocene carnivores.

Bone Processing Within the Coprolites

About 10% (n = 121) of the total coprolite sample (n = 1,250 +) was manually excavated to expose bone. This was about 90% of coprolites having bone exposed on their outer surface (total = 131, excavated n = 121). Other techniques for recognizing bone within these coprolites, such as fluoroscopy and radiography, are promising and will be the focus of future research. The excavated bone is described as follows (figs. 4-6).

Breakage

Most bones excavated from the coprolites are unidentifiable, spirally or transversely fractured fragments (see Binford, 1981) from 0.1 - 3.8 cm in length (figs.

Table 2. Measurements of postcranial bones used in this study (following von den Driesch, 1976).

SKELETAL ELEMENT	MEASUREMENT
vertebrae (centrum)[1]	breadth of cranial / caudal articular surface[2]
scapula (glenoid region)	greatest breadth of glenoid region
humerus (proximal end)	greatest breadth of proximal end[3]
humerus (distal end)	greatest breadth of distal end
radius (proximal end)	greatest breadth of proximal end
radius (distal end)	greatest breadth of distal end
ulna (proximal end)	depth across processus anconaeus
ulna (distal end)	greatest breadth of distal end[4]
pelvis (acetabulum)	length of acetabulum, including lip
femur (proximal end)	greatest breadth of proximal end[5]
femur (distal end)	greatest breadth of distal end
tibia (proximal end)	greatest breadth of proximal end
tibia (distal end)	greatest breadth of distal end
astragalus	greatest breadth[3]
calcaneum	greatest breadth
metapodial (proximal end)	greatest breadth of proximal end[3, 6]
metapodial (distal end)	greatest breadth of distal end[3, 6]
phalanges	greatest breadth of proximal end[3, 6]

1. Cervical, thoracic, and lumbar vertebrae combined, excluding caudal vertebrae.
2. Broadest unbroken surface measured. Same measurement used for all vertebrae.
3. Same measurement applied to all bones of this type regardless of taxon.
4. New measurement (see text).
5. Measurement corresponds to Bd of von den Driesch (1976) for artiodactyls.
6. All bone of this type and position grouped as a single unit.

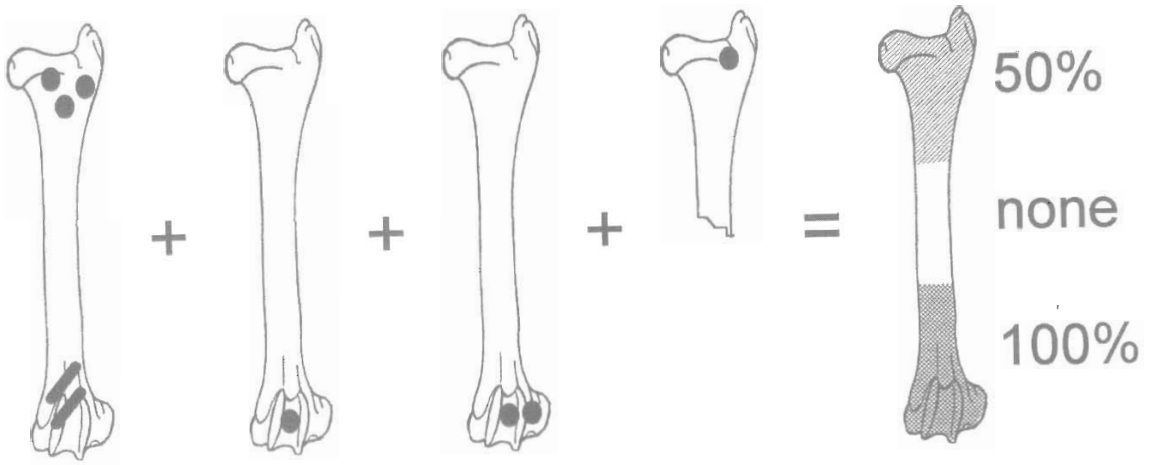


Fig. 3. Method for assessing bone processing in the Orellan sample. For any given skeletal element (femur, humerus, etc.), processed and unprocessed bones were combined to determine the processed percentage of all elements of a given type. For example, the illustrated sample of four partial and complete humeri yield proximal ends of humeri showing 50% processing, humeral shafts showing no processing, and distal ends of humeri showing 100% processing. These values are presented on figures 13-15. Dark lines and ovals represent hypothetical bone processing features.

4A-D; 5A-D; and 6A-B). Many are too nondescript to be identified to a particular element (fig. 5A). Overall, bone within the coprolites is finely to coarsely comminuted, with large fragments (> 0.5 cm) being most common. However, several examples of complete, well-preserved bones occur next to groups of bone fragments (figs. 4B and 5A). The complete bones consist of short, compact elements such as phalanges and podials, or, rarely, of small limb bones. Eleven isolated teeth have been recovered, along with one tooth-bearing partial maxilla (UNSM 121012), a partial mandible with teeth (UNSM 121005), and a crushed skull (UNSM 121013).

Articulation

Most of the bone excavated from the coprolites has been disarticulated, but there are several examples of disarticulated bones that likely represent the same individual (figs. 4B-C; 5A, 5D; and 6B). The only articulated elements recovered to date are medial and distal phalanges of a small oreodont (cf. *Miniochoerus*, UNSM 121015) and the forelimb of a small mammal (UNSM 121018).

Corrosion

Corrosion of the excavated bone appears as dissolution of compact bone and enamel and rounding of fragment edges. Many postcranial bone fragments show no evidence of dissolution, even under magnification (fig. 4A), while in others the compact bone has been dissolved by digestive fluids exposing the cancellous bone. Most of the excavated teeth show some degree of corrosion by stomach acids, such as a series of three upper molars of the small didelphid marsupial *Herpetotherium* (UNSM 121012), which show dissolution of enamel at the occlusal wear facets. Other examples are the isolated p1-4 and partial M1 of *Hesperocyon*, a small canid (fig. 5C-D). The partial M1 shows slight dissolution and rounding of its broken edges, while the premolars appear to be uncorroded.

Skeletal Representation

To date, isolated teeth, partial toothrows, postcranial bones, bone fragments, and one crushed skull have been recovered by manual preparation of the surfaces of the coprolites. The crushed skull (UNSM 121013), based on the teeth present, is a small species of *Paleolagus*. Other than small fragments, the most common skeletal elements recovered are isolated teeth (n = 12: figs. 4D; 5C-D; and 6A, 6C-D), followed by phalanges (n = 11: fig. 4A-C), partial mandibles (n = 3: figs. 5B and 6B), ribs (n = 2: figs. 4B and 5A), a maxilla (n = 1: not figured), and a femur (n = 1: fig. 4C).

Faunal Composition

The taxa recognized within the coprolites are few but diverse, and biased towards *Paleolagus*, *Leptomeryx*, and small oreodont-sized taxa. *Herpetotherium* is represented by a partial mandible with m2-m3 (fig. 5B) and the partial maxilla with M1-M3 mentioned earlier. Small and large species of *Paleolagus* (fig. 6A) are represented by isolated teeth and the crushed skull mentioned previously. *Hypisodus*, a small artiodactyl of about the same size as the large *Paleolagus*, is represented by an m2 or m3 (fig. 6C) and several phalanges (fig. 4C). *Leptomeryx*, another small (albeit slightly larger) artiodactyl, is represented by a deciduous premolar (fig. 6D) and several phalanges (fig. 4A). Two small incisors (di1) have been referred to cf. *Poebrotherium* (fig. 6B), but further comparisons are

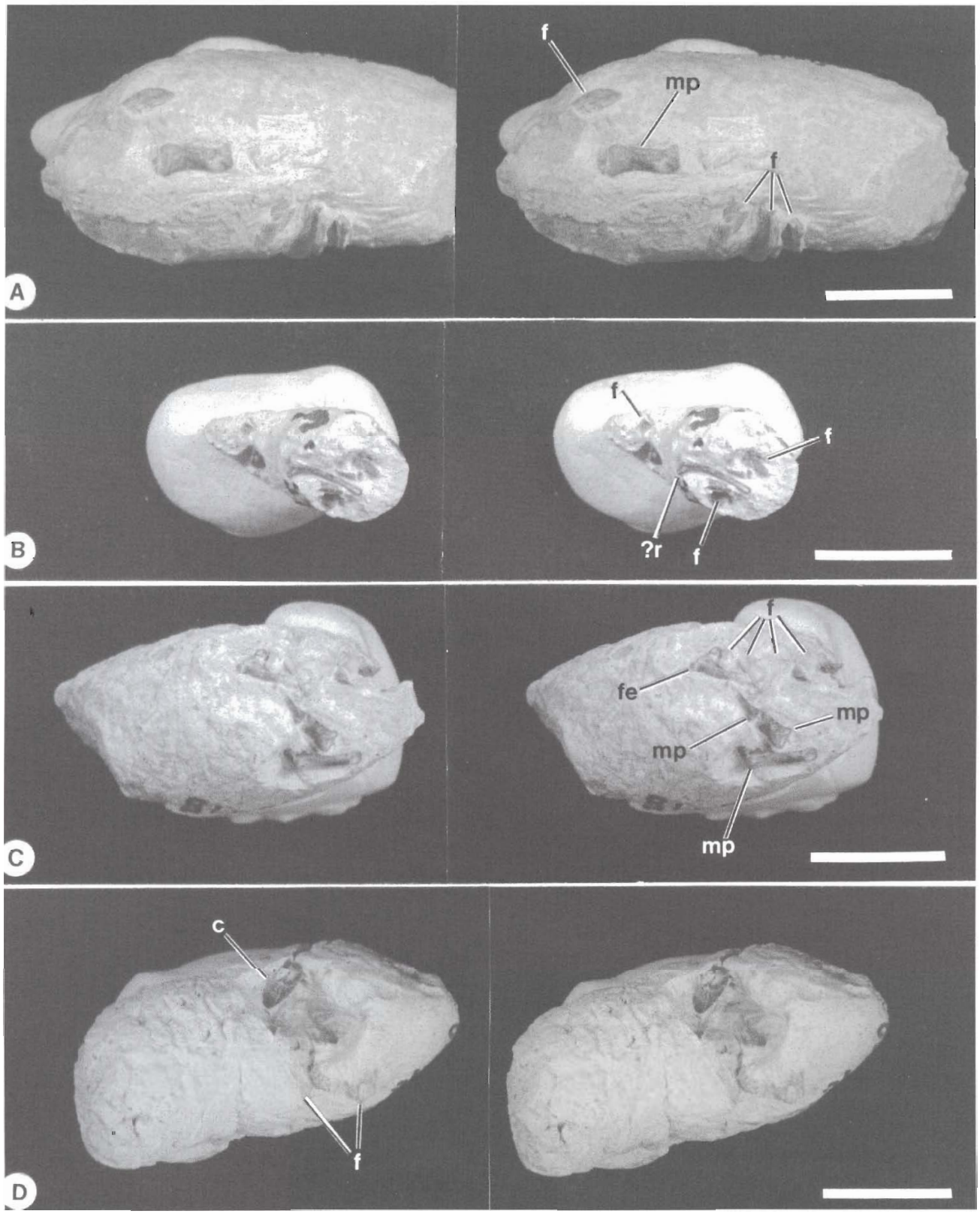


Fig. 4. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7; A) UNSM 121000; B) UNSM 121001; C) UNSM 121003; D) UNSM 121003. Symbols: f, fe, ?r, c, and mp = fragment, femur, ?rib, canine tooth, and medial phalanx, respectively. Bars = 1 cm.

needed to confirm that they do not represent *Leptomeryx* or another small artiodactyl, *Hypertragulus*. Several of the larger phalanges have been assigned to the oreodonts cf. *Merycoidodon* (UNSM 121014) and cf.

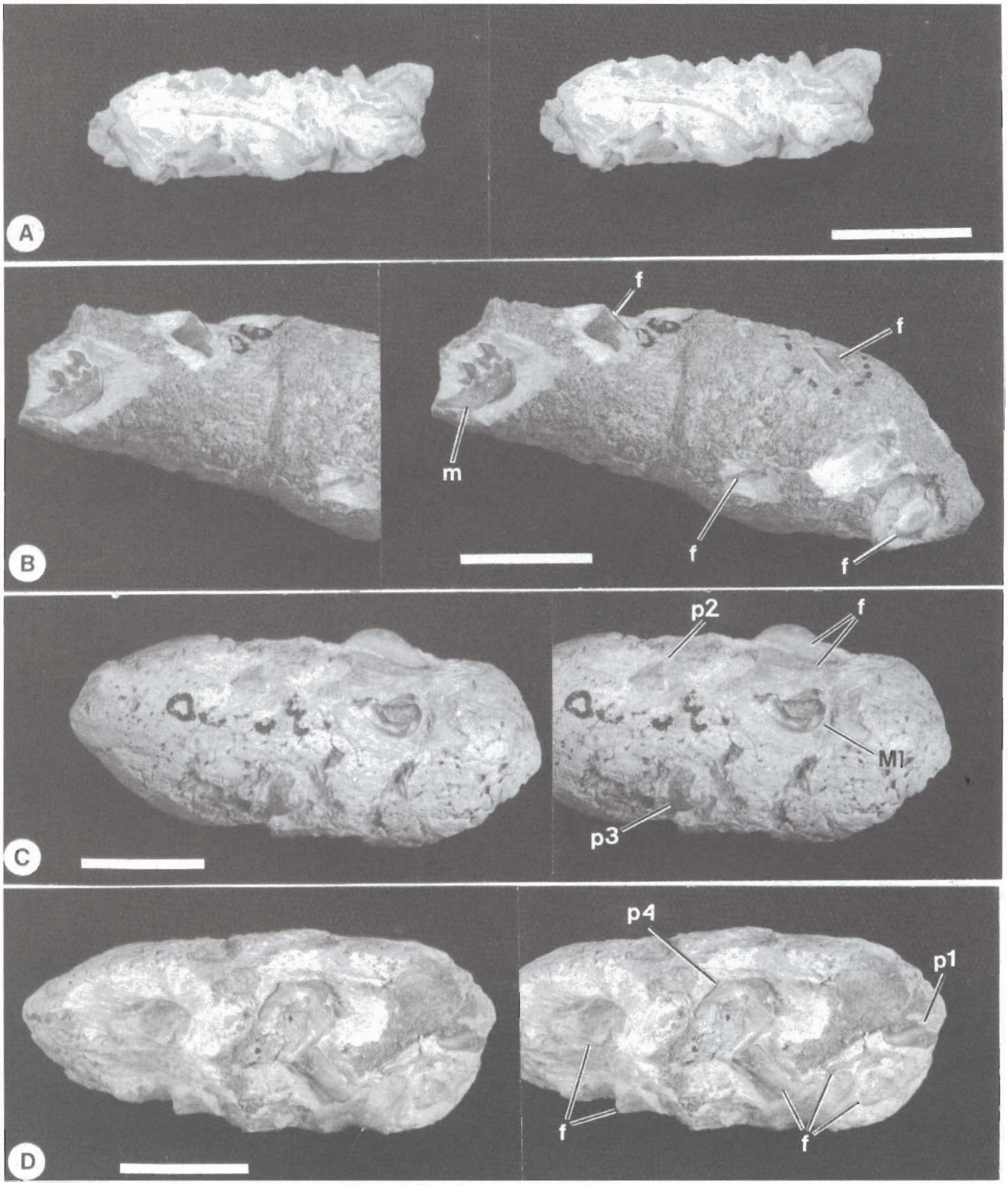


Fig. 5. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7: A) UNSM 121004; B) UNSM 121005; C) UNSM 121006; D) UNSM 121007. Symbols: f, m, p1, p2, p3, M1 = fragment, partial mandible, 1st premolar, 2nd premolar, 3rd premolar, 4th premolar, and 1st molar, respectively. Bars = 1 cm.

Miniochoerus (UNSM 121015). A single distal phalanx (UNSM 121020) was assigned to cf. *Mesohippus*. As mentioned previously, the small canid *Hesperocyon* (fig. 5C-D) is represented by four isolated premolars and a

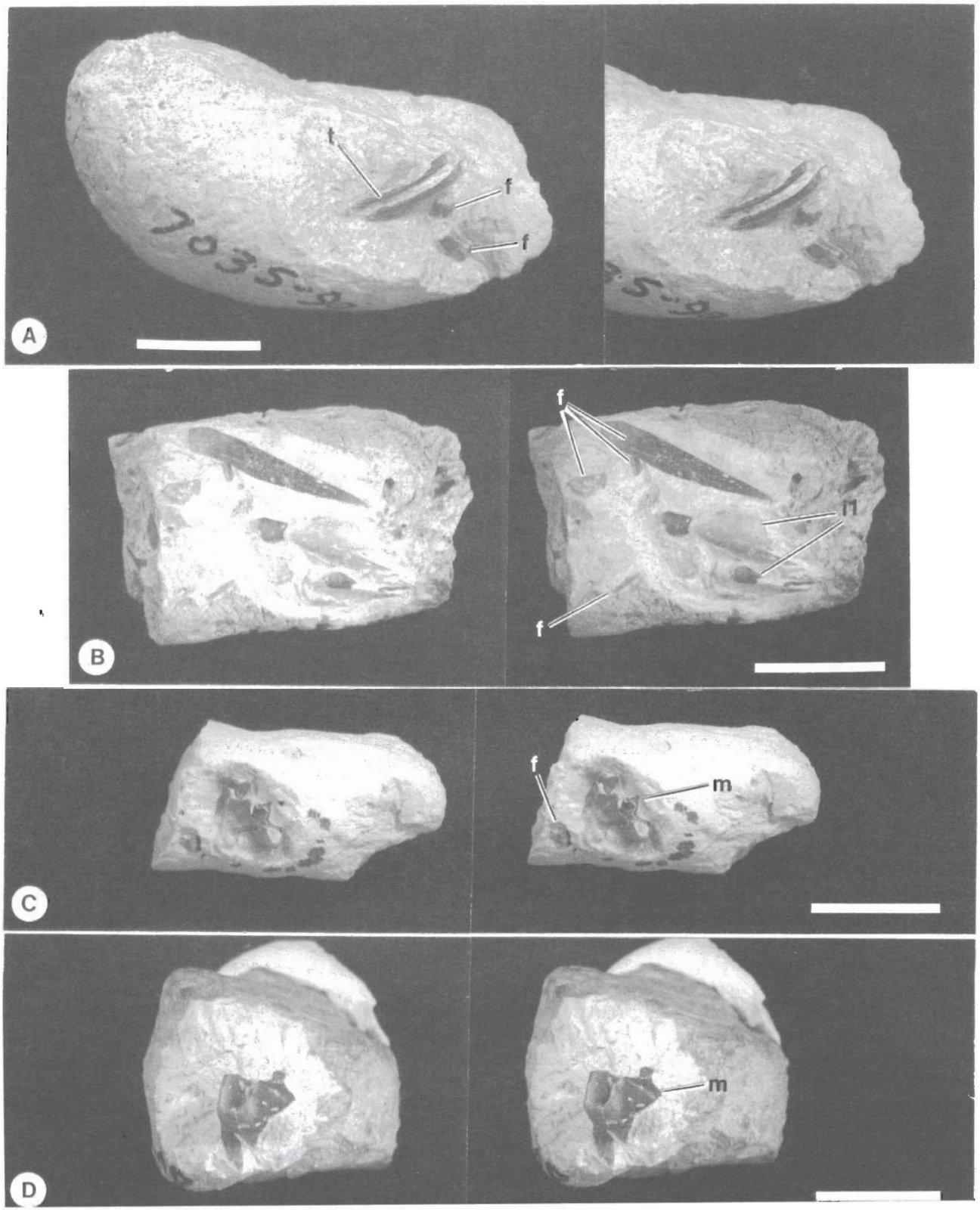


Fig. 6. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7: A) UNSM 121008; B) 121009; C) UNSM 121010; D) UNSM 121011. Symbols: f, t, i1, m = fragment, Paleolagus tooth, 1st incisior, and molar, respectively. Bars = 1 cm.

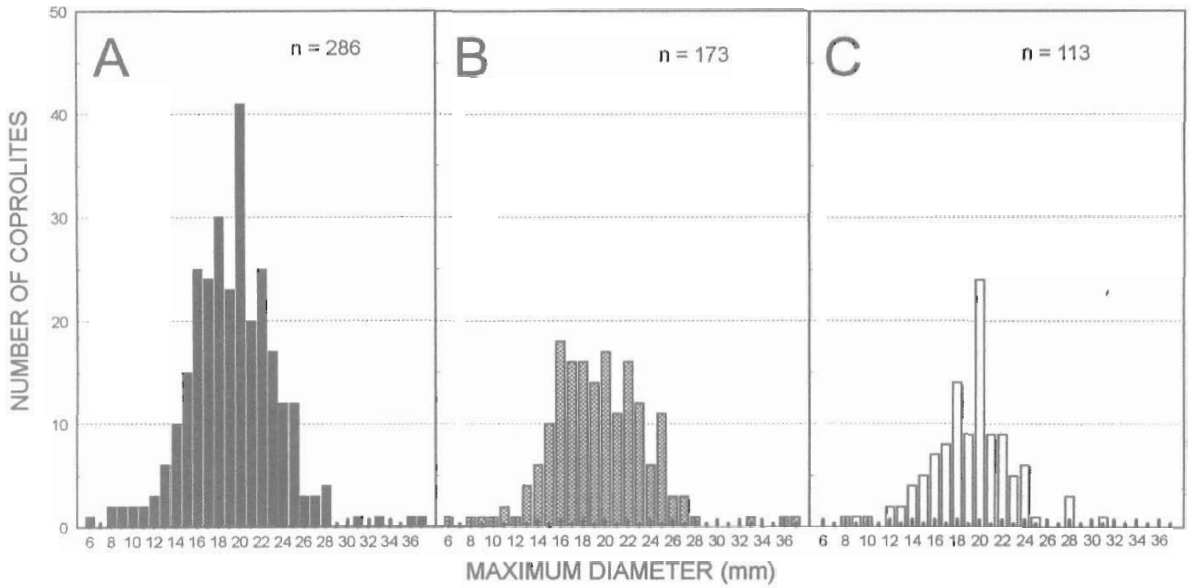


Fig. 7, A-C. Histograms showing the frequency of diameters measured in the coprolite sample collected from UNSM Sx-6 and Sx-7: A) total sample; B) coprolites in which no bone was observed; C) coprolites in which bone was observed and subsequently exposed by manual preparation.

partial M1. The well-preserved limb bones obviously represent rodents or insectivores, but the postcranial skeletons of these taxa are not well known (having been diagnosed solely on the basis of teeth) and accurately identified postcranial material was not available for comparison.

Identity of the Processing Carnivore

Based on a composite sample of 106 coprolites from the Chadron and Brule formations (*sensu* Schultz and Stout, 1955), Edwards and Yatkola (1974) concluded that White River Group coprolites were produced by at least two size classes of carnivore. Their histogram of frequency vs. size (Edwards and Yatkola, 1974: fig. 1) has three modes: a small size group (1.8-2 cm), a large size group (3-3.3 cm), and a zone of overlap (2.6-2.7 cm). Based on the same measurement of maximum diameter, the large sample of coprolites studied here yielded a histogram having a single mode at 2 cm (fig. 7A). This mode is poorly defined on a histogram produced from coprolites in which no bones were observed (fig. 7B), but a single mode of 2 cm is also present on a histogram derived from the mechanically prepared coprolites (fig. 7C).

From this analysis, I conclude that the sample of coprolites from the Orella Member at UNSM Sx-6 and Sx-7 likely represents one or more carnivores of about the same body size. Edwards and Yatkola's (1974) analysis may have indicated two distinct body sizes because their sample was collected from both the Chadron and Brule formations, which represent at least two depositional environments and their included mammalian communities. Also, as mentioned earlier, collections from the White River Group have traditionally been made by picking up material from the surface litter, which biases a sample towards larger, more conspicuous, and more complete specimens. Thus, their larger size group may be an artifact of their collecting method.

Using data from Mech (1970), Edwards and Yatkola (1974) concluded that the two body sizes of carnivores indicated by their histogram produced feces of about the same diameters as coyotes (< 2.55 cm) and wolves (2.55-3.75 cm). They asserted that assumed correlations between coprolite diameter and body size are unsupported, but their observations provide a starting point for further analysis. Based on averaged size estimates (Van Valkenburgh, 1988; Walker, 1975, p. 1152), there are several Oligocene carnivores of about the same size as the coyote (*C. latrans*, 9-12.7 kg) and the wolf (*C. lupus*, 27-79 kg). The coyote-sized taxa include the creodont *Hyaenodon crucians* (~17 kg), the nimravids *Hoplophoneus primaevus* (~16 kg) and *Dinictis felina* (~18.5 kg). This group likely includes the amphicyonid *Daphoenus vetus*, because Van Valkenburg's (1988) size estimate of 34.5 kg for this taxon is larger than is indicated by its coyote-sized skull and skeleton. The wolf-sized taxa include the large creodont *Hyaenodon horridus* (~81 kg) and the large nimravid *Hoplophoneus occidentalis* (~67.5 kg). Based on the mode of 20 mm shown by coprolite diameters from UNSM Sx-6 and Sx-7, the coprolite-producing carnivore was likely one of the larger coyote-sized carnivores.

Discussion

Andrews and Nesbit-Evans (1983) described processed bone recovered from the scats of the viverrids *Ichneumia albicauda* (white-tailed mongoose), *Cynictis penicillata* (yellow mongoose), and *Genetta genetta* (genet); the canids *Otocyon megalotis* (bat-eared fox), *Vulpes vulpes* (British red fox), *Alopex lagopus* (arctic fox), and *Canis latrans* (coyote); the mustelids *Mustela nivalis* (weasel), *M. putorius* (polecat), *M. erminea* (ermine), and *Martes martes* (pine martin); and the felids *Felis domesticus* (feral domestic cat) and *Leopardus weidi* (margay). In the following discussion, the bone in the Oligocene coprolites is compared to bone processed by these taxa. These comparisons are tentative because excavation revealed only the outermost bones within a coprolite, an accurate census of the bone within the coprolites has not been made, and there is no evidence that the excavated bone is a representative sample. To my knowledge, no comparable census of bone processing within the scats of larger carnivores has been published.

When compared to the processed bone within the scats described by Andrews and Nesbit-Evans (1983), the ratio of fragments to whole bones within the coprolites (about 15:1) is about the same as that for *C. latrans* (11.5:1) and *M. martes* (12.5:1), as opposed to 3:1 for *I. albicauda* and *O. megalotis*, 2:1 for *G. genetta*, and 1:0 for *V. vulpes* and the felids. Spirally fractured bones like those excavated from the coprolites were recovered from scats of the canids *O. megalotis*, *V. vulpes*, and *C. latrans*. The bone excavated from the coprolites further resembles bone processed by the canids in that the bone from their scats is biased towards larger fragments and taxa, but finely comminuted chips and shards are also present. This suggests the coprolite-producing carnivore may have, like extant canids, thoroughly masticated larger food items, but swallowed smaller prey whole or in large parts.

Comparison of the degree of articulation preserved within the coprolites to that described by Andrews and Nesbit-Evans (1983) indicates a further resemblance to the scats of *C. latrans* and *A. lagopus*, from which articulated elements were occasionally recovered. This is in contrast to the vivverids, from which no articulated elements were recovered; the mustelids, from which articulated remains were common; and the felids, in which the bone was comminuted beyond recognition. This degree of articulation supports the conclusion that the coprolite-producing carnivore likely swallowed its smaller prey partially intact.

The corroded bone within the coprolites, when compared to the scats described by Andrews and Nesbit-Evans (1983), most closely resembles bones processed by the mustelids, in which moderate amounts of rounding of edges and corrosion of both bones and teeth were observed. This is also in contrast to the viverrids, in which moderate to great rounding and no corrosion was observed (except for a few severely corroded examples); the canids, in which great amounts of rounding occurred and both bones and teeth were severely corroded; and the felids, in which virtually all fragments were rounded and both bones and teeth were extremely corroded. In the extant carnivores studied by Andrews and Nesbit-Evans (1983), the ingestion of hide and hair along with bones, teeth, and flesh reduced the impact of stomach acids on the ingested bone. This may have been the case for the coprolite-producing carnivore if it ate its prey whole or in parts, as suggested by the bone processing.

Comparison of the skeletal part representation within the coprolites to that within the scats described by Andrews and Nesbit-Evans (1983) revealed that the coprolites described here most closely resemble skeletal elements recovered from scats of canids. Elements within the coprolites are dominated by isolated teeth, followed by phalanges, mandibles, ribs, a maxilla, and a small femur. Bones recovered from the canid scats (in terms of actual, not relative, abundance) are mostly phalanges, followed by isolated teeth, vertebrae, metapodials, femora, humeri, and mandibles. The coprolite and canid scat assemblages are both dominated by isolated teeth and phalanges. Scats of the other taxa studied by Andrews and Nesbit-Evans (1983) had more vertebrae, more limb bones, fewer phalanges, more ribs, and more mandibles and maxillae.

Comparison of the prey fauna within the coprolites to the prey selected by the carnivores discussed by Andrews and Nesbit-Evans (1983) indicates that, like *C. latrans*, the coprolite-producing carnivore ate a variety of prey items. Taxa recovered from the coprolites range in size from small (*Herpetotherium*) to relatively large (cf. *Miniochoerus*, cf. *Merycoidodon*, cf. *Mesohippus*, *Hesperocyon*) and include at least ten genera from seven taxonomic classes of mammalian prey. Of the taxa studied by Andrews and Nesbit-Evans (1983), this level of generalized feeding was only approached by *C. latrans*, suggesting that the coprolite-producing carnivore was also a generalist feeder. Of all the Orellan carnivores, only the small canids *Hesperocyon* sp. and *Mesocyon* sp. and the amphycyonids *D. hartshornianus* and *D. vetus* had dentitions similar to that of the coyote *C. latrans* (Van Valkenburgh, 1988). Only *D. vetus* attains the body size of a coyote, and this species appears likely to have produced most of the coprolites described herein. However, based on the wide range of observed coprolite diameters (0.6-3.7 cm), carnivores of other body sizes probably contributed to the Orellan coprolite sample.

Bone Processing of the Postcranial Fragments

Preliminary inspection revealed that most of the observed alteration of the sample (for example, weathering, breakage, bone processing) occurred prior to

Table 3. Frequency of processing of individual skeletal elements. Elements not identified to taxon and minimum number of individuals not calculated (see text).

ELEMENT	NISP%[1]	GOUGE%[2]	PIT%[3]	SPALL%[4]	SCRATCH%[5]
vertebrae	289	0	3	2	>1
caudal vertebrae	70	0	0	0	0
scapula (glenoid region)	86	0	20	20	5
humerus (proximal end)	40	3	35	20	15
humerus (distal end)	147	>1	18	45	3
Radius (proximal end)	99	1	7	26	2
Radius (distal end)	52	0	17	29	2
Ulna (proximal end)	36	0	11	6	0
Ulna (distal end)	6	0	0	0	0
Pelvis (acetabulum)	78	0	16	12	1
Femur (proximal end)	82	5	5	4	1
Femur (distal end)	106	3	56	38	4
Tibia (proximal end)	55	5	13	16	2
Tibia (distal end)	150	0	7	6	3
Calcaneum	78	1	15	8	3
Astragalus	108	0	8	5	1
Metapodial (proximal end)[6]	112	0	2	2	2
Metapodial (distal end)[6]	74	0	4	0	2
phalanx (proximal end)[6]	178	0	2	1	0

1. NISP = Number of identified specimens
2. GOUGE% = Percentage of gouged elements
3. PIT% = Percentage of pitted elements
4. SPALL% = Percentage of spalled elements
5. SCRATCH% = Percentage of scratched elements
6. All elements of this type grouped.

burial in the Oligocene. Following is a description of these features, along with the distribution of preburial damage to individual skeletal elements, a description of the size groups, and the distribution of processing on different body sizes.

Non-processing Features

Non-carnivore modifications observed within the bone sample include weathering, rodent gnawing, and root etching. Damage from trampling and abrasion (see Fiorillo, 1988, 1989; Marshall, 1989) was not observed. Evidence of weathering consists of surface textures and cracks that result from bone drying out and exfoliating (Hill, 1976; Behrensmeyer, 1978). In the Orellan sample, this damage ranges from surface textures that resemble a reticulate mosaic of small cracks to deep, longitudinal cracks that penetrate through the cortical bone into underlying cancellous bone. When bone processing is superimposed over weathering surface textures, the outermost layers of cortical bone tend to splinter and give the bone surface a "rougher" appearance. Also, as bone dries, it tends to deform less plastically and breakage patterns change as a reflection of this (see below). Rodent gnawing is often difficult to distinguish from bone processing and is described in detail below. Root etching, while not common in the sample, consists of small, irregular, and intertwining etchings present on one side of the bone. Although root etching has been described (Behrensmeyer, 1978; Binford, 1981; LaGarry, 1988; Irving and others, 1989; Marshall, 1989), no analysis of its significance has been made. These surface features are the subject of continuing study, and those results will be presented elsewhere.

Bone Processing Features

Bone processing features observed within the sample consist of gouging, pitting, spalling, and transverse scratching by mammalian carnivores (table 3), and were observed on both tortoise and mammal bone. However, the processing of reptile bone in modern assemblages has not been studied, and therefore no means of drawing meaningful analogies are available. Tortoise bone is included in the following descriptions of bone processing (including table 3), but not used in subsequent analyses (tables 4 and 5, figs. 11-15).

Gouging is the least frequent type of bone processing in the sample and consists of parallel or bifurcating grooves 0.3-0.6 cm wide and 0.1-0.5 cm deep in the outer layers of compact bone. This damage is concentrated at the proximal and distal ends of the femur (figs. 8A, 8I; and 9B) and humerus, and the proximal end of the tibia (fig. 9C). It was also observed on a calcaneum (fig. 8E) and several rib fragments (fig. 10C, 10F). This damage is usually present on elements also showing pitting and spalling.

Gouging is common on bone processed by wild hyenas, less common on bone processed by wild

Table 4. Distribution and character of preburial damage to skeletal elements from UNSM Sx-6 and Sx-7.

ELEMENT	OBSERVED DAMAGE	WEATHERING
vertebrae	neural, lateral, and spinous processes broken off (most) articular processes broken off (many) edges of articular surfaces chipped (many) centrum broken transversely (some)	few are severe many are moderate few are slight few are unweathered
caudal vertebrae	neural and transverse processes chipped (few) centrum broken transversely (few)	few are slight most are unweathered
scapula	blade and spine broken off – transverse or spiral fracture (all) neck of blade bitten or scratched (some) glenoid process chipped or bitten (many)	few are severe few are moderate many are slight few are unweathered
humerus	humeral head broken or bitten off (many) lateral tuberosity broken or bitten off (many) proximal end broken off – transverse or spiral fracture (many) part or all of distal trochlea bitten or broken off (some) proximal end broken off – transverse or spiral fracture (many)	few are severe many are moderate few are slight few are unweathered
radius	proximal articular surface broken or bitten off (few) proximal end broken off – transverse or spiral fracture (some) distal articular surface broken or bitten off (very few) distal end broken off – transverse fracture (few)	few are severe few are moderate many are slight few are unweathered
ulna	proximal end broken across processus anconaeus (few) olecranon process bitten off (few) distal end broken off – transverse fracture (few)	few are moderate many are slight few are unweathered
pelvis (acetabulum)	ilium, ischium, and pubis broken off or missing (most) part of acetabulum broken or bitten off (some) lip of acetabulum chipped (many)	few are severe some are moderate some are slight some are unweathered
femur	femoral head broken or bitten off (most) greater trochanter broken or bitten off (many) proximal end broken off – transverse or spiral fracture (some) distal trochanter broken or bitten off (many) distal end broken off – transverse or spiral fracture (many)	few are severe some are moderate some are slight some are unweathered
tibia	proximal articular surface broken or bitten off (some) proximal end broken off – transverse or spiral fracture (some) distal articular surface broken or bitten off (some) distal and broken off - transverse or spiral fracture (some)	few are severe few are moderate many are slight few are unweathered
calcaneum	anterior end broken or bitten off (some) posterior end broken or bitten off (some) articular surface broken or bitten off (some)	few are severe few are moderate many are slight few are unweathered
astragalus	proximal or distal trochlea broken off (few) edges of proximal or distal trochlea chipped (many) broken transversely or longitudinally (very few)	few are moderate many are slight many are unweathered
metapodial[2]	proximal or distal trochlea broken off (few) proximal end broken off – transverse or spiral fracture (few) distal trochlea broken or chipped (very few) distal end broken off – transverse or spiral fracture (few)	few are moderate few are slight most are unweathered
phalanges[2]	proximal or distal articular surface chipped (very few) spirally or transversely broken at midpoint (very few)	few are slight most are unweathered

1. Cervical, thoracic, and lumbar vertebrae combined.
2. All elements of this type combined.

wolves, and is not typically produced by wild felids in the few species studied (Sutcliffe, 1970; Haynes, 1980a, 1980b, 1982, 1983; Hill, 1989). However, this damage has been produced by captive hyenas, wolves, tigers, and lions (Miller, 1969; Haynes, 1983). Gouges result from a carnivore dragging its canine or carnassial teeth across a bone with force sufficient to penetrate the outermost layers of compact bone (Miller,

Table 5. Size groups (I-V) assigned to taxa from UNSM Sx-6 and Sx-7. All identifications are based on teeth.

TAXON AND GROUP	COPROLITES	POSTCRANIALS	EST. BODY SIZE
GROUP I			
Herpetotherium sp.	X	?	<1 kg[2]
Peleolagus sp. (small)	X	X	<1 kg[2]
Paleogale sp	—	?	<1 kg[2]
Leptictis sp.	?	?	<1 kg[2]
Centetodon sp.	?	?	<1 kg[2]
Ischyromys sp. (small)	?	?	<1 kg[2]
Ischyromoys sp. (large)	?	?	<1 kg[2]
Pelycomys sp.	?	?	<1 kg[2]
Cedromys sp.	?	?	<1 kg[2]
Eumys sp.	?	?	<1 kg[2]
Paradjidaumo sp.	?	?	<1 kg[2]
Heliscomys sp.	?	?	<1 kg[2]
Hypisodus sp.	X	X	<1 kg[2]
GROUP II			
Paleolagus sp. (large)	X	X	~2.5 kg[2]
Hyaenodon sp. (small)	—	?	~17 kg[3]
Hesperocyon sp.	X	X	~3 kg[2]
Hoplophoneus sp. (small)	—	?	~16 kg[3]
Parictis sp.	—	?	~9 kg[2]
Leptochoerus sp.	?	?	~7 kg[2]
Miniochoerus sp.	?	X	~7.9 kg[4]
Hypertragalus sp.	?	X	~1.4 kg[4]
Laptomeryx sp.	X	X	~3 kg[4]
GROUP III			
Daphoenus sp. (large)	—	?	~34.5 kg[3]
Merycoidodon sp.	?	X	~27.7 kg[4]
Poebrotherium sp.	X	X	~30.8 kg[4]
Agriochorerus sp.	—	?	~51.3 kg[4]
Mesohippus sp.	X	X	~25 kg[4]
GROUP IV			
Hyracodon sp.	—	X	~100 kg[2]
GROUP V			
Subhyracodon sp.	—	?	~517 kg[4]

1. Body size estimates and group assignments for adults. Juveniles may fall into a smaller group.
2. Body size estimated by comparison to extant forms (see text) and Walker (1975).
3. Average body size calculated from data in Van Valkenburgh (1990).
4. Average body size calculated from data in Damuth (1990).

1969; Haynes, 1980a, 1983; Hill, 1989). If bone is fresh at the time of processing, its surface may deform plastically and the grooves will be narrow and deep (fig. 10C). However, if the bone has dried out, the outermost layers of compact bone will splinter and the gouges will be shallow and jagged (fig. 8A). Extant carnivores typically produce this damage at the proximal ends of femora, humeri, and tibiae where the largest concentrations of fatty trabecular bone are located and compact bone is thinnest. This type of damage is typical of a "moderately processed" carcass (Haynes, 1983).

Pitting is the most common type of processing within the sample (table 3), and consists of conical (fig. 8C, 8I) or wedge-shaped (fig. 8D) depressions that perforate the compact bone. Some pitting penetrates the compact bone without rupturing it, or in other cases, creates associated circular fractures around the perforation (fig. 8J). It occurs as a single puncture (figs. 8I, 8J; and 9A) or in sets of multiple or occluding punctures (figs. 8C-D, 8G; and 9H). Pitting sometimes records the outline of the damaging teeth, and may allow the identification of the processing taxon (unpublished data). Pitting within the sample is concentrated around the proximal and distal ends of limb bones (fig. 8C-D and 8I) but is present on every type of skeletal element examined except caudal vertebrae and distal ulnae. Individual pits are typically 0.1-0.3 cm wide and 0.1-0.3 cm deep, although pits as small as 0.005-cm wide and 0.005-cm deep and as large as 0.5-cm wide and 0.6-cm deep were observed.

Pitting is typically produced when a carnivore bites down and the compact bone deforms plastically (Haynes, 1983). Among extant camivorans, this type

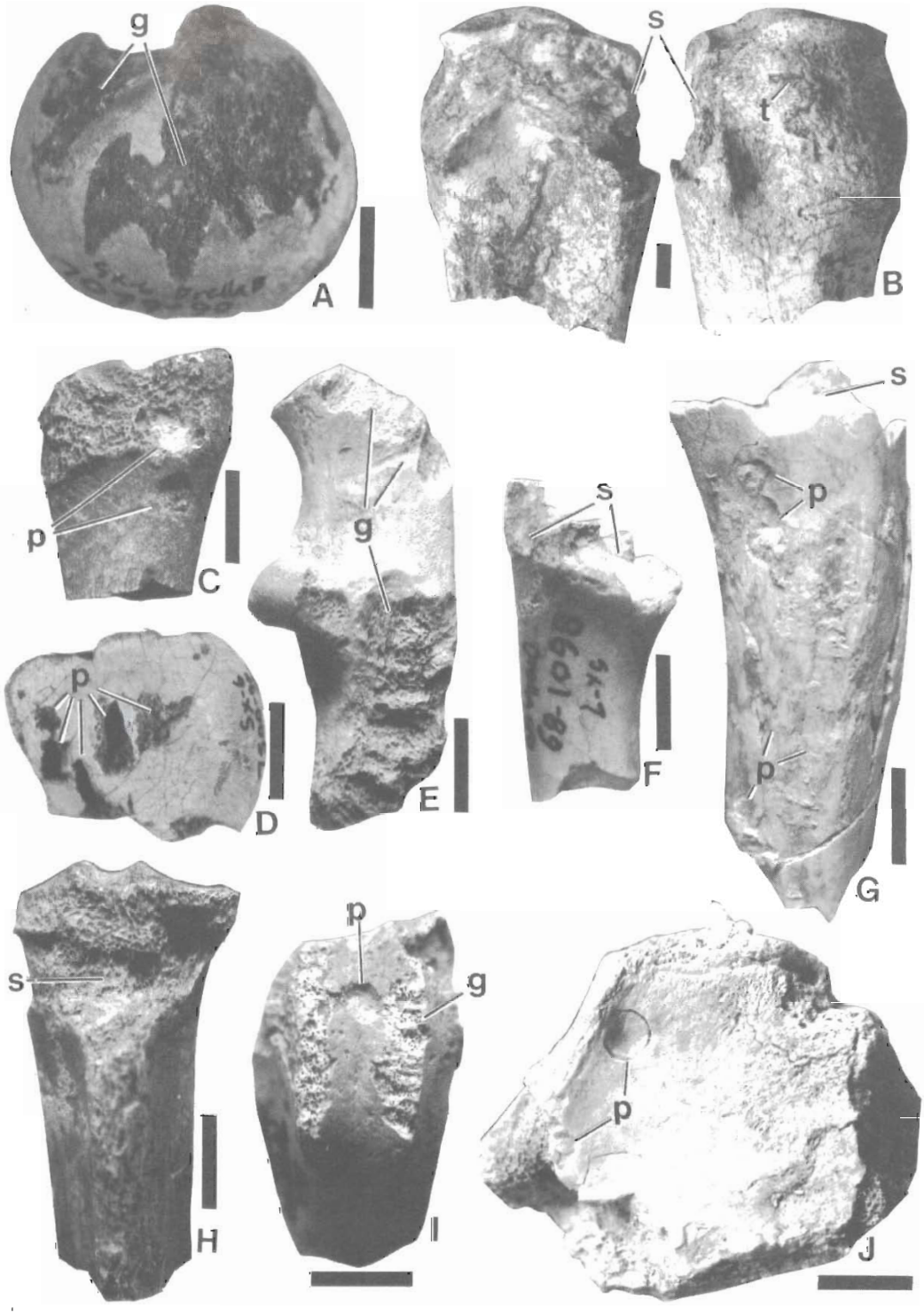


Fig. 8, A-J. Postcranial bone fragments from UNSM Sx-6 and Sx-7 showing bone processing: A) femoral head (UNSM 121210); B) proximal end of radius (UNSM 121211); C) proximal end of radius (UNSM 121212); D) humeral head (UNSM 121213); E) calcaneum, shown inverted (UNSM 121214); F) proximal end of humerus (UNSM 121215): G) proximal end of humerus (UNSM 121216); H) proximal end of tibia (UNSM 121217); I) distal end of femur (UNSM 121216); H) proximal end of tibia (UNSM 121217); I) distal end of femur (UNSM 121218); J) innominate fragment (UNSM 121219). Symbols: g, p, s = gouging, pitting, and spalling, respectively.

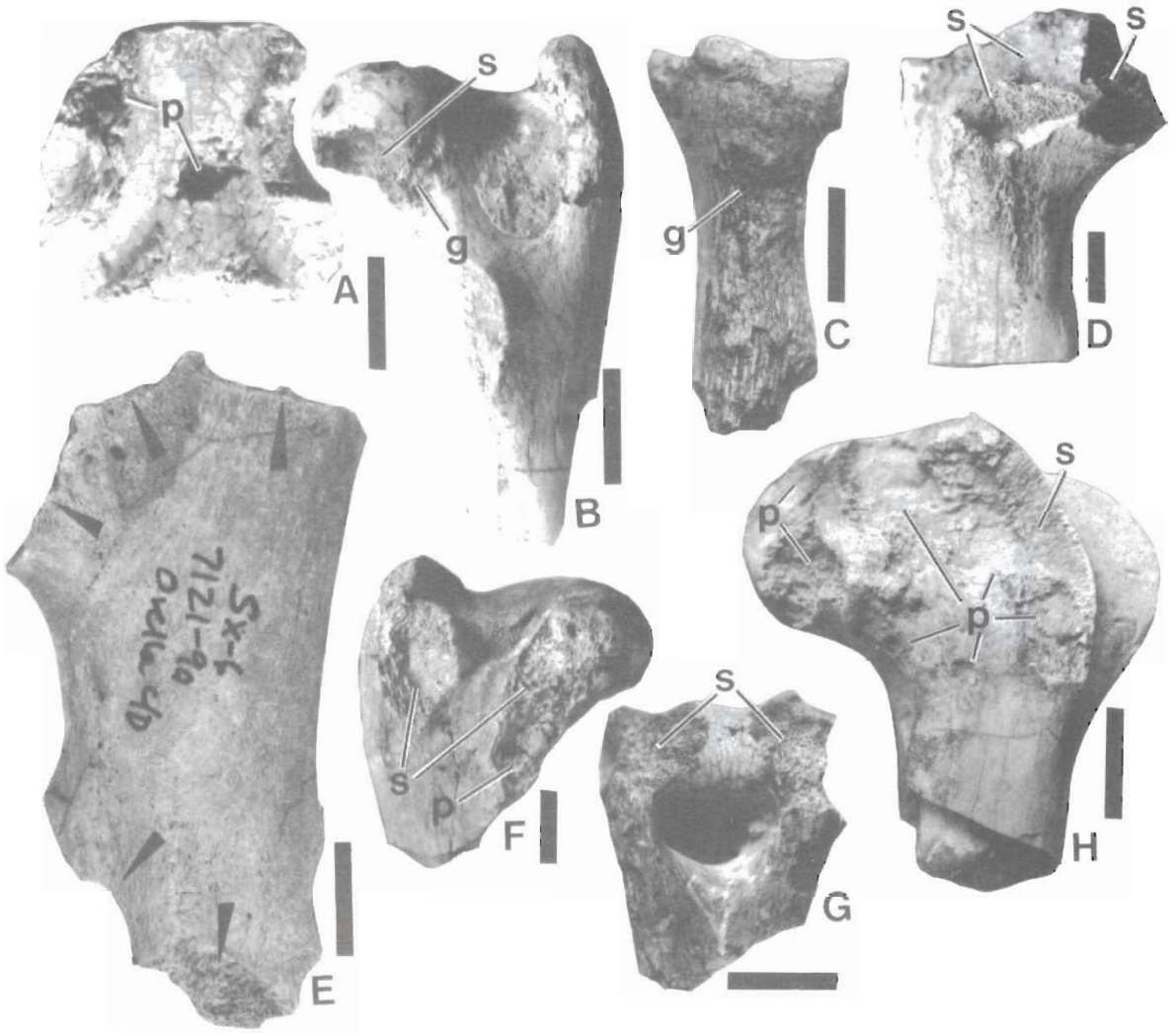


Fig. 9, A-H. Photographs of postcranial bone fragments from UNSM Sx-6 and Sx-7 showing bone processing: A) cervical vertebrae (UNSM 121220); B) proximal end of femur (UNSM 121221); C) proximal end of tibia (UNSM 121224); F) proximal end of humerus (UNSM 121225); G) distal end of humerus (UNSM 121226); H) distal end of femur (UNSM 121227). Symbols: g, p, s = gouging, pitting, and spalling, respectively.

of damage is produced by large felids, hyenas, and canids (Miller, 1969; Sutcliffe, 1970; Haynes, 1980a, 1983; Hill, 1989). Some extant ursine bears produce a large, rectangular depression rather than a conical pit (Haynes, 1983), indicating that tooth morphology may be accurately reflected by pitting when the bone deforms plastically. Pitting is most often associated with spalling (see below). This type of damage is typical of the early stages of bone processing, and in the absence of other damage it is typical of a "lightly processed" carcass (Haynes, 1983).

Spalling is second to pitting as the most common form of processing within the sample (table 3). It is concentrated at the proximal and distal ends of the major limb bones (humerus, radius, femur, tibia: figs. 8B, 8F-H; 9B, 9D, 9F-H; and 10G, 10I), and often leads to the partial or complete loss of a femoral head (figs. 8A, 8D; and 9B), an articular surface (figs. 8H, 8I; and 9F-H), or the complete removal of the proximal or distal end of a bone (figs. 8F-G; 9D; and 10G, 10I). Spalling typically occurs when a mammalian carnivore uses its canine or carnassial teeth to first puncture opposite sides of a bone; the bone then fractures, rather than deforming plastically, and a large fragment, or spall, splits off (Miller, 1969). Sometimes, but not always, remnants of the puncture produced by the teeth at their point of entry are preserved (Miller, 1969; Haynes, 1980a). Often, spalling is so pronounced that the entire end of a limb bone is bitten off, leaving a rim of jagged-edged bone at the proximal or distal end of the bone shaft, which can then record additional gnawing damage (Haynes, 1980a, 1983; Hill, 1989).

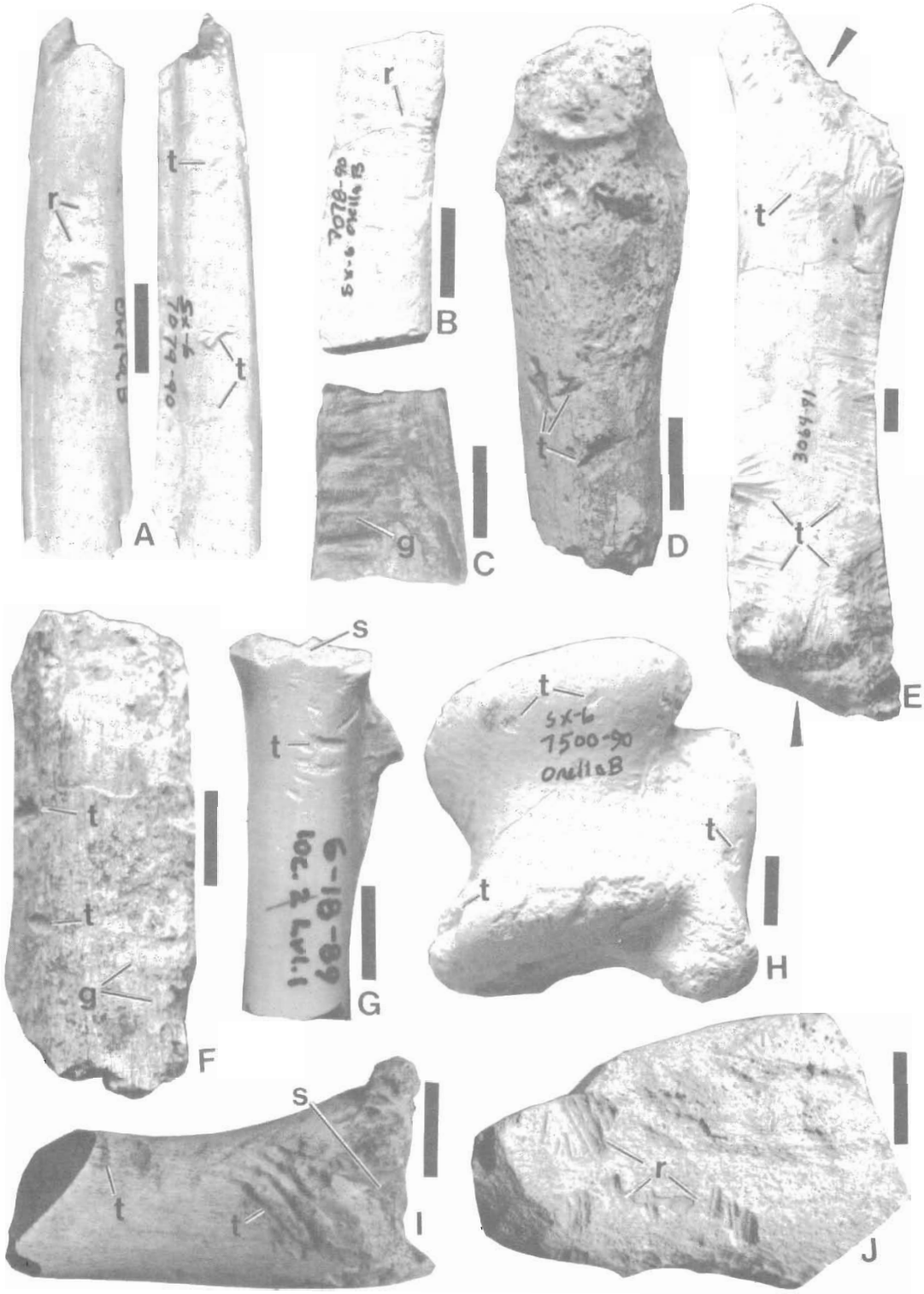


Fig. 10, A-J. Bone fragments from UNSM Sx-6 and Sx-7 showing bone processing; ***A)*** *rib fragment (UNSM* ***121228****);* ***B)*** *rib fragment (UNSM* ***121229****);* ***C)*** *? rib fragment (UNSM 121230); D) proximal end of metapodial (UNSM 121231); E) rib fragment (UNSM 121232); F) ? rib fragment (UNSM 121233);* ***G)*** *proximal end of femur (UNSM 121234); H) astragalus (UNSM* ***121235****); Symbols: g, s, t, r = gouging, spalling, transverse scratching, and rodent gnawing, respectively.*

Most large extant carnivores are capable of producing this kind of processing (Miller, 1969; Haynes, 1980a, 1983, 1985, 1988), and it is common in both extant and fossil processed bone assemblages (Miller, 1969; Haynes, 1983; LaGarry, 1988). Once damaged in this way, highly nutritious cancellous bone is exposed and is typically scooped out and consumed (Sutcliffe, 1970; Haynes, 1983; Hill, 1989). Spalling is most frequently associated with pitting (see above). Damage of this type, if restricted to missing spalls, is typical of a "moderately processed" carcass. If spalling has progressed to the point where the entire end of the limb is removed, leaving a broken rim, this damage is typical of a "heavily processed" carcass (Haynes, 1983).

Transverse scratching is the third most common form of bone processing within the sample (table 3); it consists of single and multiple sets of parallel or subparallel scratches perpendicular to the long axis of the bone (figs. 8B and 10). Transverse scratches are typically less than 0.2 cm wide and 0.1 cm deep and are usually V-shaped in cross section. They are usually less than 1 cm long (fig. 10A, 10D-I). The spacing between individual scratches in a set varies. Some are evenly spaced (fig. 10I), while others overlap (fig. 10A, lower set on right side).

Of the processing features discussed so far, transverse scratching has the most diverse origins. Transverse scratching has been attributed to rodents, canids, and felids (Miller, 1975; Haynes, 1980a, 1982, 1983; Marshall, 1989). It is typically the result of a small carnivore dragging its canines and/or incisors across the bone, in which case it is actually a small gouge (Miller, 1969). It is often produced when carnivores use their teeth to manipulate a bone to make other parts more available for processing or use their incisors to peel periosteum from the bone (Haynes, 1980b, 1982, 1983). Transverse scratching is also produced by juvenile carnivores that would typically produce gouges as adults (hyenas, wolves) but lack the jaw strength to produce other forms of damage (Sutcliffe, 1970; Haynes, 1980b, 1982; Hill, 1989). In the case of juvenile hyenas, even small pups are capable of producing damage equivalent to a much larger, adult carnivore (Sutcliffe, 1970; Hill, 1989). Damage of this type, in the absence of other kinds of processing, is typical of a "lightly processed" carcass (Haynes, 1983).

Some transverse scratching has been attributed to trampling (Behrensmeyer and others, 1989; Fiorillo, 1988, 1989). However, trample marks are usually produced by sand grains trapped between the bone and the trampling animal's feet, as hooves and claws are not hard enough to damage bone (Marshall, 1989; Fiorillo, 1988, 1989). Such marks, along with those produced by the substrate into which a bone is pressed by animal feet, appear as abrasions rather than incisions or grooves. Features of this type were not observed within the sample. This is not surprising, because the volcaniclastic silts and clays of the Orella Member would have provided a soft substrate that would reduce the effect of trampling and are likely too fine-grained to abrade bone significantly.

Rodent Gnawing

Rodent gnawing, though less common than carnivore processing, is similar in character to transverse scratching (fig. 10B, 10J). It typically consists of single or multiple sets of paired, shallow, flat grooves oriented perpendicular to the long axis of the bone. In the Orellan sample, the individual grooves within each pair are typically 0.1-0.2 cm wide, with a 0.05-0.1 cm wide ridge between them, and they are usually less than 0.1 cm deep. They have been described as being "chiseled" in appearance, which reflects the flat cutting surface of the rodent's incisors. In this sample, rodent gnawing was most common on mammal ribs and tortoise bone and carapace, and was not restricted to specific types or sizes of bone or carapace fragments. Rodent gnawing has been observed in numerous bone assemblages but has been mistaken for transverse scratching produced by carnivores, and vice-versa (Miller, 1969, 1975; Binford, 1981; Marshall, 1989). Some rodents, such as the African porcupine *(Hystrix africae-australis)*, are well known gnawers and accumulators of bone and have been observed to produce caches of bone rivaling those of hyenas in size and diversity (Sutcliffe, 1970; Brain, 1980; Klein and Cruz-Uribe, 1984). North American porcupines *(Erithizon dorsatum)* also accumulate bones in their dens in northwestern Nebraska (R. M. Hunt, personal communication).

Breakage

Assessment of bone breakage within this sample is difficult because of the damage and fragmentation produced after the bone weathered from the bedrock. Therefore, this description will focus on qualitative aspects of bone breakage using the previously mentioned criteria. Many types of preburial breakage (see Marshall, 1989) were observed, including spiral (figs. 8G; 9B; and 10A), transverse (figs. 8C and 10B), stepped (fig. 8H), uneven (fig. 10F), longitudinal, splintered (fig. 9C), scalloped edges (fig. 9E), and rounded breaks (fig. 10E). In contrast, bone breakage following fossilization and re-exposure observed in the sample is restricted to transverse (fig. 10G) and oblique (fig. 10I) breaks.

The causes of bone breakage are more diverse than the kinds of breaks that have been observed. Many kinds of bone fractures are a function of the dryness of the bone. For example, fresh bones will form spiral fractures as a result of the orientation of the bone's internal collagen matrix, and weathered bones in which the organic content is depleted will break transversely or obliquely along lines of weakness within the bone's hydroxyapatite crystal lattices (Hill, 1980; Binford, 1981; Shipman, 1981). Furthermore, weathered bones

that have even small longitudinal cracks will produce uneven, stepped, or longitudinal fractures as the cracking increases in depth (Behrensmeyer and others, 1979; Binford, 1981). Splintered breaks are produced when highly weathered bones are broken by any number of agents (Marshall, 1989). The dryness of a bone typically determines the form of breakage when bone is damaged by trampling or post-burial compression, sediment loading, cryoturbation, shrinking and swelling of clays, and soft sediment flowage (Agenbroad, 1989; Brain, 1989; Irving and others, 1989; Steele and Carlson, 1989).

All of these types of bone breakage are also produced by mammalian carnivores, and those that are adapted for the use of bone in their diet are especially destructive to bone. For example, hyenas routinely modify large bones, producing longitudinal, splintered, transverse, uneven, and spiral fractures (Sutcliffe, 1970; Binford, 1981; Hill, 1989). Some breakage is exclusively the result of bone processing by carnivores, such as scalloped edges and rounded breaks. Scalloped edges are produced when a carnivore makes successive bites around the perimeter of a thin bone such as a scapula or innominate (fig. 9E) and the thin bone breaks rather than deforming plastically. Also, rounded breaks (fig. 10E) are produced by long-term gnawing of a bone, which commonly occurs when food resources are low or bones are available to juveniles (Sutcliffe, 1970; Haynes, 1980b, 1982; Hill, 1989). Hyenas will regurgitate ingested bone, which typically is highly fragmented and has edges rounded by corrosion by stomach acids (Sutcliffe, 1970; Hill, 1989). Based on the preserved evidence and the processing criteria of Haynes (1980a, 1983) and LaGarry (1988), the only breaks in the Sx-6 and Sx-7 samples that can be attributed to bone processing with any confidence are the previously mentioned innominate with the scalloped edges and the rib with the rounded edges.

Processing of Skeletal Elements

In general, only the most robust elements or partial elements in the Orellan sample survived processing, breakage, and weathering prior to burial (tables 3, 4). Elements having several thin processes, such as vertebrae, were reduced to cylindrical remnants prior to burial. Similarly, elements with large amounts of thin bone, such as the scapula and pelvis, were reduced to the glenoid region and acetabulum, respectively. The most broken or heavily processed elements (for example, vertebrae, scapula, pelvis, humerus, femur) are most severely weathered, while the least broken and processed elements are the least weathered (for example, astragali, metapodials, phalanges).

Based on the few available studies of successive processing of the skeletal elements of large ungulates by hyenas (*C. crocuta:* Sutcliffe, 1970; Hill, 1989) and wolves (*C. lupus:* Haynes, 1980a, 1982), the removal of the head, lateral condyle, and distal trochlea of the femur, removal or damage to the head and distal tuberosities of the humerus, the removal of the ilium and the ischium from the pelvis, removal of the blade and spinous process of the scapula, and the spalling of the proximal end of the tibia indicate a "fully" to "heavily" processed carcass. In most cases the distal limb elements survive processing because they are surrounded by a lesser volume of muscle and contain little or no trabecular bone, and therefore are less desirable food items for carnivores. In addition, they often retain their covering of sinew, hide, and hair during the processing, disarticulation, and subsequent burial of the carcass (Haynes, 1980b, 1982; Hill and Behrensmeyer, 1984).

Description of Size Categories

Based on the measurements of the postcranial bone sample, I have erected five size groups. Each group includes bones (or partial elements) of a single size class regardless of taxon. With the exception of Group III, all of these groups consist of subpopulations having a single mode (figs. 11, 12). Before assigning subpopulations to size groups, I examined the distribution of modes for all of the measured elements. Several elements, such as the proximal end of the scapula (fig. 11C) and the proximal and distal ends of the humerus (fig. 11D-E) display five or more modes representing relative size groups, with the largest subpopulation occurring near the middle of the overall size distribution. This middle group likely represents the most common body size within the fauna, and is likely dominated by medium-sized ungulates (for example, oreodonts, camels, and equids).

The dominant subpopulation was used to calibrate the remaining samples having fewer than five size categories, such as the group consisting of the cervical, thoracic, and lumbar vertebrae, the caudal vertebrae, and the distal limb elements. These elements were divided into groups based on the relative positions of the dominant mode with respect to the dominant modes in the other distributions. As a result, some elements were not assigned as many size groups as others. In the case of Group III, several indistinct modes were grouped together if larger or smaller subpopulations had counterparts in the distributions for other elements. For example, modes within the size distribution for the proximal end of the tibia (fig. 12C) were matched with similarly sized modes within the distribution for the distal end of the femur (fig. 12B). Thus, all Group II bones could be reasonably matched to potentially associated bones within the entire sample. These size groups were used to construct composite representative subsamples for "very small" (Group I), "small" (Group II), "medium" (Group III), "large" (Group IV), and "very large" (Group V) animals within the fauna (table 5).

Body sizes assigned to the Orellan fauna were based on previously published size estimates, where

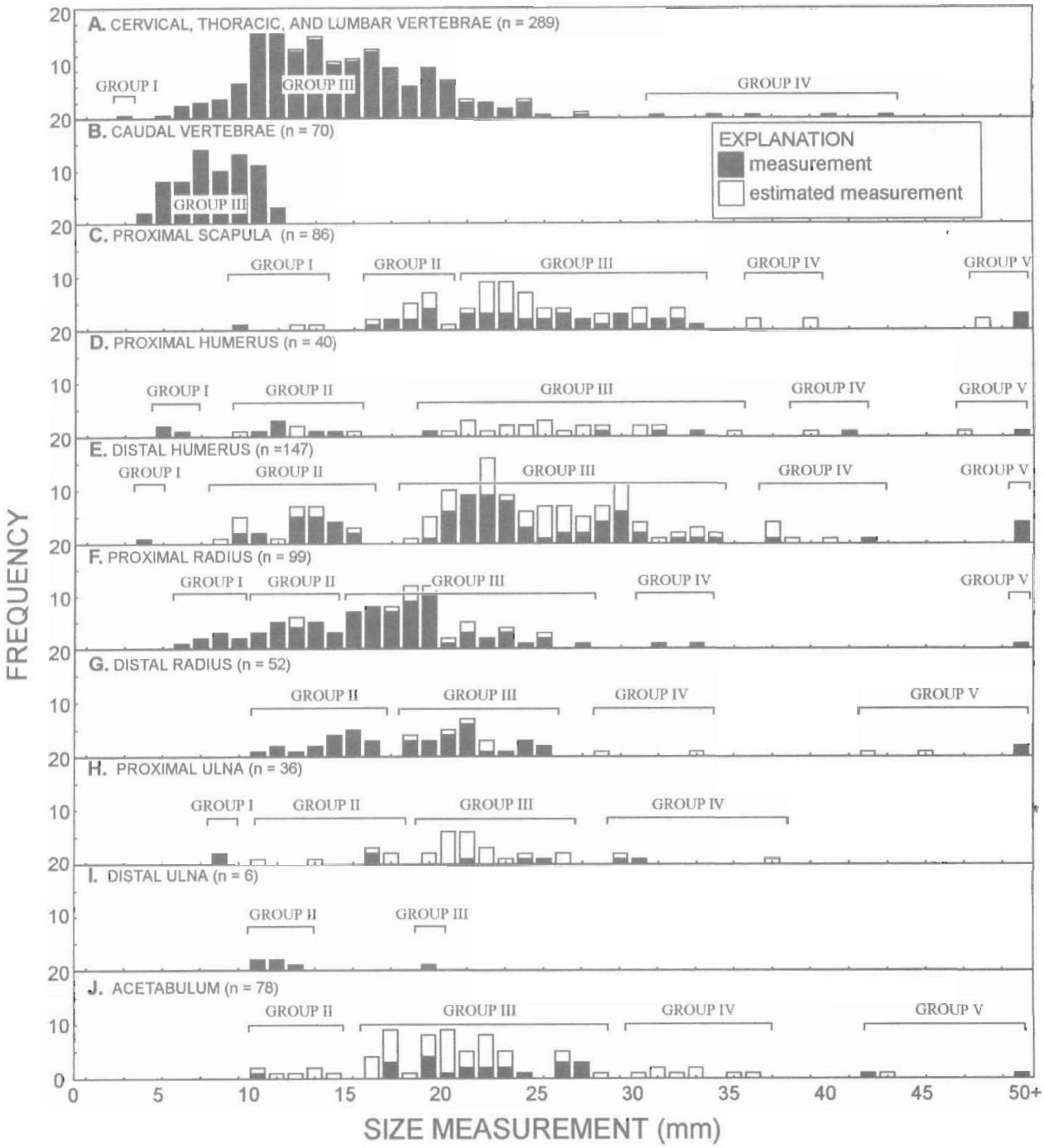


Fig. 11. Histograms derived from measurements (table 1) of bone fragments. See text for derivation of estimated values.

available, or by comparison to extant forms of about the same size and body proportions (table 5). However, the size groups used here include multiple taxa, with the number of species in each group being necessarily indeterminate. For example, bones of fetal oreodonts (cf. *Miniochoerus)* could be assigned to Group I, juveniles of the same species to Group II, and adults to Group III. The bones of taxa that are sexually dimorphic could be also placed in multiple size groups. The size groups are intended to convey a rough sense of the available body sizes contributing bones to the available "pool" for bone processing, and the sizes and group assignments for individual taxa are for the purpose of the following discussion only.

Based on body sizes assigned to the Orellan fauna, the original pool of potential prey was likely domi-

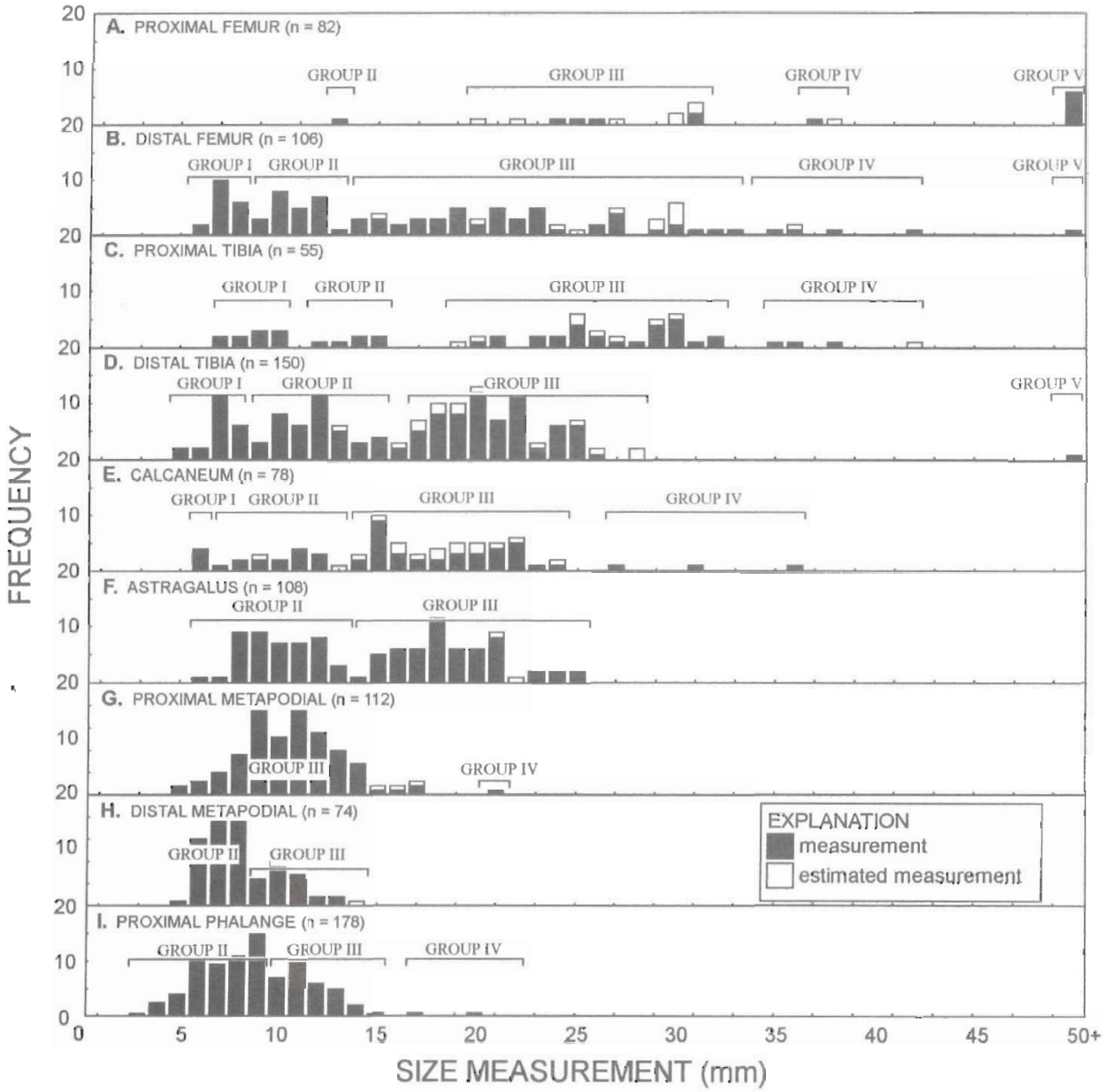


Fig. 12. Histograms derived from measurements (table 1) of bone fragments. See text for derivation of estimated values.

nated by small mammals (tables 1, 5). Based on the dentitions recovered from the "Old Floyd Hall Place," the overall distribution of body sizes within the Orellan fauna closely approximates the size distributions of animals in many modern environments, which are dominated by micromammals in both diversity and biomass (Shelford, 1964). In the absence of processes that preferentially destroy their bones, small mammals should contribute more heavily to the bone accumulating on the land surface because they typically reach sexual maturity more quickly, have larger litters, and have a shorter generation length than do larger mammals (Millar and Zammuto, 1983).

However, Groups I and II, which are based on postcranial elements rather than teeth or jaws, are severely underrepresented with respect to Group III. This is not surprising, however, because the bones of small mammals are typically preferentially destroyed by taphonomic processes prior to burial. For example, Behrensmeyer and Dechant-Boaz (1980) reported that

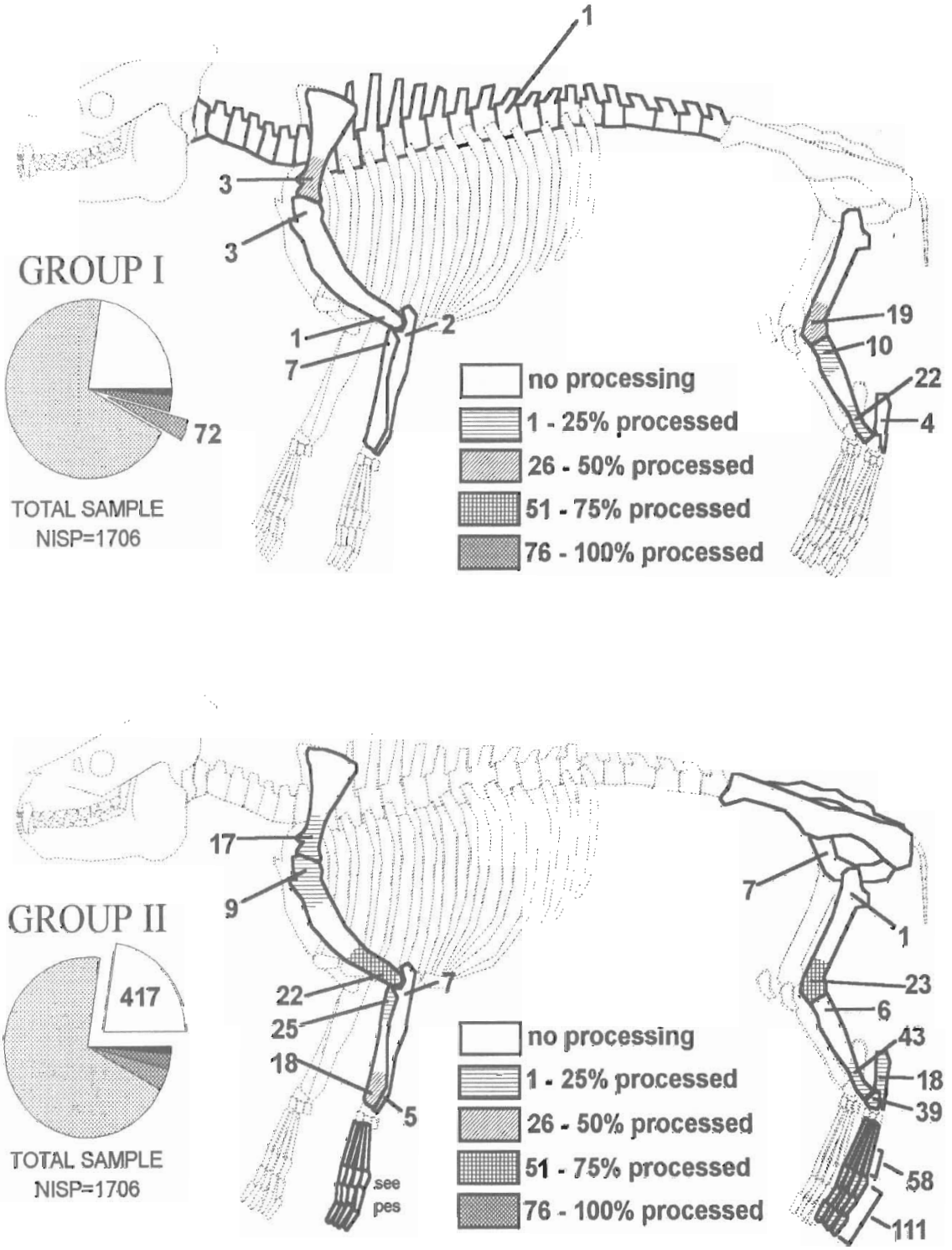
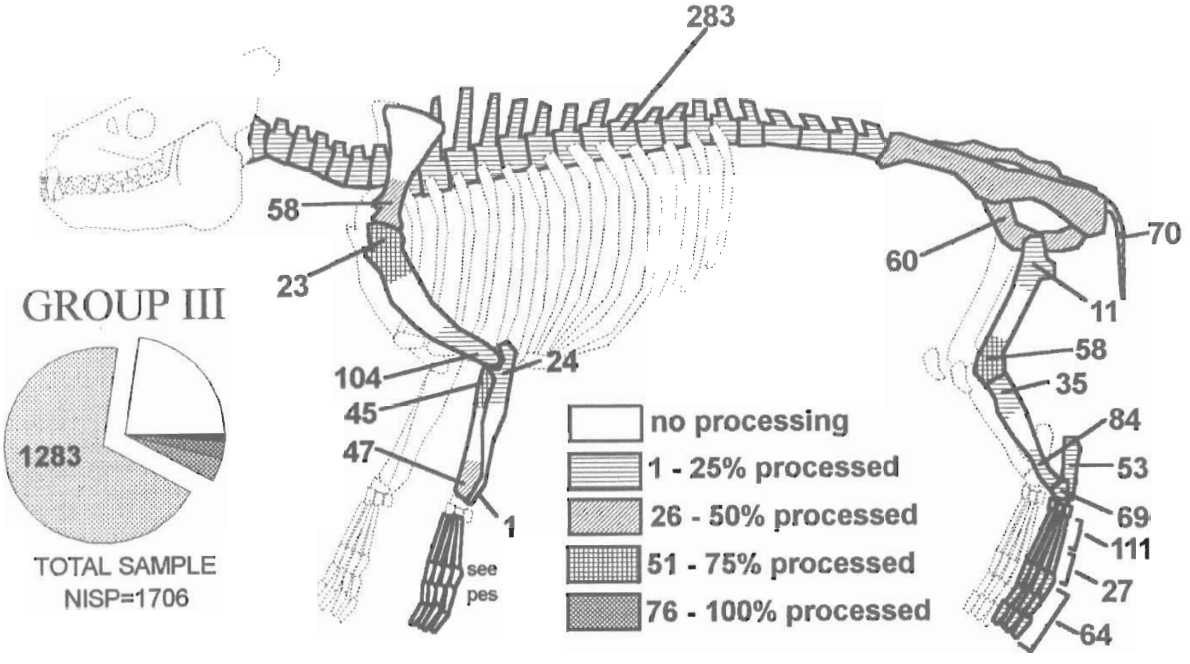


Fig. 13. Composite "skeletons" showing taxon-free groups. Dashed bones and unlabeled parts of solid bones were not present in size groups. Numerical values represent the number of identified specimens (NISP) for each size group, except value adjacent to pie slice, which is the total NISP for the size group.



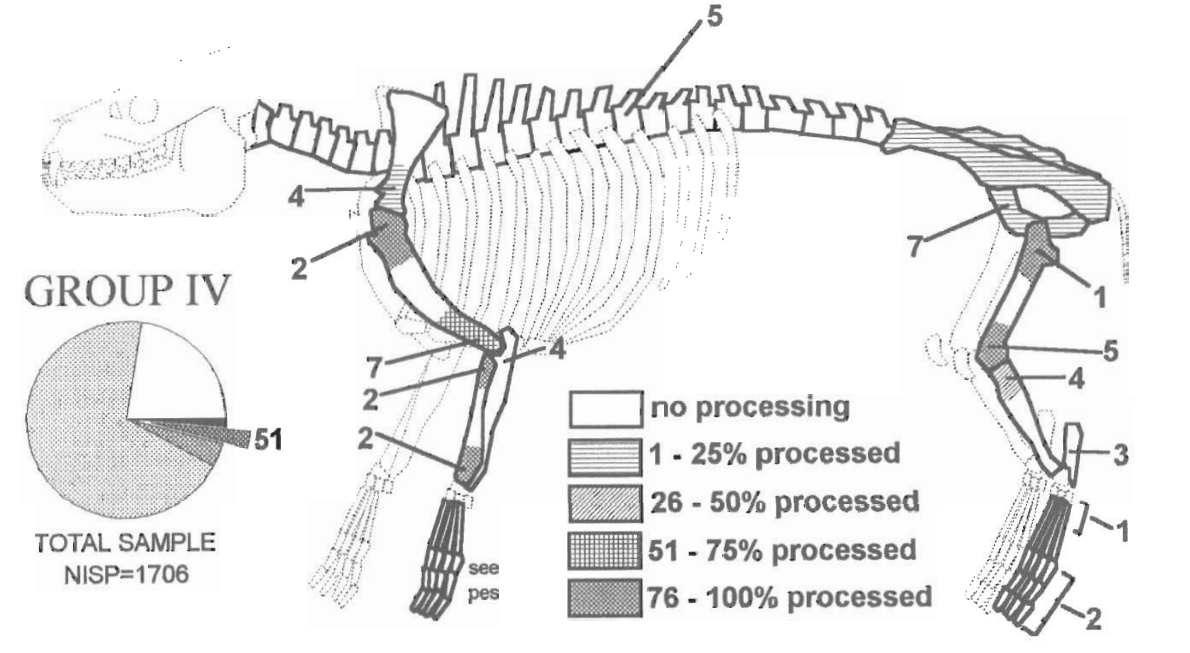


Fig. 13 (cont.). Composite "skeletons" showing taxon-free size groups. Dashed bones and unlabeled parts of solid bones were not present in the size group. Numerical values represent the number of identified specimens (NISP) for each size group, except value adjacent to pie slice, which is the total NISP for the size group.

modern East African bone assemblages were biased by the preferential destruction of smaller bones, and only taxa > 100 kg were represented in bone assemblages in the same numbers present in the living community. Animals of body sizes 15-100 kg were represented in less than expected numbers, while animals > 100 kg were represented in greater than expected numbers. Their data show that the amount of destruction increases as body size decreases (Behrensmeyer and Dechant-Boaz, 1980: fig. 5.2). Similarly, Badgely (1986) estimated that, in floodplain deposits of the Miocene Siwaliks beds of northeastern Pakistan, the subaerially

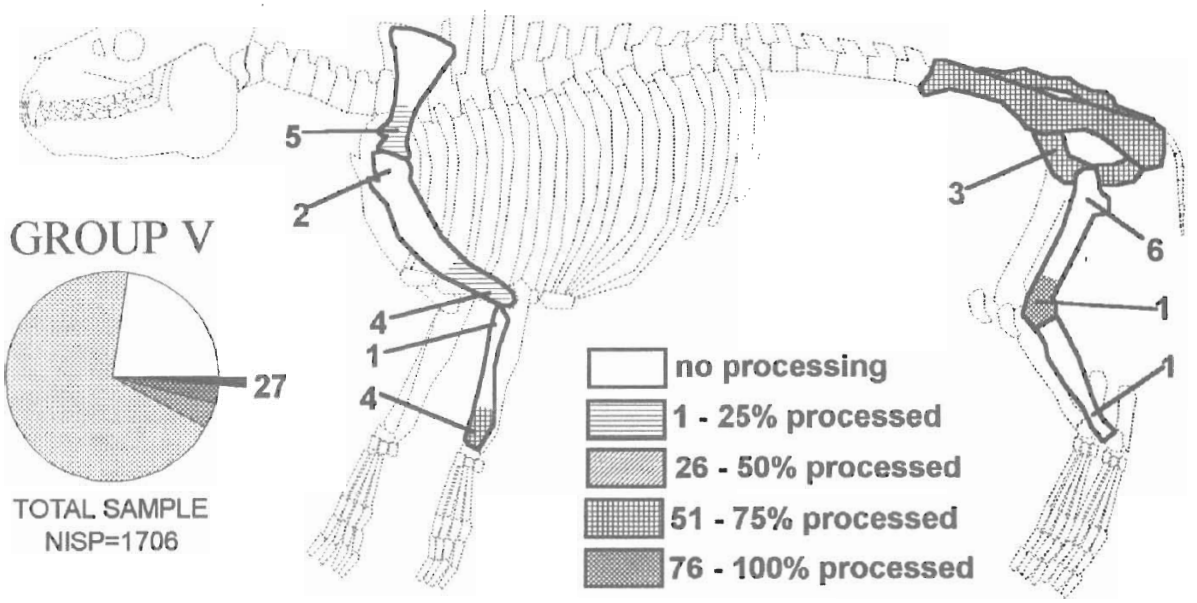


Fig. 13 (cont.). Composite "skeletons" showing taxon-free size groups. Dashed bones and unlabeled parts of solid bones were not present in the size group. Numerical values represent the number of identified specimens (NISP) for each size group, except value adjacent to pie slice, which is the total NISP for the size group. MNI = minimum number of individuals.

exposed bones of animals having body sizes < 15 kg were the first to be destroyed by weathering processes, decay, and scavenging.

Other taphonomic processes can selectively remove small bones from a bone assemblage. Voorhies (1969b) described collections from the White River Group that were dominated by squirrel-sized or smaller animals (74%: Group I), as opposed to larger animals (26%: Groups II and III). This ratio of body sizes more closely approximates that of extant mammal communities, but Voorhies considered these values to be minimum estimates because he thought his sample was winnowed by overbank floodwaters (see also Voorhies, 1969a; Behrensmeyer, 1975; Korth, 1979). Also, smaller bones are probably more damaged by weathering from the rock and subsequent exposure than are larger bones. In any case, bones of Group III are likely the best template for recording bone processing because they form the bulk of the surviving bone sample and represent a significant part of the Orellan mammal fauna.

Distribution of Processing on Size Groups

When compiled on composite "skeletons" representing each of the five size groups (fig. 13), the patterns of bone processing within each group are readily apparent. In general, bone processing was concentrated at the shoulder, elbow, wrist, hip, knee, and ankle joints, with few notable exceptions. Group I mammals show little processing of the forelimb, and were processed at the glenoid region of the scapula but not at the proximal end of the femur or at the elbow and wrist joints. The hindlimb was processed at the knee and ankle joints but not the hip joint. It is possible the scapulae were processed after disarticulation from the humerus but is more likely the lack of processed humeri results from the poor preservation of Group I elements. Group II mammals show the same overall pattern as the other groups, except none of the recovered proximal tibiae were processed. As in Group I mammals, this is likely an artifact of preservation. The pattern of bone processing at joints within the major muscle masses is clearly established in groups III-V.

Bone processing of large ungulates by extant carnivores begins during the initial feeding episode following the death of the prey, which varies widely in length, depending on the number of conspecific participants in the kill, the population density of competing predators, and the overall availability of prey resources (Mech, 1970; Kruuk, 1972, 1975; Schaller, 1972; Kingdon, 1977; Peterson, 1977). In general (see Haynes, 1980a, 1982, 1985, 1988), the initial processing is concentrated at the large pectoral and pelvic muscle masses, the nasal region, the throat and neck, the thoracic and abdominal viscera, the rump and anus, and the braincase. The initial, or "light" (terminology of Haynes, 1982) processing of a carcass incidentally damages the skeleton in these regions. Because large ungulate carcasses usually lie on their sides while being consumed by carnivores, during this initial stage the fore and hind limbs on the uppermost side of the carcass are often detached as a unit from the carcass, while

those underneath the carcass remain until later stages of processing. Processing then proceeds to more thoroughly remove flesh from these areas and continues on to areas containing less meat, such as the flanks of the vertebral column and the middle parts of the fore and hind limbs. During this stage of "moderate" or "full" processing, the glenoid region of the scapula, the proximal ends of the femur and humerus, the innominate, and the ribs are well processed. "Heavy" processing of the carcass begins when most of the meat has been removed from the skeleton, and bone becomes the primary remaining source of nutrition. It is in this stage that clearer distinctions in bone processing capabilities and indications of resource availability emerge, as the skeleton is severely damaged, or in extreme cases, completely consumed. Both the hyena (*C. crocuta)* and the wolf (*C. lupus)* routinely process prey carcasses to this degree.

Discussion

Although Orellan carnivores do not have direct analogs among the large extant carnivores typically studied in assessments of bone processing (see Van Valkenburgh, 1988), some general statements can be made about the character of the processed Orellan bone assemblage. All of the common forms of processing described by Haynes (1980a, 1983) in extant assemblages are present within the Orellan bone sample (figs. 8-10, tables 3, 4). Using the uniformitarian approach, the relative frequencies of the types of bone processing within the Orellan assemblage can be compared to assemblages processed by extant carnivorans. The Orellan assemblage is dominated by pitting, followed by spalling, transverse scratching, and gouging, and the few bones in which the entire proximal or distal end were bitten off show sharply broken edges that were not gnawed and rounded by additional processing. Haynes (1983: table 2) characterized the bone processing abilities of extant hyenas, canids, ursids, and felids based on the relative degree and frequency of bone processing they inflict, and the functional constraints of their dentition. Using the limited number of extant "styles" of processing available, the Orellan sample closely resembles "wolf-like" processing in the high degree of pitting, spalling, and transverse scratching preserved on the bone and the jagged edges remaining on bone shafts. This is in contrast to "hyena-like" processing, which proceeds past pitting and transverse scratching and is dominated by the removal of the ends of limb bones and the rounding of the edges of the remaining shaft. Some kinds of bone breakage are diagnostic of "hyena-like" processing, but the causes of breakage within the Orellan sample are unclear and may be revealed by further study. The Orellan assemblage least resembles "felid-like" processing, which is dominated by transverse scratching, knife-like pits and gouges, and bitten-off ends of limb bones.

Haynes (1983) has stated that, for extant carnivores, in order for a carcass or carcass assemblage to contain species-diagnostic damage, it must be heavily processed. This is because most carnivores are capable of inflicting light amounts of processing, whereas few species have sufficient size and jaw strength to heavily process a bone assemblage. Also, many carnivores are capable of inflicting haphazard damage to a bone assemblage, whereas intensive processing can reveal species-diagnostic patterns. However, because Orellan carnivores do not have direct extant analogs (see Van Valkenburgh, 1988), it is doubtful that species-diagnostic processing, if present in the Orellan sample, would be recognized. However, the relative degree of processing recorded on the Orellan sample can be compared to that inflicted by extant bone processing carnivores.

Processing increases (from "light" to "moderate" or "moderate" to "heavy") when there are more predators using a carcass or when prey are less available (Haynes, 1980b, 1982). Also, some taxa characteristically inflict greater amounts of processing with less effort, such as the difference between processing by felids, wolves, and hyenas. The Orellan sample, based on the amount of "moderately" and "heavily" processed bones (tables 3, 4), likely represents a composite sample having an average state of "moderate" or "full" processing.

What may not be readily appreciated is that the recording of carnivore-induced processing is a function of scale. For example, hyenas, lions, wolves, and bears routinely process the bones of bison, caribou, water buffalo, and other large ungulates. If the only prey carcasses available to such large carnivores were oreodont-sized, these smaller carcasses might be consumed entirely and no "residue" of the carcass would be available for burial, fossilization, and subsequent study. Carcass remnants such as those in the Oligocene assemblage studied here (table 5) could be "heavily" processed by proportionately smaller carnivores.

Recognition of types, amounts, and degrees of processing is a useful first step in the analysis of bone modification. However, any discussion of bone processing would be remiss without exploring the identity of potential bone processors. Although extant carnivores differ in size, feeding habits, jaw strength, and tooth design, Binford (1981) hypothesized that bone modification patterns will not vary between species; rather the magnitude of the capability to process bone will be the primary variable. In contrast, Haynes (1980b, 1983) argued that this may be an overly simplistic assumption. Because of the highly variable dentitions within extant families of carnivores, Haynes (1983) was able to identify types and frequencies of damage diagnostic at the level of family. The variation in the dentitions of extinct carnivore leaves open the possibility of diagnosing some types of processing based on dental anatomy alone. The following discussion addresses this possibility with regard to Orellan

carnivores.

The Orellan carnivore guild is well known from dental, cranial, and postcranial material (Mellet, 1977; Wang, 1994; Baskin and Tedford, 1996; Bryant, 1996; Hunt, 1996; Wang and Tedford, 1996), and based on their dentitions some carnivores may be deemed more or less likely to have processed the Orellan bone assemblage. The creodonts *Hyaenodon horridus* and *H. crucians* have dentitions consisting of large incisors, massive canines, robust premolars, and bladelike molars. These teeth would likely produce a processing signature resembling a blending of "felid-like" and "hyena-like" features, such as large conical pits (premolars), large punctures (canines), wide and shallow (premolars) or knife-like gouges (molars), and bitten-off ends of limb bones (molars). The nimravids *Hoplophoneus primaevus*, *H. occidentalis*, and *Dinictis felina* have dentitions consisting of small incisors, saber-like canines, reduced premolars, and bladelike carnassials. These taxa would likely produce a "felid-like" processing signature because their teeth closely resemble those of extant felids, except that it is unlikely that their large canines could be used to process bone (eliminating conical pitting and canine-induced gouging). Also, their canines would likely restrict the use of their incisors (less transverse scratching). The canids *Hesperocyon* (jackal-sized) and *Mesocyon* sp. (fox-sized), and the amphicyonids *Daphoenus hartshornianus* (fox-sized) and *D. vetus* (coyote-sized) have dentitions consisting of moderately sized incisors, canines, premolars, and molars, much like small wolves or coyotes. Based on the anatomy of their teeth, these taxa would likely produce a "wolf-like" processing signature, albeit on a smaller scale.

These conclusions are supported by Van Valkenburgh (1988) who, based on comparisons to the dental anatomy of trophic guilds of extant carnivorans, characterized the hyaenodonts and nimravids as having diets consisting of 70-100% meat, and the amphicyonids having diets consisting of 50-70% meat, with the remainder consisting of fruit and insects. Her analysis indicates a high degree of meat specialization on the part of hyaenodonts and nimravids, and generalist feeding habits on the part of amphicyonids. In the same analysis, she characterizes the extant wolf as a meat specialist, but much of the work cited herein has demonstrated that wolf-like dentitions are easily capable of processing bone. Interestingly, based on Van Valkenburgh's (1988) analysis, the Orellan carnivore guild lacked a species being functionally adapted, like modem hyenas, for the processing of bone and having bone as a major part of its diet. Based on the results of this study, such a taxon need not have been present for Orellan bone to be processed. In addition, wear patterns on the premolars of hyaenodonts suggest that they were durophagous and likely filled this niche.

Based on the preceding descriptions of the processed bone assemblage, the discussions of the character of the "style" and degree of processing, and the suites of potential processing signatures described above, it is possible to suggest the dominant bone processors of the Orellan sample. The dominance of conical pitting, spalling, transverse scratching, and the small amounts of gouging and severed ends of limb bones indicate a "wolf-like," or perhaps more correctly, "canid-like" style of processing dentions. Furthermore, the presence of tiny conical pits on Group I bones, and proportionately larger conical pits on Group II, III, and IV bones, indicate that several taxa having similar dentitions were the processors of the Orellan bone. It seems likely then that the Orellan carnivores with the most canid-like dentitions, namely *Hesperocyon*, *Mesocyon*, *Daphoenus hartshornianus*, and *Daphoenus vetus*, were the dominant processors of the Orellan sample. It is surprising that the Orellan assemblage did not display a more "hyena-like" signature, as would be expected with the durophagous hyaenodonts in the fauna. However, hyaenodonts may have had a low population density, may have processed bone completely, leaving no "residue," or may not have frequented the floodplain environment relative to the other bone processors.

Whether these animals processed the Orellan bone assemblage during the initial feeding, or contributed to the overall processing over a long period of time by systematically or haphazardly scavenging is unclear. Some studies of bone processing by extant carnivores have been able to distinguish between predation and scavenging (Haynes, 1980, 1982, 1983) while others have not (Miller, 1969; Sutcliffe, 1970). Kingdon (1977) stated that in attritional carcass assemblages, the results of predation and scavenging are inseparable. However, this study indicated that Oligocene carnivores targeted highly nutritive skeletal parts for consumption as do many modern carnivorans. The matter of whether or not these taxa were scavengers is a subject for additional study.

The reliability of the conclusions reached in this study and the level of resolution are conditioned to some degree by the amount of time averaging present within the sequence of depositional environments from which the fossils were collected. Also, in any paleoecological reconstruction, the limits imposed by taphonomic biases on the inferences and interpretations drawn from taphonomic data must be addressed before making broader generalizations. Many taphonomic processes can bias a fossil sample prior to its discovery and study (see Olson, 1980; Shipman, 1981; Marshall, 1989). Such biases are introduced by: 1) the mode of death; 2) destructive forces after death but prior to burial; 3) burial processes; 4) diagenesis; 5) exhumation and exposure; and 6) discovery and collection. In this study, (1) was of no concern because bone processing is a distinctly post-mortem process.

Consideration of (2) was the principal emphasis of this study. I attempted to reduce or eliminate (5)

and (6) by using a sampling method that retrieved all of the fossil material, or as much of it as could be acquired. The two biases of concern, then, are (3) and (4).

Voorhies (1969b) stated that the most reliable paleoecological reconstructions are those based upon collections from thin but widespread floodplain deposits of relatively uniform lithology, such as those of the White River Group. This view was shared by Edwards and Yatkola (1974), who attributed the excellent preservation of coprolites within the Orella Member to be partly due to the fine-grained sediments, the relatively low energy of the depositional environment, and the contribution of eolian volcaniclastic sediment to the burial and subsequent fossilization of coprolites. According to Badgely (1986), vertebrate fossil samples from floodplain deposits are largely autochthonous, having accumulated in place with a minimum of preburial transport, and typically better represent the range of body sizes present in ancient communities. While the fine-grained volcaniclastic deposits making up the Orella Member may not exactly correspond to the epiclastic fine-grained sediments of most modern floodplains in the style of sedimentation, the preservation of mammal bone in these settings probably is generally comparable. Episodic, low-energy sheet flow over level surfaces by water moving silt- and clay-sized sediment is common to both environments.

The low energy of Orellan floodplain deposits explains how Edwards and Yatkola (1974) were able to recover *in situ* clusters of coprolites preserved in their original orientations. They commented that these coprolites, which were originally soft enough to record the outlines of the vegetation on which they were dropped, would not have remained intact and undisturbed under any but the lowest energy conditions. These observations indicate that, in terms of the area sampled, deposition of the Orella Member did not significantly bias the bone assemblage with the exception of possibly winnowing Group I bones from the sample locality (see previous discussion).

In her study of time averaging in fluvial assemblages, Behrensmeyer (1982) estimated that for a floodplain assemblage, the amount of time involved approximates 100-10,000 years, and is in large part a function of the length of time present within each diastem, or the interval between flooding events that bury the bone that has accumulated on the land surface. Based on paleosols, the Scenic Member of Brule Formation in the Big Badlands of South Dakota, which is similar to the Orella Member in age, stratigraphic position, lithology, and depositional environment (Clark and others, 1967; LaGarry, 1998), required a minimum of 81,700 years to be deposited and pedogenically modified (Retallack, 1983). The "entisols" and "inceptisols" within the Scenic Member likely supported herbaceous and early successional vegetation. Terry and others (1995) recognized only "entisols" within the overbank clayey siltstones and silty claystones of the Orella Member, suggesting that the development of vegetation and the time occurring between flood events was about of equivalent duration. Based on radiometrically dated ashes and magnetostratigraphic correlations, the Orellan NALMA lasted 1.7 million years (Prothero and Whittlesey, 1998), and although no correspondence between the Orella Member and the Orellan NALMA is implied here, these values serve to constrain the duration of the period of accumulation for the Orellan sample studied here.

Summary and Conclusions

In this paper I have shown that the large, likely autochthonous sample of coprolites and postcranial bone fragments from the Orella Member of the Brule Formation at UNSM localities Sx-6 and Sx-7 had been processed during the early Oligocene by mammalian carnivores over a period of more than 80,000 but less than 1.7 million years. Based on the degree of bone breakage, corrosion by stomach acids, bone articulation, skeletal part representation, and prey fauna composition, the Orellan coprolites were probably produced by a carnivore having a body size and feeding habits similar to the coyote, *Canis latrans*. Based on the body sizes and dentitions within the Orellan carnivore guild, the large amphicyonid *Daphoenus vetus* probably produced most of the coprolites. Based on the frequency and style of bone processing observed in a large sample of postcranial fragments from the same interval and locality, the bone assemblage was moderately processed by carnivores of several body sizes having canid-like dentitions, that exhibited "wolf-like" processing behaviors.

Based on body sizes and dentitions within the Orellan carnivore guild, the canids *Hesperocyon* and *Mesocyon*, and the amphicyonids *Daphoenus hartshornianus* and *D. vetus* likely produced most of the bone processing observed in the sample. The uniformitarian approach is limited in its application in this study because the Orellan and extant carnivoran faunas are not directly analogous. This study has demonstrated, however, that such direct evidence as tooth marks is, once recognized, sufficient to establish which taxa and size categories were processed, to what degree the bones were processed, characterize bone processing in terms of an extant bone processor, and indicate which taxa are the likeliest bone processors.

Haynes (1980b) stated that extant carnivores, like humans, leave enduring evidence of their behavior in the bone residues they produce — these residues can reflect the carnivore's ethology and the availability of animals making up the residue. His studies have shown that different living carnivore species can damage bones distinctively because of anatomical, me-

chanical, and behavioral differences, and each may have a processing signature. However, if extinct carnivores had such processing signatures, the bone residue preserved in the rock record is likely a composite of all of the processing that occurred in the vicinity and interval being sampled. Thus, all such assemblages are likely to contain a mixed signal reflecting bone processing by all species having access to the unburied bone. Since the discovery of individual kill sites are unlikely (see comments by Haynes, 1988), the consistent use of a region over long periods of time may leave a residue reflecting the habits and preferences of the species contributing most regularly to the processing of the composite assemblage. At best, only the activities of the dominant processor may be recovered. However, if past carnivores selected particular size groups of prey, and the sample can be divided into the appropriate size groups, the signature of the dominant processor of each size group may be revealed by careful analysis.

In the concluding section of "Fossils in the Making," Behrensmeyer and Hill (1980) commented:

> *New field sampling programs . . . are essential to the growth of paleoecology. There is a need for more large, carefully documented fossil samples from single localities, and there is also a need for multiple smaller samples that can reveal persistent patterns of skeletal part and taxonomic occurrences. Quarriable bone concentrations often result from unusual circumstances of death and burial, and thus may be limited in their representation of original paleocommunity characteristics. . . . Smaller samples which tap the 'background' of fossil occurrences in a deposit can provide a different kind of sample, perhaps containing more reliable information on the original overall community.*

This study was an initial attempt at using such a "background" sample to examine the composite residue left by Oligocene carnivores. While this study is necessarily limited in the amount of detail that can be revealed, this approach provides a method for inferring aspects of the behavior of extinct carnivores that would otherwise be unavailable for study. The application of the methods described here to other stratigraphically and geographically restricted bone samples may reveal patterns of bone processing that are of general paleoecologic and taphonomic importance.

Acknowledgments

This work would not have been possible without the understanding and cooperation of Mr. Bruce Quintard, owner of the "Old Floyd Hall Place." I thank N. C. Guyon, W. B. Wells, M. R. Myers, and C. E. Rudnick for their assistance in collecting the samples used in this study. I thank Rob Skolnick for the preparation of the fossil material within the coprolites. I thank J. A. Kinsey for assistance measuring coprolites, and L. A. LaGarry for assistance measuring the large sample of mammalian bones. I thank R. M. Hunt, Jr. and B. E. Bailey for help identifying the rarer taxa from the "Old Floyd Hall Place." This research was supported by Challenge Cost-Share Agreements 02-07-91-013, 02-07-92-025, 02-07-93-011, and 02-07-94-015 between the Nebraska National Forest and the University of Nebraska-Lincoln; the Conservation and Survey Division's STATEMAP project; the University of Nebraska State Museum's M. E. Green Fieldwork Scholarship; and the Nebraska Geological Society's Yatkola-Edwards Research Grant. This research was part of a doctoral dissertation supervised by R. M. Hunt, Jr. at the University of Nebraska-Lincoln. R. M. Hunt, Jr., M. R. Voorhies, D. A. Loope, A. Joern, R. J. Zakrzewski, L. A. LaGarry, A. R. Fiorillo, and C. A. Flowerday reviewed the manuscript.

References

Agenbroad, L. D., 1989, Spiral fractured mammoth bone from nonhuman taphonomic processes at Hot Springs Mammoth Site, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 139-148.

Andrews, P., and Nesbit-Evans, E. M., 1983, Small mammal bone accumulations produced by mammalian carnivores: Paleobiology, v. 9, p. 289-307.

Badgely, C., 1986, Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan: Paleobiology, v. 12, p. 119-142.

Baskin, J. A., and Tedord, R. H., 1996, Small arctoid and feliform camivorans, *in* Prothero, D. R., and Emry, R. J., eds.,. The Terrestrial Eocene-Oligocene Transition in North America: Cambridge University Press, Cambridge, United Kingdom, p. 486-497

Behrensmeyer, A. K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: Bulletin of the Museum of Comparative Zoology, v. 146, p. 473-578.

_____, 1978, Taphonomic and ecologic information from bone weathering: Paleobiology, v. 1, p. 150-162.

_____, 1982, Time resolution in fluvial vertebrate assemblages: Paleobiology, v. 8, p. 211-227.

Behrensmeyer, A. K., and Dechant-Boaz, D. E., 1980, The recent bones of Amboseli Park, Kenya, in relation to East African Paleoecology, *in* Behrensmeyer, A. K., and Hill, A. P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 72-92.

Behrensmeyer, A. K., Gordon, K. D., and Yanagi, G. T., 1989, Nonhuman bone modification in Miocene fossils from Pakistan, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 99-120.

Behrensmeyer, A. K., and Hill, A. P., 1980, Conclusion; *in* Behrensmeyer, A. K., and Hill, A. P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 299-305.

Behrensmeyer, A. K., and Kidwell, S. M., 1985, Taphonomy's contributions to paleobiology: Paleobiology, v. 11, p. 105-119.

Behrensmeyer, A. K., Western, D., and Dechant-Boaz, D., 1979, New perspectives in vertebrate paleoecology from a recent bone assemblage: Paleobiology, v. 5, p. 12-21.

Binford, 1981, Bones: Ancient Men and Modern Myths: Academic Press, New York, 320 p.

Brain, C. K., 1980, Some criteria for the recognition of bone-collecting agencies in African caves, *in* Behrensmeyer, A. K., and Hill, A. P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 108-130.

Bryant, H. R., 1996, Nimravidae, *in* Prothero, D. R., and Emry, R. J., eds., The Terrestrial Eocene-Oligocene Transition in North America: Cambridge University Press, Cambridge, United Kingdom, p. 453-475.

Clark, J., 1937, The stratigraphy and paleontology of the Chadron Formation in the Big Badlands of South Dakota: Carnegie Museum Annals, v. 25, p. 261-350.

_____, 1954, Geographic designation of the members of the Chadron Formation in South Dakota: Carnegie Museum Annals, p. 197-198.

Clark, J., Beerbower, J. R., and Kietzke, K. K., 1967, Oligocene sedimentation, stratigraphy, paleoecology, and paleoclimatology in the Big Badlands of South Dakota: Fieldiana Geology Memoirs, v. 5, 157 p.

Damuth, J., 1990, Problems in estimating body masses of archaic ungulates using dental measurements, *in* Damuth, J., and MacFadden, B. J., eds., Body Size in Mammalian Paleobiology: Cambridge University Press, Cambridge, United Kingdom, p. 229-254.

Darton, H. H., 1899, Preliminary report on the geology and water resources of Nebraska west of the one hundred and third meridian, *in* United States Geological Survey Nineteenth Annual Report 1897-1898, pt. 4, p. 719-814.

Driesch, A., von den, 1976, A guide to the measurement of animal bones from archaeological sites: Peabody Museum Bulletin 1, 135 p.

Edwards, P., 1973a, A qualitative comparison of the chemical composition of recent feces and coprolites: Proceedings of the 83rd Annual Nebraska Academy of Sciences, p. 32.

_____, 1973b, Qualitative x-ray diffraction and x-ray fluorescence analysis of some Oligocene coprolites: Contributions to Geology, v. 12, p. 25.

Edwards, P., and Yatkola, D., 1974, Coprolites of White River (Oligocene) carnivorous mammals – origin and paleoecologic and sedimentologic significance: Contributions to Geology, v. 13, no. 2, p. 67-73.

Emry, R. J., Bjork, P. R., and Russell, L. S., 1987, The Chadronian, Orellan, and Whitneyan North American land mammal ages, *in* Woodburne, M. O., ed., Cenozoic Mammals of North America: Geochronology and Biostratigraphy: University of California Press, Berkeley, p. 118-152.

Evanoff, E., Prothero, D. R., and Lander, R. H., 1992, Eocene-Oligocene climatic change in North America: the White River Formation near Douglas, east-central Wyoming, *in* Prothero D. R., and Berggren, W. A., eds., Eocene-Oligocene Climatic and Biotic Evolution: Princeton University Press, Princeton, New Jersey, p. 116-130.

Falkenbach, C. H., and Schultz, C. B., 1951, Suggested correlations of the Oligocene of Nebraska and South Dakota: Fifth Field Conference of the Society of Vertebrate Paleontology Guidebook, p. 47-50.

Fiorillo, A. R., 1988, Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska: Contributions to Geology, v. 26, p. 57-97.

_____, 1989, An experimental study of trampling – implications for the fossil record, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 61-72.

Gifford-Gonzalez, D., 1989, Overview – modern analogs: developing an interpretive framework, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 42-52.

Gingerich, P. D., 1989, New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming – composition and diversity in a rarely sampled high-floodplain assemblage: University of Michigan Papers in Paleontology, v. 28, 98 p.

Harvey, C., 1960, Stratigraphy, sedimentation, and environment of the White River Group of the Oligocene of northern Sioux County, Nebraska: doctoral dissertation, University of Nebraska-Lincoln, 151 p.

Hatcher, J. B., 1893, The *Titanotherium* beds: American Naturalist, v. 27, p. 204-221.

Haynes, G., 1980a, Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones: Paleobiology, v. 6, p. 341-351.

_____, 1980b, Prey bones and predators – Potential ecologic information from analysis of bone sites: Ossa, v. 7, p. 75-97.

_____, 1982, Utilization and skeletal disturbance of North American prey carcasses: Arctic, v. 35, p. 266-281.

_____, 1983, A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones: Paleobiology, v. 9, p. 164-172.

_____, 1985, On watering holes, mineral licks, death, and predation, *in* Mead, J., and Meltzer, D., eds., Environments and Extinctions – Man in Late Gla-

cial North America: Center for the Study of Early Man, Orono, Maine, p. 53-71.

_____, 1988, Mass deaths and serial predation – comparative taphonomic studies of modern large mammal death sites: Journal of Archaeological Science, v. 15, p. 219-235.

Hill, A., 1976, On carnivore and weathering damage to bone: Current Anthropologist, v. 17, p. 335-336.

_____, 1979, Disarticulation and scattering of mammal skeletons: Paleobiology, v. 5, p. 261-274.

_____, 1980, Early post-mortem damage to the remains of some contemporary East African mammals, *in* Behrensmeyer, A. K., and Hill, A. P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 131-152.

_____, 1989, Bone modification by modem spotted hyenas, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 169-178.

Hill, A., and Behrensmeyer, A. K., 1984, Disarticulation patterns of some modern East African mammals: Paleobiology, v. 10, p. 366-376.

Hunt, R. M., Jr., 1978, Depositional setting of a Miocene mammal assemblage, Sioux County, Nebraska (U.S.A.): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 24, p. 1-52.

_____, 1988, Report on paleontological excavations at Agate Fossil Beds National Monument undertaken by the University of Nebraska State Museum from June 25, 1985 to August 16, 1986: National Park Service/University of Nebraska-Lincoln (Supplemental Agreement No. CA-6000-5-8032), 60 p.

_____, 1990, Taphonomy and sedimentology of Arikaree (lower Miocene) fluvial, eolian, and lacustrine paleoenvironments, Nebraska and Wyoming – a paleobiota entombed in fine-grained volcaniclastic rocks, *in* Lockley, M., and Rice, A., eds., Volcanism and Fossil Biotas: Geological Society of America Special Paper 244, p. 69-111.

_____, 1996, Amphicyonidae, *in* Prothero, D. R., and Emry, R. J., eds., The Terrestrial Eocene-Oligocene Transition in North America: Cambridge University Press, Cambridge, United Kingdom, p. 476-485.

Irving, W. N., Jopling, A. V., and Kritsch-Armstrong, I., 1989, Studies of bone technology and taphonomy, Old Crow Basin, Yukon Territory, *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 347-380.

Janis, C. M., 1990, Correlation of cranial and dental variables with body size in ungulates and macropodoids, *in* Damuth, J., and MacFadden, B. J., eds., Body Size in Mammalian Paleobiology: Cambridge University Press, Cambridge, United Kingdom, p. 255-300.

Kingdon, J., 1977, East African Mammals IIIa – Carnivores: Academic Press, New York, 476 p.

Klein, R. G., 1982, Age (mortality) profiles as a means of distinguishing hunted species from scavenged ones in ancient communities: Paleobiology, v. 8, p. 151-158.

_____, 1983, The computation of ungulate age (mortality) profiles from dental crown heights: Paleobiology, v. 9, p. 70-78.

_____, and Cruz-Uribe, K., 1984, The analysis of animal bones from archeological sites: University of Chicago Press, Chicago, 266 p.

Korth, W. W., 1979, Taphonomy of microvertebrate assemblages: Carnegie Museum Annals, v. 48, p. 235-285.

Kruuk, H., 1972, The spotted hyena – a study of predation and social behavior: University of Chicago Press, Chicago, 335 p.

_____, and Turner, M., 1967, Comparative notes on predation by lion, leopard, cheetah, and wild dog in the Serengeti area, East Africa: Mammalia, v. 31, p. 1-27.

LaGarry, H. E., 1988, Taphonomic evidence of predation and scavenging of *Teleoceras* (Mammalia: Rhinocerotidae), with a description of the Camelidae from the Minium Quarry local biota of north-central Kansas: master's thesis, Fort Hays State University, Hays, Kansas, 78 p.

_____, 1998, Lithostratigraphic revision and redescription of the Brule Formation (White River Group), northwestern Nebraska, *in* Terry, Jr., D. O., LaGarry, H. E., and Hunt, R. M. Jr., eds., Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene of North America): Geological Society of America Special Paper 325, p. 63-92.

LaGarry, H. E., and Hunt, R. M., Jr., 1992, 1991 Paleontological resource survey of the Oglala National Grassland (Roundtop 7.5' Quadrangle), Sioux County, Nebraska: USDA Forest Service/University of Nebraska-Lincoln, Challenge Cost-Share Agreement No. 02-07-91-013, 26 p.

LaGarry, H. E., and Hunt, R. M., Jr., 1993, 1992 Paleontological resource survey of the Oglala National Grassland (Roundtop, Horn, and Orella 7.5' Quadrangles), Sioux and Dawes counties, Nebraska. USDA Forest Service/University of Nebraska-Lincoln, Challenge Cost Share Agreement No. 02-07-92-025, 65 p.

LaGarry, H. E., and LaGarry, L. A., 1997a, Geologic map of the Sherrill Hills (Wyoming-Nebraska) USGS 7.5' quadrangle: University of Nebraska-Lincoln Conservation and Survey Division Open-File Map No. 53, 1:24,000 map and explanatory booklet.

_____, 1997b, Geologic map of the Bodarc (Nebraska) USGS 7.5' quadrangle: University of Nebraska-Lincoln Conservation and Survey Division Open-File Map No. 61, 1:24,000 map and explanatory booklet.

_____, 1997c, Geologic map of the Chadron West (Nebraska) USGS 7.5' quadrangle: University of Ne-

braska-Lincoln Conservation and Survey Division Open-File Map No. 65, 1:24,000 map and explanatory booklet.

_____, 1997d, Geology of the Montrose, Orella, Wolf Butte, Roundtop, and Horn 7.5' USGS quadrangles, Sioux and Dawes counties, Nebraska: University of Nebraska-Lincoln Conservation and Survey Division Open-File Report No. 48, 156 p.

Legendre, S., 1986, Analysis of mammalian communities from the late Eocene and Oligocene of southern France: Palaeovertebrata, v. 18, p. 191-212.

Legendre, S., and Roth, C., 1988, Correlation of carnassial tooth size and body weight in recent carnivores: Historical Biology, v. 1, p. 85-98.

Marshall, L., 1989, Bone modification and the "laws of burial;" *in* Bonnichsen, R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 7-26.

Matthew, W. D., 1899, A provisional classification of the freshwater Tertiary of the west: American Museum of Natural History Bulletin, v. 12, p. 19-75.

_____, 1909, Faunal lists of the Tertiary Mammalia of the west: U. S. Geological Survey Bulletin, v. 361, p. 91-138.

Mech, L. D., 1970, The Wolf – Ecology and Behavior of an Endangered Species: Natural History Press, New York, 384 p.

Meek, F. B., and Hayden, F. V., 1857, Descriptions of new species and genera of fossils, collected by Dr. F. V. Hayden in Nebraska Territory, with some remarks on the Tertiary and Cretaceous formations of the northwest, and the parallelism of the latter with those of other portions of the United States and Territories: Proceedings of the Academy of Natural Science of Philadelphia for 1857, p. 117-148.

_____, 1861, Descriptions of new Lower Silurian (primordial), Jurassic, Cretaceous, and Tertiary fossils, collected in Nebraska, by the exploring expedition under the command of Capt. Wm. F. Raynolds, U. S. Topographical Engineer, with some remarks on the rocks from which they were obtained: Proceedings of the Academy of Natural Science of Philadelphia, v. 13, p. 415-447.

Mellet, J. S., 1974, Scatological origin of microvertebrate fossil accumulations: Science, 185, p. 349-350.

_____, 1977, Paleobiology of North American *Hyaenodon* (Mammalia: Creodonta): Contributions to Vertebrate Evolution, v. 1, p. 1-134.

Millar, J. S., and Zammuto, R. M., 1983, Life histories of mammals – an analysis of life tables: Ecology, v. 64, p. 631 -635.

Miller, D. R., 1979, Wolf-caribou-human interactions on the taiga of north-central Canada during winter, *in* Klinghammer, E., ed., The Behavior and Ecology of Wolves: Garland STPM Press, New York, p. 93-116.

Miller, G., 1969, A study of cuts, grooves, and other marks on recent and fossil bone, I – animal tooth marks: Tebiwa, v. 12, p. 20-26.

_____, 1975, A study of cuts, grooves, and other marks on recent and fossil bone, II – weathering cracks, fractures, splinters, and other natural phenomena, *in* Swanson, E., ed., Lithic Technology: Moulton Publishing, The Hague, Netherlands, p. 211-226.

Olson, E. C., 1980, Taphonomy – its history and role in community evolution, *in* Behrensmeyer, A. K., and Hill, A. P., eds., Fossils in the Making: University of Chicago Press, Chicago, p. 5-19.

Osborn, H. F., 1929, Titanotheres of ancient Wyoming, Dakota, and Nebraska: U. S. Geological Survey Monograph 55, 953 p.

Peterson, R. O., 1977, Wolf ecology and prey relationships on Isle Royal: National Park Service Scientific Monograph Series, v. 11, p. 1-210.

Prothero, D. R., 1994, The Eocene-Oligocene Transition: Columbia University Press, New York, 291 p.

Prothero, D. R., and Emry, R. J., 1996, The Terrestrial Eocene-Oligocene Transition in North America: Cambridge University Press, Cambridge, United Kingdom, 690 p.

Prothero, D. R., and Swisher, C. C., III, 1992, Magnetostratigraphy and geochronology of the terrestrial Eocene-Oligocene transition in North America, *in* Prothero, D. R., and Berggren, W. A., eds., Eocene-Oligocene Climatic and Biotic Evolution: Princeton University Press, Princeton, New Jersey, p. 46-73.

Prothero, D. R., and Whittlesey, K. E., 1998, Magnetic stratigraphy and biostratigraphy of the Orellan and Whitneyan land mammal "ages" in the White River Group, *in* Terry, D. O., Jr., LaGarry, H. E., and Hunt, R. M., Jr., eds., Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene of North America): Geological Society of America Special Paper 325, p. 39-62.

Retallack, G. J., 1983, Late Eocene and Oligocene paleosols from Badlands National Park, South Dakota: Geological Society of America Special Paper 193, 82 p.

_____, 1997, Neogene expansion of the North American prairie: Palaios, v. 12, p. 380-390.

Savage, D. E., and Russell, D. E., 1983, Mammalian Paleofaunas of the World: Addison-Wesley Publishing Company, Reading, Massachusetts, 432 p.

Schaller, G. B. ,1972, The Serengeti Lion: University of Chicago Press, Chicago, 480 p.

Schultz, C. B., and Falkenbach, C. H., 1968, The phylogeny of the oreodonts, pts. 1-2: Bulletin of the American Museum of Natural History, v. 39, p. 1-498.

Schultz, C. B., and Stout, T. M., 1938, Preliminary remarks on the Oligocene of Nebraska: Geological Society of America Bulletin, v. 49, p. 1921.

_____, 1955, Classification of Oligocene sediments in Nebraska: Bulletin of the University of Nebraska State Museum, v. 4, p. 17-52.

Schultz, C. B., Tanner, L. G., and Harvey, C., 1955, Paleosols of the Oligocene of Nebraska: Bulletin of the University of Nebraska State Museum, v. 4, p. 1 -16.

Scott, K. M., 1990, Postcranial dimensions of ungulates as predictors of body mass, *in* Damuth, J., and MacFadden, J., eds., Body Size in Mammalian Paleobiology: Cambridge University Press, Cambridge, United Kingdom, p. 301-336.

Scott, W. B., 1940, The mammalian fauna of the White River Oligocene – pt. 4, Artiodactyla: Transactions of the American Philosophical Society (new series), v. 28, p. 363-746.

_____, 1941, The mammalian fauna of the White River Oligocene – pt. 5, Perissodactyla: Transactions of the American Philosophical Society (new series), v. 28, p. 747-980.

Scott, W. B., and Jepsen, G. L., 1936, The mammalian fauna of the White River Oligocene – pt. 1, Insectivora and Carnivora: Transactions of the American Philosophical Society (new series), v. 28, p. 1-153.

Shelford, V. E., 1964, The Ecology of North America: University of Illinois Press, Urbana, 610 p.

Shipman, P., 1981, The Life History of a Fossil – an Introduction to Taphonomy and Paleoecology: Harvard University Press, Cambridge, United Kingdom, 222 p.

Sinclair, W. J., 1921, The "turtle-oreodon" layer or "red layer," a contribution to the White River Oligocene: Proceedings of the American Philosophical Society, v. 60, p. 457-466.

Steele, D. G., and Carson, D. L., 1989, Excavation and taphonomy of mammoth remains from the Duewall-Newberry Site, Brazos County, Texas, *in* Bonnichsen R., and Sorg, M. H., eds., Bone Modification: Center for the Study of the First Americans, Orono, Maine, p. 413-430.

Stevens, M. S., and Stevens, J. B., 1996, Merycoidodontinae and Miniochoerinae, *in* Prothero, D.R., and Emry, R.J., eds., The Terrestrial Eocene-Oligocene Transition in North America, Cambridge University Press, Cambridge, United Kingdom, p. 498-573.

Sutcliffe, A. J., 1970, Spotted hyena – crusher, gnawer, digester of bones: Nature, v. 227. p. 1110-1113.

Swinehart, J. B., Souders, V. L., DeGraw, H. M., and Diffendal, R. F., Jr., 1985, Cenozoic paleogeography of western Nebraska, *in* Flores, R. M., and Kaplan, S. S., eds., Cenozoic Paleogeography of West-Central United States. Society of Economic Paleontologists and Mineralogists (Rocky Mountain Section), Rocky Mountain Paleogeography Symposium 3, p. 209-229.

Terry, D. O., Jr., 1998, Lithostratigraphic revision and correlation of the lower part of the White River Group: South Dakota to Nebraska, *in* Terry, D. O., Jr., LaGarry, H. E., and Hunt, R. M., Jr., eds., Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene of North America): Geological Society of America Special Paper 325, p. 15-38.

Terry, D. O., Jr., and LaGarry, H. E., 1998, The Big Cottonwood Creek Member – a new member of the Chadron Formation in northwestern Nebraska, *in* Terry, D. O., Jr., LaGarry, H. E., and Hunt, R. M., eds., Depositional Environments, Lithostratigraphy, and Biostratigraphy of the White River and Arikaree Groups (Late Eocene to Early Miocene of North America): Geological Society of America Special Paper 325, p. 117-142.

Terry, D. O., Jr., LaGarry, H. E., and Wells, W. B., 1995, The White River Group revisited – vertebrate trackways, ecosystems, and lithostratigraphic revision, redefinition, and redescription, *in* Flowerday, C. A., ed., Geologic Field Trips in Nebraska and Adjacent Parts of Kansas and South Dakota: University of Nebraska-Lincoln Conservation and Survey Division Guidebook 10, p. 43-57.

Thomasson, J. R., Zakrzewski, R. J., LaGarry, H. E., and Mergen, D. E., 1990, A late Miocene (late early Hemphillian) biota from northwestern Nebraska: National Geographic Research, v. 6, p. 231-244.

Van Valkenburgh, B., 1988, Trophic diversity in past and present guilds of large predatory mammals: Paleobiology, v. 14, p. 155-173.

_____, 1990, Skeletal and dental predictors of body mass in carnivores; *in* Damuth, J., and MacFadden, B. J., eds., Body Size in Mammalian Paleobiology: Cambridge University Press, Cambridge, United Kingdom, p. 181-206.

Voorhies, M. R., 1969a, Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming Contributions to Geology Special Paper 1, 69 p.

_____, 1969b, Sampling difficulties in reconstructing Late Tertiary mammalian communities: Proceedings of the North American Paleontological Convention, pt. E, p. 454-468.

Walker, E. P., 1975, Mammals of the World, third edition, v. I and II: Johns Hopkins University Press, Baltimore, 1,500 p.

Wang, X., 1994, Phylogenetic systematics of the Hesperocyoninae (Carnivora: Canidae): American Museum of Natural History Bulletin, v. 221, p. 1 - 207.

Wang, X., and Tedford, R. H., 1996, Canidae, *in* Prothero, D. R., and Emry R. J., eds., The Terrestrial Eocene-Oligocene Transition in North America: Cambridge University Press, Cambridge, United Kingdom, p. 433-452.

Wanless, H. R., 1922, Lithology of the White River sedi-

ments: Proceedings of the American Philosophical Society, v. 62, p. 663-669.

_____, 1923, The stratigraphy of the White River beds of South Dakota: Proceedings of the American Philosophical Society, v. 63, p. 191-267.

Ward, F., 1922, The geology of a portion of the Badlands: South Dakota Geological and Natural History Survey Bulletin, v. 11, 80 p.

Weigelt, J., 1989, Recent Vertebrate Carcasses and Their Paleobiological Implications (translated by Schaefer, J.): University of Chicago Press, Chicago, 188 p.

Wells, W. B., Terry, D. O., Jr., and LaGarry, H. E., 1995, Stratigraphic implications of a fluvial origin for the "nodular zones," Brule Formation (Orella Member), northwestern Nebraska: Geological Society of America Abstracts with Programs, v. 27, p. 95.

Wood, A. E., 1937, The mammalian fauna of the White River Oligocene – pt. 2, Rodentia: Transactions of the American Philosophical Society (new series), v. 28, p. 155-269.

_____, 1940, The mammalian fauna of the White River Oligocene – pt. 3, Lagomorpha: Transactions of the American Philosophical Society (new series), v. 28, p. 271-362.

Wood, H. E., Clancy, R. W., Clark, J., Colbert, E. H., Jepsen, G. L., Reeside, J. B., Jr., and Stock, C, 1941, Nomenclature and correlation of the North American continental Tertiary: Geological Society of America Bulletin, v. 52, p. 1-48