Taphonomic Evidence of Bone Processing from the Oligocene of Northwestern Nebraska

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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 km²) and Sx-7 (0.05 km²) 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 northeastern 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 Remes, 1953; Emery 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, biostratigraphy, and paleoecology (Matthew, 1899, 1909; Sinclair, 1921; Weigelt, 1922, 1923; Galen, 1922; Scott and Jensen, 1935; Clark, 1937, 1939; Wood, 1937, 1940; Scott, 1940; Krider, 1941; Schatz and Stutt, 1950; Clark and others, 1967; Schieck and Falkenbach, 1969). 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 Klein, 1988).

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 carnivore and bone assemblages of East Africa.

In the broad belt of Africa, it is evident that predators have found numerous abandoned prey. The carcasses of crocodiles have been torn apart and the parts carried off... a curious sort of sorting takes place. The bones have been taken into and then ground by re- doers... Where the remains of prey pile up, the predators' droppings are scattered everywhere. Carnivores have the habit, noticed by Bödtig, of forming bone depositions. We could not otherwise explain why the fossil skulls and lower jaw fragments of Hyaenodon, Canis, Pachycrocuta, and Mesocarnus 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 preference, selective consumption of skeletal elements, introduction or removal of preferred orientation, cutting of bone at den sites, and selective consumption of prey age classes (Steuell, 1975; Hill, 1976, 1979, 1980; Haynes, 1980a, 1980b, 1982, 1983, 1988, 1990; McKittrick, 1982, 1983; Andrew and Nesbitt, 1983; Klein and Cruz-Uribe, 1984; Hill and Behrensmeyer, 1984).

However, 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, alteration 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, 1989; Hunt, 1978, 1988, 1990; Thomasson and others, 1990; and some authors have used a uniformitarian approach (see Cifelli-Gonzalez, 1989) to qualitatively compare modifications produced by extant and fossil taxa (for example, Hayes, 1985b, 1987; Haynes, 1988a, 1988b, 1990) and Behrensmeyer and others (1987) have commented on the (as yet unquantified) 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 mammal 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 volcanlastic claystones and siltstones, limestones, and eolianic 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, 1881).
Hatcher, 1953; Darton, 1899, 1903, 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, 1993, 1997). In northwestern Nebraska, these rocks are exposed as steep cliffs and discontinuous outcrops north of the Pine Ridge escarpment (see LaGarry and LaGarry, 1997d).

The Brule Formation of Northwestern Nebraska

The Brule Formation was first described by Darton (1896), but the stratigraphic classification of Schultz and Janes (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 Swinney and others (1955) later added the "brown siltstone" member for discussion, see LaGarry, 1998.

Stratigraphy

Schultz and Stout (1955) subdivided the Orella Member, consisting of 56 to 85 m of interbedded massive clay slates, laminated clay slats, nodular sandstone, siltstone, claystone, gyttja, gypsiferous paleosols, and channel sandstones. Their Orella Member was subdivided into the Orella "A," "B," "C," and "D," based on the distribution 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 (1955) Orella Member was used to define the Orellan North American land mammal age, or NALMA (Wood and others, 1941), and was divided biostratigraphically based on the biochronologically defined Orellan NALMA (early Oligocene) as characterized by Clark and others (1967). In LaGarry's (1998) lithologic reinterpretation, the Orella Member consists of thinly interbedded sheet sandstones with a few massive volcanioclastic clayey siltstones and silty claystones, and channel sandstones, laminated and massive volcanioclastic silty claystones that filled and overrode outcrop sheet sandstones and volcanioclastic siltstone deposits. The Orella Member consists of thinly interbedded sheet sandstones, laminated and massive volcanioclastic clayey siltstones and silty claystones, and channel sandstones, laminated and massive volcanioclastic clayey siltstones, and laminated volcanioclastic siltstone members, and channel sandstones, laminated volcanioclastic siltstones, as the uppermost part of the underlying Chadron Formation, which consists of 8 to 10 m of volcanioclastic siltstone members, 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 Clark and others, 1967). 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 fossil sample used in this study was collected from rocks that were classified as "Orella A" and "Orella C," and it is within the biochronologically defined Orellan NALMA (early Oligocene) as characterized by Clark and others (1967).

Depositional Environment

Harvey (1960) and Terry and others (1965) interpreted the Orella Member to be a sequence of stacked "couplets" of thin overbank sheet sandstones and volcanioclastic siltstone that filled and overrode outcrop sheet sandstones and volcanioclastic siltstones that filled and overrode cut-and-fill palaeochannel sequences during two or more separate and alternating periods of incision and backfilling. Harvey's (1962) interpretation was of cyclic deposition within nested palaeovalleys. However, Terry and others (1965) suggested that the Orella Member was deposited during a period of complex overlapping and episodic cutting and filling. Schultze and Stout (1955) and Schultze and others (1955) subdivided the Orella Member into the stratigraphic positions of what they interpreted to be palaeosols. In contrast, Clark and others (1967) argued that there were no palaeosols within the Orella Member, and that the Orella Member was dominated by overbank sheet deposition rather than pedogenesis. More recently, Schultze and Stout (1955) and Schultze and others (1955) subdivided the Orella Member into the stratigraphic positions of what they interpreted to be palaeosols. In contrast, Clark and others (1967) argued that there were no palaeosols 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 (1935).

"Old Floyd Hall Place" The Orella Member is 26-29 m thick at Schultz and Stout's (1939) type area at Toadstool Geologic Park in northeastern Sioux County, but it pinches out to the west and the base of the Pine Ridge egress near Chadron, Nebraska, to the east (LaGarry and LaGarry, 1997a, 1997b). The "Old Floyd Hall Place" is located 4 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 volcanioclastic 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). 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.

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.
expenses are present between exposures, greatly fa-
cilitating 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 the preservation of bone fragments indicated that little, if any, bone was present within
these sediments at this locality.

Assessment of Bone Processing

Traditionally, fossils are collected from the White
River Group by picking up surface litter one piece at a
time or collecting in sift 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 3), within small areas of 0.08 km² and
0.09 km² of UNSM 5x-4 and 5x-7, respectively (fig. 2).
These areas were sampled in 1989, 1990, and 1991. The
resulting samples were observed for study, and con-
stituted of a mixture of fossilized jaws, teeth, fragmen-
tary postcranial bones of mammals and turtles, tere-
tre shell fragments, coprolites, animal scats, and bits of
modern vegetation (fig. 2). Fossil material was placed in a 0.406 mm screen while adhering clay resid-
dues were rinsed off. This was not “screen washing,”
in that no sediment was processed with the fossil ma-
terial. The screening process provided a virtually sedi-
ment-free sample, as if it had been removed from a
paved surface. The fossil material was judged to have
been eroded from the clayey siltstones because sand-
stone within the Orella Member is well-cemented, as
are bones within the sandstones. Preliminary inspec-
tion of the sample showed that none of the postcranial
fragments had adhering remnants of sandstone or ce-
ment, which is more resistant to weathering than the
assessible 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
sample showed evidence of breakage prior to burial or
diagenetic alteration from the bedrock and subsequent subaerial exposure
produced sharp breaks that expose cleavage faces of
within the bone. These breaks interrupt the pattern of
diagenetic staining from the bedrock. These studies
pointed towards larger, more easily seen fragments after weathering from the beds. 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, 1983). 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 mam-

mals have been recognized from the White River
Group since the 1920s (Bidleman, 1921; Wanless, 1923).
These coprolites are cylindrical, unsegmented masses
that often contain bones and teeth (Edwards and Yatkola, 1994). 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,
1979a, 1979b; Edwards and Yatkola, 1974; Retallack,
1983, 1987; Wethera, 1991). Few studies have ad-
ressed the processing of prey bone during ingestion,
digestion, and excretion by extant mammalian carni-
vores (Mellett, 1974; Andrews and Nodro, 1983). In
order to make comparisons with existing studies,
the coprolites were prepared by mechanically excavat-
ing 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
whether possible, the identity of the prey species. I esti-

ated the general body size of the carnivore(s) that
excreted the coprolites by measuring the maximum
diameter of complete coprolites and partial coproli-
tes in which the maximum diameter was preserved,
and then compared these data to the extant scato-
logical record.
notching, burrowing by insect larvae, and scratch- 
ing and breakage by trampling (Miller, 1969, 1975; Hill, 
These modifications, where present, were described. 
these features were recognized through vi-
sual inspection of the sample, and the character and 
potential origins of those features present in the sample 
will be discussed below.

Body Size Determination

Extant mammalian carnivores select a particular 
range of prey body sizes (Kruuk and Turner, 1967; 
Meek, 1976; Kruuk, 1972; Schaller, 1972; Kingsford, 
1977; Peterson, 1977; Miller, 1979; Haynes, 1982). For 
examples, lions in the Serengeti Plains of eastern Af-
rica most frequently prey on zebra and wildebeest, 
having body sizes from 100-300 kg, whereas 
leopards most frequently prey on Thomson's gazelles, 
impala, and reedbuck having body sizes from 10-100 
kg (Kruuk and Turner, 1967). Extant carnivores are also 
opportunistically and will pursue, either, typically smaller, 
prey when it is available (Kruuk and Turner, 1967; 
Kingsdon, 1977). However, body size and availability, 
rather than membership in a particular taxonomy, 
group, determine the preferred prey of extant carni-
vores. 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 fur-
ther 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 Clifford-
Geddes, 1969). However, heavily processed assem-
blages are a "residue" of the original sample of prey 
carcasses and may consist of only a few scrapes or un-

Therefore, assigning processed bones to groups of 
any kind is problematic. Nevertheless, the compo-
sition 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 estimat-
ing body size are available, such as measuring the di-
ame of the femoral shaft (Gingerich, 1989) or (for 
carnivores) the length of the lower carnassial 
(legendos, Bibe: Legendre and Sutcli, 1988). Rates of 
vivisection, cranial, body length, and postcranial bone 
measurements have also been used (Olmust, 1980; Jutus, 
1990; Scott, 1990; Van Valkenburgh, 1990). These 
techniques require securely identified or well-
preserved skeletal material for the most accurate re-
sults, 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 comparisons. 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 postcraniaal 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).

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

<table>
<thead>
<tr>
<th>SKELETAL ELEMENT</th>
<th>MEASUREMENT</th>
</tr>
</thead>
<tbody>
<tr>
<td>vertebrae (total)</td>
<td>breadth of centrum cranial articular surface</td>
</tr>
<tr>
<td>scapula (glenoid region)</td>
<td>greatest breadth of glenoid region</td>
</tr>
<tr>
<td>humerus (proximal end)</td>
<td>greatest breadth of proximal end</td>
</tr>
<tr>
<td>radius (proximal end)</td>
<td>greatest breadth of proximal end</td>
</tr>
<tr>
<td>radius (distal end)</td>
<td>greatest breadth of distal end</td>
</tr>
<tr>
<td>ulna (proximal end)</td>
<td>deepest point proximal articular surface</td>
</tr>
<tr>
<td>ulna (distal end)</td>
<td>greatest breadth of distal end</td>
</tr>
<tr>
<td>pelvis (pubic symphysis)</td>
<td>length of acetabulum, including lip</td>
</tr>
<tr>
<td>femur (proximal end)</td>
<td>greatest breadth of proximal end</td>
</tr>
<tr>
<td>femur (distal end)</td>
<td>greatest breadth of distal end</td>
</tr>
<tr>
<td>tibia (proximal end)</td>
<td>greatest breadth of proximal end</td>
</tr>
<tr>
<td>tibia (distal end)</td>
<td>greatest breadth of distal end</td>
</tr>
<tr>
<td>astragali</td>
<td>greatest breadth</td>
</tr>
<tr>
<td>calcaneum</td>
<td>greatest breadth</td>
</tr>
<tr>
<td>metacarpal (proximal end)</td>
<td>greatest breadth of proximal end</td>
</tr>
<tr>
<td>metacarpal (distal end)</td>
<td>greatest breadth of distal end</td>
</tr>
<tr>
<td>phalanges</td>
<td>greatest breadth of proximal end</td>
</tr>
</tbody>
</table>

1. Cervical, thoracic, and lumbar vertebrae combined, excluding cranial vertebrae.
2. Broadest unbroken surface measured. Some measurements are for all vertebrae.
3. Some measurements applied to all bones of this type regardless of taxon.
4. New measurement (see text).
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 121065), 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 erosion by stomach acids, such as a series of three upper molars of the small chilotheriid 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 Herpestes, a small canid (fig. 5C-D). The partial M1 shows slight dissolution and rounding of its broken edges, while the premolars appear to be uneroded.

Skeletal Representation
To date, isolated teeth, partial tooth rows, postcranial bones, bone fragments, and one crushed skull have been recovered by manual preparation of the surfaces of the coprolites. The crushed skull (UNSM 121113), 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 = 72; figs. 4B-C; and 6A-D and 6B), 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, Lepomeryx, and small oreodont-sized taxa. Herpetotherium is represented by a partial mandible with m2-m3 (fig. 6B) and the partial maxilla with M1-M3 mentioned earlier. Small and large species of Paleolagus (fig. 4A) are represented by isolated teeth and the crushed skull mentioned previously. Hesperus, a small artiodactyl of about the same size as the large Paleolagus, is represented by an m2 or m3 (fig. 4C) and several phalanges (fig. 4C). Lepomeryx, another small (slightly larger) artiodactyl, is represented by a deduced premolar (fig. 4D) and several phalanges (fig. 4A). Two small incisors (d11) have been referred to cf. Poebatherium (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 121003; 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, Hypeutragulus. Several of the larger phalanges have been assigned to 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.

*Miniochirus* (UNSM 121015). A single distal phalanx (UNSM 121030) was assigned to *cf. Metochirus*. As mentioned previously, the small canid *Hesperocyon* (Fig. 5C-4D) is represented by four isolated premolars and a
Fig. 6. Stereo pair photographs of coprolites from UNSM Sx-6 and Sx-7: A) UNSM 123006; B) 123007; C) UNSM 123009; D) UNSM 123011. Symbols: f, l, m = fragment, Paleolagus tooth, 1st incisor, and molar, respectively. Bars = 1 cm.
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 Yakola (1974) concluded that White River Group coprolites were produced by at least two size classes of carnivores. Their histogram of frequency vs. size (Edwards and Yakola, 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 Orilla Member at UNSM Sx-6 and Sx-7 likely represents one or more carnivores of about the same body size. Edwards and Yakola’s (1974) analysis may indicate 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 Yakola (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 Valkenburg, 1988; Walker, 1975, p. 1952), there are several Oligocene carnivores of about the same size as the coyote (C. latrans, 9-12.7 kg) and the wolf (C. lycaon, 27-79 kg). The coyote-sized taxa include the creodont Hyaenodon crucinns (~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 harriensis (~81 kg) and the large nimravid Amphicyon pristodontalis (~63 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 Cryptoprocta ferox (yellow mongoose), Cryptoprocta ferox (white-tailed mongoose), Cryptoprocta ferox (genet); the canids Canis lupus (gray wolf), Canis lupus (red fox), Vulpes vulpes (British red fox), Vulpes vulpes (Arctic fox), and Canis lupus (coyote); the mustelids Mustela visna (weasel), M. putorius (polecat), M. erminea (ermine), and Martes martes (stone marten); and the felids Felis catus (domestic cat) and Leptailurus serval (Serval). 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 1:1) is about the same as that for C. latrans (1:1.51) and M. martes (2:2.81), as opposed to 3:1 for L. africanus and O. genetta, 2:1 for G. genetta, and 1:1 for V. vulpes and the felids. Sphally fractured bones like those excavated from the coprolites were recovered from scats of the canids O. genetta, 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 toward larger fragments and taxa, but finely comminuted chips and shards are also present. This suggests the coprolite-producing carnivore may have, like certain 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 closer resemblance to the scats of C. latrans and A. inexpectus, from which articulated and isolated elements were recovered. This is in contrast to the viverrids, 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 processed bone described by Andrews and Nesbit-Evans (1983), most closely resembles bone processed by the mustelids, in which moderate amounts of rounding occurred and both bones and teeth were severely corroded; and the canids, in which virtually all fragments were rounded and both bones and teeth were extremely corroded. In the wild carnivores studied by Andrews and Nesbit-Evans (1983), the ingestion of hide and hair along with bones, teeth, and fur 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 number, 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 faunas within the coprolites to the prey selected by the carnivores discussed by Andrews and Nesbit-Evans (1983) indicates that the C. latrans, the coprolite-producing carnivore, ate a variety of prey items. Tissue recovered from the coprolites ranges in size from small (D. hartskovianus) to relatively large (C. hesperocyon, cf. Megalocyon, cf. Mesocyon, Hesperocyon) and includes at least ten genera from four taxonomic classes of mammalian prey. Of the taxa studied by Andrews and Nesbit-Evans (1983), this level of generalization was only approached by C. latrans, suggesting that the coprolite-producing carnivore was also a generalist feeder. Of all the Carnivora, only the small canids Hesperocyon sp. and Mesocyon sp. and the amphicyonids O. bulbivolum and D. series had densities in an area similar to that of the coyote C. latrans (Van Valkenburgh, 1988). Only D. series 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 Oligocene coprolite sample.

Bone Processing of the Postcranial Fragments

Preliminary inspection revealed that most of the observed attention of the sample (for example, weathering, brecciation, 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).

<table>
<thead>
<tr>
<th>ELEMENT</th>
<th>NISP%</th>
<th>GOUGE%</th>
<th>PIT%</th>
<th>SPALL%</th>
<th>SCRATCH%</th>
</tr>
</thead>
<tbody>
<tr>
<td>vertebrae</td>
<td>289</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>&gt;1</td>
</tr>
<tr>
<td>caudal vertebra</td>
<td>70</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>scapula (glenoid region)</td>
<td>86</td>
<td>0</td>
<td>20</td>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>humerus (proximal end)</td>
<td>40</td>
<td>0</td>
<td>35</td>
<td>20</td>
<td>15</td>
</tr>
<tr>
<td>Radius (proximal end)</td>
<td>147</td>
<td>1</td>
<td>18</td>
<td>45</td>
<td>3</td>
</tr>
<tr>
<td>Radius (distal end)</td>
<td>99</td>
<td>1</td>
<td>7</td>
<td>26</td>
<td>2</td>
</tr>
<tr>
<td>Ulna (proximal end)</td>
<td>52</td>
<td>0</td>
<td>17</td>
<td>29</td>
<td>2</td>
</tr>
<tr>
<td>Ulna (distal end)</td>
<td>36</td>
<td>0</td>
<td>11</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Fibia (proximal end)</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fibia (distal end)</td>
<td>78</td>
<td>0</td>
<td>16</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Femur (proximal end)</td>
<td>32</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Femur (distal end)</td>
<td>106</td>
<td>3</td>
<td>36</td>
<td>38</td>
<td>4</td>
</tr>
<tr>
<td>Tibia (proximal end)</td>
<td>55</td>
<td>5</td>
<td>13</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Tibia (distal end)</td>
<td>150</td>
<td>0</td>
<td>7</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Calcaneum</td>
<td>75</td>
<td>1</td>
<td>15</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Asteragalus</td>
<td>108</td>
<td>0</td>
<td>8</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Metapodial (proximal end)</td>
<td>112</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Metapodial (distal end)</td>
<td>74</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>phalanx (proximal end)</td>
<td>4/8</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

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.

Non-processing Features
Non-carnivore modifications observed within the bone sample include weathering, rodent gnawing, and root etching. Damage from trampling and abrasion (see Figs. 8A, 8B, 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. As bones dry, this tends to deform less plastically and breakage patterns change as a result (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 by Behrensmeyer, 1978; Rinfield, 1981; LaGarry, 1981; 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. 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 bones dry, this tends to deform less plastically and breakage patterns change as a result (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 by Behrensmeyer, 1978; Rinfield, 1981; LaGarry, 1981; 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.
<table>
<thead>
<tr>
<th>ELEMENT</th>
<th>OBSERVED DAMAGE</th>
<th>WEATHERING</th>
</tr>
</thead>
<tbody>
<tr>
<td>vertebra</td>
<td>neural, lateral, and spino processes broken off (most)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>articular processes broken off (many)</td>
<td>many are moderate</td>
</tr>
<tr>
<td></td>
<td>edges of articular surfaces chipped (many)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>central beam broken transversely (some)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td>caudal vertebra</td>
<td>neutral and transverse processes chipped (few)</td>
<td>few are slight</td>
</tr>
<tr>
<td></td>
<td>central beam broken transversely (few)</td>
<td>most are unweathered</td>
</tr>
<tr>
<td>scapula</td>
<td>blade and spine broken off - transverse or spiral fracture (all)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>neck of blade bitten or scratched (some)</td>
<td>many are moderate</td>
</tr>
<tr>
<td></td>
<td>glenoid process chipped or bitten (many)</td>
<td>few are slight</td>
</tr>
<tr>
<td></td>
<td>few are unweathered</td>
<td></td>
</tr>
<tr>
<td>humerus</td>
<td>humeral head broken or bitten off (many)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>lateral tuberosity broken or bitten off (many)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>part or all of distal trochanter broken or bitten off (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>proximal end broken off - transverse or spiral fracture (many)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td></td>
<td>distal articular surface broken or bitten off (very few)</td>
<td></td>
</tr>
<tr>
<td>radius</td>
<td>proximal articular surface broken or bitten off (few)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>proximal and distal end - transverse or spiral fracture (some)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>distal articular surface broken or bitten off (few)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse fracture (few)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td>ulna</td>
<td>proximal end broken, bosses processes anomalous (few)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>olecranon process broken off (few)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse fracture (few)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td>pelvis</td>
<td>ilium, ischium, and pubis broken off or missing (very few)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>part of acetabulum broken or bitten off (nearly all)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>lip of acetabulum chipped (many)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td></td>
<td>few are moderate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>some are slight</td>
<td></td>
</tr>
<tr>
<td></td>
<td>none are unweathered</td>
<td></td>
</tr>
<tr>
<td>femur</td>
<td>femoral head broken or bitten-off (most)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>greater trochanter broken or bitten off (many)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>proximal and distal end - transverse or spiral fracture (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>distal trochanter broken or bitten off (many)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (some)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>distal articular surface broken or bitten off (some)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td>tibia</td>
<td>proximal articular surface broken or bitten off (some)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td></td>
<td>proximal end broken off - transverse or spiral fracture (some)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>distal articular surface broken or bitten off (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (some)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td>calcaneum</td>
<td>anterior end broken or bitten off (some)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>posterior end broken or bitten off (nearly all)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>articular surface broken or bitten off (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (some)</td>
<td>few are unweathered</td>
</tr>
<tr>
<td></td>
<td>few are slight</td>
<td></td>
</tr>
<tr>
<td></td>
<td>few are unweathered</td>
<td></td>
</tr>
<tr>
<td>astragalus</td>
<td>proximal or distal trochlea broken off (few)</td>
<td>few are severe</td>
</tr>
<tr>
<td></td>
<td>edges of proximal or distal trochlea chipped (many)</td>
<td>many are unweathered</td>
</tr>
<tr>
<td></td>
<td>broken transversely or longitudinally (very few)</td>
<td>many are unweathered</td>
</tr>
<tr>
<td>metatarsal</td>
<td>proximal or distal trochlea broken off (few)</td>
<td>few are moderate</td>
</tr>
<tr>
<td></td>
<td>proximal and distal end - transverse or spiral fracture (some)</td>
<td>many are slight</td>
</tr>
<tr>
<td></td>
<td>distal trochanter broken or chipped (very few)</td>
<td>most are unweathered</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (few)</td>
<td>few are slight</td>
</tr>
<tr>
<td></td>
<td>distal end broken off - transverse or spiral fracture (few)</td>
<td></td>
</tr>
<tr>
<td>phalanges</td>
<td>proximal or distal articular surface chipped (very few)</td>
<td>few are slight</td>
</tr>
<tr>
<td></td>
<td>spirally or transversely broken at midpoint (very few)</td>
<td>most are unweathered</td>
</tr>
</tbody>
</table>

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

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

Wolves, and is not typically produced by wild fields in the few species studied (Scientific, 1980; Haynes, 1980a, 1980b, 1982, 1983; Hill, 1989). However, this damage has been produced by captive hyenas, wolves, tigers, and lions (Miller, 1969; Haynes, 1983). Grooves result from a carnivore dragging its canine or carnassial tooth across a bone with force sufficient to penetrate the outermost layers of compact bone (Miller, 15
### Table 5. Size groups (I-V) assigned to taxa from UNSM Sx-6 and Sx-7. All identifications are based on teeth.

<table>
<thead>
<tr>
<th>TAXON AND GROUP</th>
<th>COPROLITES</th>
<th>POSTCRANIALS</th>
<th>EST. BODY SIZE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GROUP I</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herpetotherium sp.</td>
<td>X</td>
<td>?</td>
<td>&lt;1 kg²</td>
</tr>
<tr>
<td>Palaeolemur sp. (small)</td>
<td>X</td>
<td>?</td>
<td>&lt;1 kg²</td>
</tr>
<tr>
<td>Palaeolemur sp.</td>
<td>?</td>
<td>?</td>
<td>&lt;1 kg²</td>
</tr>
<tr>
<td>Canetodora sp.</td>
<td>?</td>
<td>?</td>
<td>&lt;1 kg²</td>
</tr>
<tr>
<td>Hylaeomys sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Leptictis sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Ischyromys sp (small)</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Ischyromys sp (large)</td>
<td>?</td>
<td>?</td>
<td>&lt;1 kg²</td>
</tr>
<tr>
<td>Pelycopus sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Cedrornis sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Eumys sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Paradjidambo sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Heliscomys sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td>Hypisodus sp.</td>
<td>?</td>
<td>?</td>
<td>4 kg²</td>
</tr>
<tr>
<td><strong>GROUP II</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeolemur sp. (large)</td>
<td>X</td>
<td>X</td>
<td>-2.5 kg²</td>
</tr>
<tr>
<td>Pseudoherds sp.</td>
<td>?</td>
<td>?</td>
<td>&lt;17 kg²</td>
</tr>
<tr>
<td>Hyaenodon sp. (small)</td>
<td>?</td>
<td>?</td>
<td>-17 kg²</td>
</tr>
<tr>
<td>Hoplophoneus sp.</td>
<td>?</td>
<td>?</td>
<td>-16 kg²</td>
</tr>
<tr>
<td>Pteron sp.</td>
<td>?</td>
<td>?</td>
<td>-9 kg²</td>
</tr>
<tr>
<td>Leptictidion sp.</td>
<td>?</td>
<td>?</td>
<td>-7 kg²</td>
</tr>
<tr>
<td>Minioclerherds sp.</td>
<td>?</td>
<td>?</td>
<td>-7.9 kg²</td>
</tr>
<tr>
<td>Hypisodus sp.</td>
<td>?</td>
<td>?</td>
<td>-1.4 kg²</td>
</tr>
<tr>
<td>Leptomyxys sp.</td>
<td>Y</td>
<td>X</td>
<td>-3 kg²</td>
</tr>
<tr>
<td><strong>GROUP III</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphoerds sp. (large)</td>
<td>?</td>
<td>?</td>
<td>-34.5 kg²</td>
</tr>
<tr>
<td>Merostomotherds sp.</td>
<td>?</td>
<td>X</td>
<td>-27.7 kg²</td>
</tr>
<tr>
<td>Poebrotherds sp.</td>
<td>?</td>
<td>X</td>
<td>-30.8 kg²</td>
</tr>
<tr>
<td>Agriotheres sp.</td>
<td>?</td>
<td>?</td>
<td>-51.3 kg²</td>
</tr>
<tr>
<td>Mesohippus sp.</td>
<td>?</td>
<td>X</td>
<td>-25 kg²</td>
</tr>
<tr>
<td><strong>GROUP IV</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hyaenodon sp.</td>
<td>?</td>
<td>?</td>
<td>-100 kg²</td>
</tr>
<tr>
<td><strong>GROUP V</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subhyracodon sp.</td>
<td>?</td>
<td>?</td>
<td>-517 kg³</td>
</tr>
</tbody>
</table>

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).
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 121213); C) proximal end of radius (UNSM 121213); D) humeral head (UNSM 121213); E) calcaneum, shown inverted (UNSM 121214); F) proximal end of humerus (UNSM 121215); G) proximal end of humerus (UNSM 121214); H) proximal end of tibia (UNSM 121217); I) distal end of femur (UNSM 121216); J) proximal end of tibia (UNSM 121217); K) distal end of femur (UNSM 121218); L) innominate fragment (UNSM 121219). Symbols: g, p, s = gouging, pitting, and spalling, respectively.
of damage is produced by large felids, hyenas, and canids (Miller, 1969; Sudbury, 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, 10J), and often leads to the partial or complete loss of a femoral head (figs. 8A, 8B, and 9B), an articular surface (figs. 8F-H; 9F-H), or the complete removal of the proximal or distal end of a bone (figs. 8F-H; 9F-H; and 10G, 10J). 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 5x-6 and 5x-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; LeGarry, 1988). Once damaged in this way, highly nutritious cancellous bone is exposed and is typically scraped out and consumed (Sutcliffe, 1970; Haynes, 1983b, 1988). Spalling is most frequently associated with pitting (see above). Damage of this type, if restricted to missing apatite, 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. 8D and 10). Transverse scratches are typically less than 0.2 cm wide and 0.1 cm deep and are usually Valoped in cross section. They are usually less than 1 cm long (figs. 10A, 10D-H). The spacing between individual scratches in a set varies. Some are evenly spaced (fig. 10E), while others overlap (fig. 10A, lower set on right side).

Of the processing features discussed so far, transverse scratching has the least diverse origins. Transverse scratching has been attributed to rodents, canids, and felids (Miller, 1976; Haynes, 1980a, 1982, 1983; Marshall, 1989). It is typically the result of a small carnivore, such as coyote or red fox, gnawing 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, 1983b, 1988). Transverse scratching is also produced by juvenile carnivores that would typically produce gouges and is typically scooped out and consumed (Sutcliffe, 1970; Hays, 1983b, 1988). Spalling is most frequently associated with pitting (see above). Damage of this type, if restricted to missing apatite, is typical of a "moderately processed" carcass (Haynes, 1983).

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that have even small longitudinal cracks with produce uneven, stepped, or longitudinal fractures as the cracking increases in depth (Binford, 1981). Splintered breaks are produced when highly weathered bones are broken by any number of agents (Marshall, 1989). The dynamics of bone typically determines the form of breakage when bone is damaged by trampling or post-burial compression, sediment loading, cryoturbation, or freeze-thaw cycles (Ager, 1989; Brain, 1989; Irving and others, 1989; Scaife and Carlson, 1989).

Some breaks are exclusively the result of bone processing by carnivores, such as scapula and pelvis, head, cranial, and mandibular bones. The differences in the Sx-6 and Sx-7 samples that can be attributed to burial. Similarly, elements with large amounts of bone breaks rather than deforming plastically. Also, rounded breaks (fig. 120) are produced by long-term graveling of bones, which commonly occurs when food resources are low or bones are available to herbivores (Sutcliffe, 1970; Haynes, 1980, 1982; Hill, 1989). Hyenas typically break up 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 (Haynes, 1980a, 1983) and Lacy (1988), the only breaks in the Sx-6 and Sx-7 samples that can be attributed to bone processing with 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, 1987), the removal of the head, lateral condyle, and distal trochlear of the femur, removal or damage to the head and distal tuberae 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 includes 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 sources for carnivores. In addition, they often retain their covering of skin, hair, and hair during the processing, disarticulation, and subsequent burial of the carcass (Haynes, 1980b; 1983; Hill and Sutcliffe, 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 taxa. With the exception of Group 3, all of these groups exist 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-1) display five or more modes representing relative size groups, with the largest subpopulation occurring near the middle of the overall size distribution. The categories represent relatively size categories, with the largest subpopulation occurring near the middle of the overall size distribution. 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 modes 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. 12D). Then, 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 means 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
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 also be 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-

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**Fig. 11.** 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
distributions 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 small mammals 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 accumu-
la�ing on the land surface because they typically reach
sexual maturity more quickly, have larger litters, and
have a shorter generation length than do larger mam-
mals (Millar and Zammuto, 1983).

However, Groups I and II, which are based on
postcranial elements rather than teeth or jaws, are se-
verely 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. 12. Histograms derived from measurements (Table 1) of bone fragments. See text for derivation of estimated values.
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.
modem East African bone assemblages were biased by the preferential destruction of smaller bones, and only taxa > 100 kg were represented in greater than expected num-
bers. 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
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 (1969a) described collections from the White River Group that were dominated by squirrel-sized or smaller animals (75% Group I), as opposed to larger animals (25% 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, 1969b; Behrensmeyer, 1975; Kenobi, 1989).

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 II mammals 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 humerus 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 humeri 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, 1972; Kreutz, 1972; 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 cranial 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 the 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. Procuring then proceeds to more thoroughly remove flesh from these areas and continues on to areas containing less meat, such as the sides of the vertebral column and the middle parts of the fore and hind limbs. During this stage of "moderate" or "full" processing, the gleans region of the scapula, the proximal ends of the femur and humerus, the inframandibular, 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, 1989a, 1989b), 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. 6-10, tables 3, 4). Using the uniformitarian approach, the presence of these forms of processing within the Orellan assemblage can be compared to assemblages processed by extant carnivores. 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 was bitten off show sharp broken edges that were not grooved and caused by additional processing. Haynes (1983; table 2) characterized the bone processing abilities of extant hyenas, bears, canids, and felids based on the relative location 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 shafts. 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 carcase or carcase 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 strength to heavily process a bone assemblage. Also, many carnivores are capable of inflicting haemaphagous 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, 1989b), 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, 1980a, 1982). Also, some taxa characteristically inflict greater amounts of processing with less effort, such as the differences 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, bears, wolves, and lions routinely process the bones of bisons, caribou, water buffalo, and other large ungulates. If the only prey carcasses available to such large carnivores were Woodward-sized, these smaller carcasses might be considered entirely and no "footprint" 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 proportionally smaller carnivores. Recognition of the various degrees of processing is a useful first step in the analysis of bone modification. However, any discussion of bone processing would be useless 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 (1980a, 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.
The Orellan carnivore guild is well known from dental, cranial, and postcranial material (Mellott, 1971; Wang, 1989a; Bakhshi and Tedford, 1994; Bryant, 1994; Hunt, 1982; Wang and Tedford, 1986), 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. occidentalis have dentitions consisting of small incisors, robust premolars, and blade-like molars. These teeth would likely produce a processing signature resembling a blending of "felid-like" and "hyena-like" features, such as large conical premolars, large canines, and blade-like molars. 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 C. sp. (tiger-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 extant caniforms, characterized the Orellan taxa as having teeth and dentitions resembling those of extant canids, canines, and premolars, except for the presence of large conical pits and small amounts of gouging and severed ends of limb bones. If such a taxon were present, it is possible to suggest the dominant bone processing signature of the "style" and degree of processing, and the suites of potential processing signatures described above, is it possible to suggest the dominant bone processing signature of the "style" and degree of processing, and the suites of potential processing signatures described above. It is possible that the Orellan carnivores with the most "canid-like" dentitions, namely Hyaenodon, Hesperocyon, and Daphoenus hartshornianus, 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 had bone processing complete without the need for "residuals," or may have been expected to process bone assemblage during the initial feeding, or contributed to the overall processing over a long period of time by systematically or haphazardly scavenging in situ. Some studies of bone processing by extant carnivores have been able to distinguish between predation and scavenging (Haynes, 1953, 1982, 1975) while others have not (Miller, 1969; Sutcliffe, 1970). Kingdon (1977) stated that in situations in which 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 carnivores. The method whether or not a site was scavenger is a subject for additional study.

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 in situ. Some studies of bone processing by extant carnivores have been able to distinguish between predation and scavenging (Haynes, 1953, 1982, 1975) while others have not (Miller, 1969; Sutcliffe, 1970). Kingdon (1977) stated that in situations in which 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 carnivores. The method whether or not a site was scavenger 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 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; 3) destructive forces after death; 4) destruction; 5) digestion; 6) abrasion and exposure; and 7) 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 ac-
quired. The two biases of concern, then, are (5) and
(6).

Voorhies (1969b) stated that the most reliable pal-
 aeontological reconstructions are those based upon col-
lections from this but widespread floodplain de-
posits of relatively uniform lithology, such as those of the White River Group. This view was shared by
Edwards and Yatkola (1974), who attributed the excel-
 lent preservation of coprolites within the Orella Mem-
ber to be partly due to the fine-grained sediments, the
relatively low energy of the depositional environment, and the contribution of silt and clay-sized sediment to the burial and subsequent fossilization of coprol-
ites. According to Badgely (1986), vertebrate fossil
samples from floodplain deposits are largely autoch-
thonous, having accumulated in place with minimal
or preburial transport, and typically better represen-
t the range of body sizes present in ancient communities. While the fine-grained volcaniclastic deposits making up the Orella Member may not exactly corre-
spond to the episcopal fine-grained sediments of many
modern floodplains in the style of sedimentation, the
preservation of mammal bone in these settings prob-
ably is generally comparable. Episodic, low-energy
sheet flow over level surfaces by water moving silt-
and clay-sized sediment is common to both environ-
ments. 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 undis-
turbed under any but the lowest energy conditions.
These observations indicate that, in terms of the area
sampled, deposition of the Orella Member did not sig-
ificantly bias the bone assemblage with the exception
of possibly winnowing Group I bones from the sample
studied here.

In her study of time averaging in fluvial assem-
bles, Behrensmeyer (1982) estimated that for a flood-
plain assemblage, the amount of time involved ap-
proximates 100–10,000 years, and is in large part a func-
tion of the length of time present within each diastem,
the interval between flooding events that bury the
sediment. Based on radiometrically dated ashes and magnetostratigraphic correlations, the
Orellan NALMA lasted 1.7 million years (Prothero and
Whitehouse, 1988), and although no correspondence
between the Orella Member and the Orellan NALMA
is implied here, this provides some evidence 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 actinomorphous sample of coprolites and postcranial bone fragments from the Orella Member of the Brule Formation at UNSM localities 2967 and 2968 had been processed during the early Oligocene by mammalian carnivores over a period of more than 1.7 million years. Based on the degree of bone
breakage, erosion by stomach acids, bone articula-
tion, skeletal part representation, and prey fauna com-
position, the Orellan coprolites were probably pro-
duced 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, amphi-episodic Daphoenus prob-
ably produced most of the coprolites. Based on the fre-
quency and style of bone processing observed in a
large sample of postcranial fragments from the same
interval and locality, the bone assemblage was moder-
ately processed by carnivores of several body sizes
having well-defined dentitions that exhibited "end-like" processing conditions.

Based on body sizes and dentitions within the Orellan carnivore guild, the canids Hesperocyon and
Mephitax, and the amphi-episodic Daphoenus hespero-
cyonidus and D. vetus likely produced most of the bone processing observed in the sample. The uni-
formitarian approach is limited in its application in
this study because the Orellan and extant carnivora-humanus are not directly analogous. This study has dem-
sharize, however, that such indirect evidence as tooth
marks is, on a recognized, sufficient to establish which
taxa and the categories were processed, to what de-
gree the bones were processed, characteristic bone pro-
cessing in terms of an extant bone processor, and indi-
cate which taxa are the beneficient bone processors.

Haynes (1980a) stated that extant carnivores, like humans, leave and using 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 the living carnivore species can damage
bone distictively because of anatomical, me-
chemical, 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, 1989), 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 revealed. However, if 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.

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 unattainable 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 paleoecological and taphonomic importance.

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