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The influence of post-burial environment and plant-bone interactions on vertebrate preservation: an experimental taphonomic study

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Abstract of the Dissertation

The influence of post-burial environment and plant-bone interactions on vertebrate preservation: an experimental taphonomic study

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Differential preservation of bone due to varying local-to-global terrestrial environmental conditions is recognized as a pervasive bias throughout the fossil record. Furthermore, the distribution of these environments has varied considerably through time, profoundly affecting what is preserved in the fossil record, and where. Little is known regarding how environment-specific decay and diagenesis affect terrestrial bone preservation, and ultimately our reconstructions of paleoecology, diversity, and biogeography. To investigate short-term processes critical in the decay and diagenesis of buried bone, I performed a 14-month controlled taphonomic experiment which explored the individual and collective effects of 1) sediment hydrology and organic content [sand vs. silt/humus], 2) bone size [deer vs. rabbit vertebrae], and 3) plant association [gymnosperm vs. angiosperm] in controlled laboratory microcosms. Data included the measurement of leachate for calcium (Ca) using DCP-AES, sediment pH, bone mass change, and CT scanning to quantify changes in bone density. Results show that plant type, sediment type, and bone size all significantly interact to influence bone decay, with the effect depending on the context. Sediment type had the strongest influence overall, driving differences in pH, anoxia, mass/density loss, and Ca leaching. Plants were found to release substantial amounts of Ca, but did not differ by type. This experiment suggests that the process of bone decay: 1) is reduced by the presence of plant material, 2) depends on the surface area to volume ratio of a bone, and 3) is sediment specific: high-flow sand-dominated sediments erode bone at a high rate, while low-flow silt/humus-dominated sediments affect bone more slowly. Comparison of experimental data with fossil vertebrate distribution from the Late Jurassic Morrison Formation of North America suggests that the same factors are important for fossil preservation, but environmental differences exert a strong control over these processes. Furthermore, changes to local environmental conditions brought about by global climate patterns may have a profound impact on fossil preservation, affecting the spatial distribution of vertebrate remains over geologic time. This study has important implications for taphonomic interpretation of individual fossil sites, facies control of fossil preservation, and even large-scale paleobiogeographic reconstructions.

Dedication

This dissertation is dedicated to my family for always supporting me. To Summer, for always being there when I needed you. And to my friends and colleagues, who have been like a second family, without whom I would not have remained sane. I must also recognize my advisor, Catherine Forster, for letting me choose my own path.

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Chapter 1–Introduction

> "Anything that happens, happens. Anything that, in happening, causes something else to happen causes something else to happen. Anything that, in happening, causes itself to happen happens again. All of this, however, doesn't necessarily happen in chronological order."
>
> From "Mostly Harmless" by Douglas Adams

1. TAPHONOMIC PROCESSES

Following death, most organisms decompose completely and are recycled back into the local environment through multiple biotic and abiotic pathways. Of course, if this did not occur the world would have been overrun with the remains of the once living long ago. Under most circumstances this recycling process is thorough and (geologically speaking) fast-acting. On rare occasions the decomposition process is slowed by environmental conditions, such as rapid burial and water immersion, which prevent decay agents from acting effectively. Should these conditions persist, some portion of the remains may survive long enough for a secondary build-up of materials (usually minerals) to stabilize the remains. This suite of reactions can be loosely grouped together under the umbrella term "fossilization". Fossilization can be thought of as a race between decomposition processes and preservative processes working at different time scales. In most cases decomposition is rapid and wins out, but in the rare cases that preservative processes outpace decay, a fossil will develop.

The study of decomposition, preservation, and their mutual effect on fossilization potential is the purview of taphonomy. As first described by Efremov (1940), taphonomy includes all aspects of the passage of organisms from the biosphere into the lithosphere.

Taphonomy studies the physical and chemical processes that act on, and subsequent changes that occur to, once-living remains, including loss and decay of tissues, scattering of remains, physical breakage (fragmentation), transport, burial, diagenesis (alteration or replacement of original tissue), and discovery (Behrensmeyer et al. 2000, Lyman 1994, Martin 1999).

1.1 Surface and Subsurface Taphonomic Processes

The immediate environment plays an important role in directing the course of alterations to body tissues (including bone), the rate at which they occur, and the short-term survival of remains (for examples see Andrews 1995, Behrensmeyer 1978, Briggs and Kear 1993a, Fernández-Jalvo et al. 2002, Lyman 1994, Martin 1999, Pfretzschner 2006, Trueman et al. 2004). Factors affecting long-term survival can not be directly observed, however inferences drawn from archeological and fossil assemblages suggest that these, too, are influenced by environmental conditions (for examples see Hedges and Millard 1995, Hulbert et al. 1996, Nielsen-Marsh et al. 2007, Pfretzschner 2004, Pike et al. 2001). The preservation of vertebrate fossils is understood using approaches based on physical and/or chemical processes affecting remains. Research on these processes is further partitioned among those occurring at the surface and those following burial (subsurface).

At the surface bones from different taxa and of different size may be preferentially preserved or destroyed due to variation in physical processes, such as differential consumption, transport, and trampling, which may remove whole components of the biota from the potential fossil assemblage (Andrews 1995, Aslan and

Behrensmeyer 1996, Coard and Dennell 1995, Elder and Smith 1988, Lyman 1994). Chemical alteration to vertebrate tissues, especially bone, also occurs during surface exposure and may take place in concert with, or independent of, physical modifications (Fernández-Jalvo et al. 2002, Trueman et al. 2004). Modifications to vertebrate tissues by surface processes prior to burial have important repercussions for post-burial diagenesis and fossil preservation potential (Fernández-Jalvo et al. 2002, Nielsen-Marsh and Hedges 1997).

Following burial, physical processes acting on remains include invertebrate consumption, plant root attack, and sediment compaction (Bader et al. 2009, Lyman 1994, Martin 1999, Nicholson 1998, Smoke and Stahl 2004, Wilborn 2007). Chemical processes are often complex and involve alterations to both the mineral apatite and organic collagen fractions through autolytic, dissolution, and recrystallization mechanisms (Clarke 2004, Hedges 2002, Nielsen-Marsh and Hedges 1997, Pfretzschner 2006, Pike et al. 2001). The combined effect of the above chemical processes is capable of selectively removing individual bones, skeletons, or taxa, however our understanding of the bias imposed by subsurface processes within and between different environments remains poorly understood compared to our knowledge of surface processes. Whether subsurface taphonomic processes enhance or counteract patterns of bias imposed through surface processes remains to be determined. This gap in understanding means we may only be accounting for a fraction of the bias existing in the formation of the terrestrial vertebrate fossil record.

1.2 Understanding the Factors Responsible for Preservation

In order to elucidate these factors, taphonomic research employs the following approaches: 1) observation and experimentation on extant remains, 2) analysis of fossil remains, and 3) mathematical models.

A uniformitarian approach provides powerful diagnostic tools for interpreting many features of fossil assemblages (Andrews 1995, Behrensmeyer 1978, 1982, Behrensmeyer and Kidwell 1985, Cutler et al. 1999). Most taphonomic studies have dealt with observations on natural systems or performed experiments under natural conditions at the sediment-atmosphere or sediment-water interface (Andrews and Cook 1985, Aslan and Behrensmeyer 1996, Austin and Vivanco 2006, Boaz and Behrensmeyer 1976, Burnham et al. 2005, Davis and Briggs 1998, Demko et al. 1998, Elder and Smith 1984, Fernández-Jalvo et al. 2002, Ioannidou 2003, Kerbis Peterhans et al. 1993, Llona and Andrews 1999, Rich 1989, Sept 1994, Soja et al. 2004, Tappen 1994, Tappen 1992, Trueman et al. 2004, Weigelt 1989, Wuttke 1983). A smaller number of studies have examined the diagenetic behavior of buried remains under natural conditions (Bell et al. 1996, Child 1995, Dent et al. 2004, Hedges 2002, Henderson 1987, Nicholson 1996, Nicholson 1998, Nielsen-Marsh and Hedges 1999, Pfretzschner 2004). However, the difficulty in manipulating and controlling individual factors in complex natural systems make it difficult to know what factor or combination of factors is responsible for observed processes and results.

Direct observations on fossilized vertebrate remains include studies on the differential preservation of particular elements, structures, and tissues. Mineralized tissues such as bone and eggshell are preserved much more frequently than non-

mineralized tissues, although under certain conditions spectacular soft-tissue preservation can occur (e.g., Dal Sasso and Signore 1998, Grellet-Tinner 2005, Schweitzer et al. 2007, Wegweiser et al. 2004, Zhou et al. 2003). Buried vertebrate remains that become fossilized can be exposed to a multitude of environmental conditions over time as the surrounding burial environment continues to change. Remains may be reworked into adjacent strata, transported to new environments, and/or encounter shifting biogeochemical conditions (some of which result from decay of the organism itself). These factors, which may occur days to millions of years after burial or fossilization, can obscure the original environmental signature making it difficult to systematically study the environmental pathways necessary for preservation *post hoc* (Clarke 2004, Wings 2004).

Complex mathematical models based on the physicochemical properties of tissues, sediment, and porewater have been used to predict both the short- and long-term behavior of organic tissues after burial. In modeling complex biogeochemical reactions, researchers have compartmentalized the tissue-sediment-porewater system into separate domains. Many studies have focused on mineral-porewater interactions, ignoring or discounting the role of organic fraction loss and microbial influence in decomposition (Hedges and Millard 1995, Pike et al. 2001, Wang and Cerling 1994). Others have looked only at collagen loss through chemical degradation (Collins et al. 1995). While aspects of each mathematical model have been observed in many bones (fossil and modern) and environments, the factors that drive decomposition–be it hydrology, microbial attack, bone structure/chemistry, etc.–has yet to be satisfactorily addressed.

1.3 A New Direction for Taphonomic Research

Taphonomic research should ideally be applicable to the study of more than a single fossil type, assemblage, locality, taxon, or environment. Taphonomic studies should have a broader context in order to reveal common patterns of preservation and examine spatiotemporal trends in preservation. This knowledge can in turn be applied to understanding broader-scale climatic, environmental, and ecological context during fossil assemblage formation.

This approach requires an understanding of how small-scale processes (those operating directly on the remains) ultimately influence the structure of fossil assemblages. Primary among these is the effect of biogeochemical conditions in the post-burial environment on ossified vertebrate tissues (i.e., bone, teeth). Post-burial biogeochemical conditions directly impact decomposition and diagenesis by controlling the biotic and abiotic processes acting on remains (Berna et al. 2004, Child 1995, Fernández-Jalvo et al. 2002, Hedges 2002, Nicholson 1998, Nielsen-Marsh et al. 2007, Reiche et al. 2003).

Paleoecology relies on accurate interpretations of fossil assemblages to reconstruct past ecosystems. The environmental specificity of surface and subsurface processes allows taphonomic data to be applied to understanding past environmental settings and ecological relationships among taxa, including diversity, habitat preferences, and rank abundance (Behrensmeyer et al. 2000, Blob and Fiorillo 1996, Cutler et al. 1999, Dodson et al. 1980, Martin et al. 1999, Moore et al. 2007). The information gained from past ecosystems has important consequences for how we view biogeographic and evolutionary patterns over time. In other words, understanding the proximal

environmental factors that affect organic preservation ultimately impacts all larger scale paleoecological interpretations, such as ecosystem reconstruction and faunal diversity patterns. Such patterns help us understand how climate and tectonics help direct evolution and may be important for understanding periods of major climatic upheaval and mass extinction (Behrensmeyer et al. 1992, DiMichele et al. 2004, Jablonski and Sepkoski 1996).

1.4 Description of the Dissertation

This dissertation grew out of an interest in large-scale fossil distribution patterns and their perceived relationship with climate patterns. While working on a project studying the distribution of dinosaur fossils I noticed an interesting correlation between the areas of highest diversity and climate type (biome). This diversity pattern strongly differs from the present unimodal diversity pattern, where biodiversity is centered on the equator and decreases towards the poles. The Mesozoic pattern appears bimodal with highest diversity located over the midlatitudes, and is demonstrated by both animal and plant fossils. This could be interpreted as evidence of a biota evolving under a globally warm "hot house", providing a response unlike that currently observed under our interglacial "cold house" conditions. However, the biome where the highest Mesozoic diversity is found also supported the types of environments most beneficial for vertebrate preservation (Rees et al. 2004). Therefore, this Mesozoic biodiversity pattern may be the result of large-scale taphonomic bias rather than a reflection of the actual living biodiversity gradient. In seeking to address this problem, my research focuses on the following questions:

1. Through what mechanisms do different biogeochemical conditions in the post-burial environment affect the decomposition of vertebrate bone (Chapters 2 and 3)?
2. Which biogeochemical conditions, or combination of conditions, are necessary for bone preservation (Chapter 2)?
3. Is vertebrate fossil preservation correlated with the distribution of particular paleoenvironmental and/or biogeochemical indicators in the fossil record (Chapter 4)?
4. Through what mechanisms are small-scale biogeochemical processes linked to large-scale vertebrate fossil distribution patterns? What, if any, effect does this have on our understanding of paleobiodiversity (Chapter 5)?

In designing this dissertation I wanted to examine not only the biogeochemical aspects of fossil preservation, but also how variation in these factors may scale up to affect fossil distribution patterns at the landscape level and above. A major goal of this work is to provide the necessary framework for others interested in investigating these and similar questions in the future.

1.5 Organization of the Dissertation

This work consists of two main parts. The first part consists of Chapters 2 and 3, which describe a controlled, laboratory-based taphonomy experiment examining the effects of various factors (bone size, sediment hydrology, plant type) on bone decomposition. The experimental design, methods, and major results are found in Chapter 2. Chapter 3 includes a detailed description of physical changes to each bone

from the experimental treatments, including mass measurements, volumetric water displacement, and density change using computed tomography (CT). The potential application of this method for future taphonomic studies is discussed. The second part consists of Chapters 4 and 5, looking at the larger-scale implications of the small-scale processes examined in the first part. In Chapter 4 large-scale vertebrate fossil distribution patterns of the Late Jurassic Morrison Formation were analyzed using multivariate statistical methods. Chapter 5 examines the theoretical origin and structure of a hierarchical relationship between climate and fossil preservation patterns, including the effect this interaction may have on actual versus reconstructed paleobiodiversity. Chapter 6 contains a discussion of conclusions and future directions. Appendices at the end collect data used in Chapters 2 through 4.

Chapter 2–Experimental Taphonomic Analysis of Bone Decomposition under Different Environmental Conditions

ABSTRACT

While studies of surface taphonomic processes have provided a wealth of information, this represents only a part of the fossilization pathway and an empirical understanding of post-burial processes remains incomplete. Laboratory-based taphonomic experiments have been used successfully to study decay and diagenesis, providing critical information on fossilization mechanisms. To investigate short-term processes critical in the decay and diagenesis of buried bone, a 14-month controlled taphonomic experiment was performed that explored the individual and collective effects of 1) sediment hydrology [sand vs. silt/humus], 2) bone size [deer vs. rabbit vertebrae], and 3) plant association [gymnosperm vs. angiosperm] in controlled laboratory microcosms. Data included the measurement of leachate for calcium (Ca) using DCP-AES, sediment pH, bone mass change, and quantification of bone density change using CT imaging. Plant type, sediment type, and bone size all significantly interact to influence bone decay, with the effect depending on the context. Sediment type had the strongest influence overall, driving differences in pH, anoxia, mass/density loss, and Ca leaching. Plants were found to release substantial amounts of Ca, but did not differ by type. This experiment suggests that the process of bone decay: 1) is reduced by the presence of abundant plant material, 2) is strongly dependent on the surface area to volume ratio of a bone, and 3) is sediment specific: porous high-flow sediments erode bone at a high rate, while semipermeable low-flow sediments affect bone more slowly. This study has important implications for

taphonomic interpretation of individual fossil sites, understanding facies control of fossil preservation, and the use of vertebrate fossil data in large-scale paleobiogeographic reconstructions.

2.1 INTRODUCTION

Many studies have established a connection between prevailing environmental factors on sediment surfaces and their effect on the potential for the preservation of vertebrate remains (Andrews 1995, Andrews and Cook 1985, Aslan and Behrensmeyer 1996, Behrensmeyer 1978, Davis and Briggs 1998, Fernández-Jalvo et al. 2002, Kerbis Peterhans et al. 1993, Lyman 1994, Sept 1994, Tappen 1994, Trueman et al. 2004, Weigelt 1989). However, the effect of subsurface conditions on buried remains varies between environments (Dent et al. 2004, Henderson 1987, Jans et al. 2002, Nicholson 1998, Nielsen-Marsh et al. 2007, Pfretzschner 2006, Smith et al. 2007) and may play an equal or greater role in determining preservation but has received far less attention and remains inadequately understood.

The various approaches to bone taphonomy have resulted in different, and sometimes conflicting, predictions regarding the processes and conditions driving bone decomposition. Hedges (2002) and Hedges and Millard (1995) suggest that dissolution of bone apatite by water is the primary pathway of decomposition and diagenesis, with collagen loss playing a minor role. However, others contend that collagen decomposition is the most important pathway of bone decomposition, with mineral loss occurring as a byproduct (Child 1995, Nicholson 1996). Alternatively, the decomposition pathway may

depend on environmental conditions: alkaline environments attack collagen first, while acidic environments attack bone mineral first (Fernández-Jalvo et al. 2002). While lacking a consensus, what this body of research does suggest is that sediment type and hydrology, vegetation, and body size all play a role in bone preservation.

Sediment type and hydrology are important drivers of vertebrate decomposition (Hedges 2002, Lillie and Smith 2007, Pike et al. 2001, Reiche et al. 2003) by controlling saturation, flow rate, pH, solute concentration, oxygen content, and microbial activity of porewater (Falter and Sansone 2000, Gordon and Buikstra 1981, Henderson 1987, Rockhold et al. 2005, Sharma and McInerney 1994). Depending on the combination of these conditions percolating groundwater (and its microbiota) can rapidly remove the mineral (Gordon and Buikstra 1981, Hare 1980, Nicholson 1998) and/or organic components of bone (Andrews 1995, Hedges and Millard 1995, Henderson 1987), weakening the overall integrity of skeletal elements.

The effect of differences in plant community on vertebrate preservation is overlooked in current taphonomic studies, despite its important role in determining sediment and soil properties. Plant roots excrete a variety of organic acids, which mobilize metabolically necessary minerals for absorption (Berner et al. 2004, Cochran and Berner 1996, Raven et al. 1999). The decomposition of plant material decreases porewater pH due to the release of secondary metabolites (Yavitt and Fahey 1986) and may result in the creation of humus, a recalcitrant by-product of plant decay (Berg and McClaugherty 2003). Humics may prevent bacterial digestion of collagen by cross-linking with it (van Klinken and Hedges 1995). Plant species differ significantly in leaf structure and composition, which influences nutrient cycling dynamics among

communities (Enright 1999, Enriquez et al. 1993, Knops et al. 2002, Pereira et al. 1998). Furthermore, the functional group to which a plant belongs (deciduous/perennial, tree, shrub, grass) or its living environment (tropical, temperate, boreal) have a larger impacts on plant physiognomy and secondary metabolites than phylogeny (Aerts 1997, Berg and McClaugherty 2003, Cornelissen et al. 2004, Hobbie et al. 2006).

Overall body size and individual bone size are known to play a large role in preservation potential. Smaller bones are almost always destroyed before larger bones through surface and subsurface processes (Andrews 1995, Behrensmeyer 1978, Nicholson 1998, Von Endt and Ortner 1984). Additionally, a positive relationship exists between bone mass (size), density, and preservation potential (Behrensmeyer 1978, Behrensmeyer 1988, Dirrigl 2001, Lam and Pearson 2005, Lyman 1994).

Experimental research under controlled laboratory conditions is necessary to accurately define the contribution of different environmental factors to vertebrate decomposition and the mechanisms driving observed patterns. This approach has been used successfully for invertebrate taphonomy (Briggs and Kear 1993a, b, Kear et al. 1995, Martin et al. 2005, Sagemann et al. 1999) and some studies of this type exist for terrestrial vertebrates (Haslam and Tibbett 2009, Stokes et al. 2009, Tibbett et al. 2004), however only two experiments directly address bone preservation (Daniel 2003, Von Endt and Ortner 1984). The laboratory taphonomic experiment described here was designed with two goals in mind: 1) to examine the singular and collective effects of specific environmental parameters on bone decay, and 2) to provide a quantitative, controlled experimental model for studying modes of preservation and diagenesis in vertebrate tissues.

2.2 DESCRIPTION OF EXPERIMENT

2.2.1 Experimental Design

Based on a literature review the three environmental factors that play the largest known role in bone decomposition and diagenesis are as follows:

1) Sediment hydrology: Two types of experimental burial matrix were created to mimic common but contrasting generalized depositional environments: i) a High Flow/Low Organic (HF/LO) matrix representing a fluvial channel environment and ii) a Low Flow/High Organic (LF/HO) matrix representing an organic-rich soil.
2) Bone size: Two different sized vertebrae, from deer (large) and rabbit (small).
3) Plant presence and type: The overall effect of presence or absence of vascular plant material in the post-burial environment was considered. Plant material was divided into angiosperm and gymnosperm treatments.

2.2.2 Hypotheses and Predictions

To test the effects of these three environmental factors on bone decay, a series of hypotheses were developed.

Hypothesis I

H_1: The Low Flow/High Organic (LF/HO) matrix will preserve interred bone of both sizes better than the High Flow/Low Organic (HF/LO) matrix.

H_0: There will be no discernable relationship between degree of decay and the type of experimental matrix.

Predictions: The abundant organics and small grain size of LF/HO matrix will lead to a lower pH (≤6), widespread anoxia, and slow flow rate will support local saturation surrounding the bone, counteracting mineral removal and resulting in generally well-preserved bone. Large grain size and open pore structure of HF/LO matrix will result in near-neutral pH (~7), low anoxia, and high flow rate supporting greater leaching of bone tissue components and resulting in poor preservation.

Hypothesis II

H_1: The deer and rabbit vertebrae will be poorly preserved in the presence of plant material and well preserved in experimental matrix alone.

H_0: There will be no difference in bone preservation between matrix types with and without plant material.

Predictions: The presence of plant material will lead to lower porewater pH, which will enhance the decay of bone regardless of sediment type.

Hypothesis III

H_1: Bones interred with angiosperm material will be better preserved than bones interred with gymnosperm material.

H_0: Differences between plant treatments will be non-significant. Any effects of differing phytochemistry between angiosperm and gymnosperm material will be minor compared to the overall effect of plant presence on the buried bone.

Predictions: The decay of gymnosperm material will create more acidic porewater in the experimental matrix and leach more bone mineral than angiosperm material. This effect should be more pronounced in HF/LO matrix than LF/HO matrix treatments.

Hypothesis IV

H_1: The smaller rabbit vertebrae will be poorly preserved compared to the much larger deer vertebrae.

H_0: There will be no difference in preservation quality between rabbit and deer vertebrae.

Predictions: Despite decaying at the same rate deer vertebrae will lose a smaller proportion of their mass and density due to having a smaller surface area-to-volume ratio than rabbit vertebrae leading to differential preservation between deer and rabbit vertebrae when buried under the same conditions.

2.3 MATERIALS AND METHODS

2.3.1 Treatment Descriptions

Matrix Type

Each experimental matrix was created by mixing different proportions of sand, silt, and peat derived from common sources. The sand and peat (*Sphagnum* sp.) were purchased from a home supply store and the silt was collected from a Pleistocene glacial loess deposit near Dyersburg, Tennessee. HF/LO matrix contains 90% sand and 10% silt by volume, while LF/HO matrix contains 20% sand, 40% silt, and 40% peat by volume. This method of creating stock sediment types was used in order to maintain tighter

control over sediment composition, reduce variation between treatments, and prevent the effects of locality-specific sediment characteristics.

Bone Size

Farm-raised adult rabbit (*Oryctolagus cuniculus*, sex unknown) and white-tailed deer (*Odocoileus virginianus*, female) vertebrae were used. Deer and rabbit vertebrae differ in mass by an order of magnitude (average rabbit=1.3 g, deer=28.2 g). Initial mass and volume measurements are available in Table 3.2. Cervical and thoracic vertebrae were chosen because they share a similar morphology across most tetrapod taxa and are often preserved as fossils. Before use all vertebrae were mechanically separated and cleaned of flesh by hand with scalpel, scissors, and forceps.

Plant Type

Modern representatives of the major gymnosperm, fern, and angiosperm families were used. Gymnosperm and fern families used in this study were grouped into a single treatment (henceforth "gymnosperms") and included members of the Taxodiaceae, Cycadales, Cyatheaceae and Osmundaceae. Angiosperm families included the Magnoliaceae, Lauraceae, and Arecaceae. One representative of each family was used. Leaves from each group were obtained from the greenhouse and campus of Stony Brook University (Long Island, NY), washed with deionized water, toweled dry, and cut into 12 cm lengths. Plant treatments received a total of 7 g of mixed leaves from the angiosperm or gymnosperm group. An approximately equal proportion of each species was included in their respective treatment group.

2.3.2 Experimental Apparatus

Experimental treatments containing all combinations of the three parameters (plus controls) were synthesized and placed into individual containers (12 experimental treatments and 6 control, see Table 2.1). Each treatment was replicated three times for a total of 54 experimental containers, each consisting of the following items:

- A 2-liter plastic soda bottle with bottom removed, cleaned, and inverted to form a funnel-shaped outlet.
- 1.5 liters of experimental matrix.
- In addition to microbes already presumably present in the experimental matrix, an additional innoculation of ca. 2 mL from: i) water that had contained raw chicken skin and sat outdoors for one week; and ii) dark, organic-rich mud from a sump pond on the Stony Brook campus, increased the diversity of microbial decomposers.
- A 15 × 15 cm square of landscape cloth covering the bottle outlet to prevent sediment loss.
- A polypropylene nozzle glued to the soda bottle cap and screwed onto the bottle outlet (former bottle mouth) for attachment to drainage system.

Each container was connected to a one-way water delivery and collection system made of lengths of clear plastic Tygon™ tubing and polypropylene T-joints (The Tapho-O-Matic, Figure 2.1). All treatments were run in the laboratory at a constant temperature (~18˚ C) and water-moisture level, since variations in these parameters have been found to have a large effect on the rate of chemical reactions related to diagenesis (Andrews 1995). Deionized (DI) water was delivered through a system of PVC piping maintained matrix

saturation at all times. DI water pH was maintained at the level of natural rainwater (5.6-5.7) using an automatic pH controller (AZOO Soho pH Controller) attached to a CO_2 tank with a regulator and solenoid system (Milwaukee model MA957), which was attached to an aquarium CO_2 reactor kept in the main DI water feeder tank. The pH of the water tank was recorded from the pH controller on a daily basis. After passing through a container, water was drained via vinyl tubing into a sink and not recycled.

Bone and plant material were placed in the approximate middle of the container, towards the center, to maintain as equal a volume as possible of sediment on all sides surrounding the material. Each vertebra was placed with the spinous process facing upwards, parallel to water flow. When interred together with bone, plant material was arrayed in a mat underneath the vertebra in contact with the centrum (Figure 2.1A).

Table 2.1: Description of experimental and control treatments used in this project. HF/LO=High Flow/Low Organic, LF/HO=Low Flow/High Organic.

		Experimental Matrix	
		HF/LO	**LF/HO**
Treatment	**Angiosperm+Bone**	Rabbit w/ plants *3 replicates*	Rabbit w/ plants *3 replicates*
		Deer w/ plants *3 replicates*	Deer w/ plants *3 replicates*
	Gymnosperm+Bone	Rabbit w/ plants *3 replicates*	Rabbit w/ plants *3 replicates*
		Deer w/ plants *3 replicates*	Deer w/ plants *3 replicates*
	Bone Alone	Rabbit only *3 replicates*	Rabbit only *3 replicates*
		Deer only *3 replicates*	Deer only *3 replicates*
	Angiosperm Alone	Plants only *3 replicates*	Plants only *3 replicates*
	Gymnosperm Alone	Plants only *3 replicates*	Plants only *3 replicates*
	Matrix Control	No bone or plants *3 replicates*	No bone or plants *3 replicates*

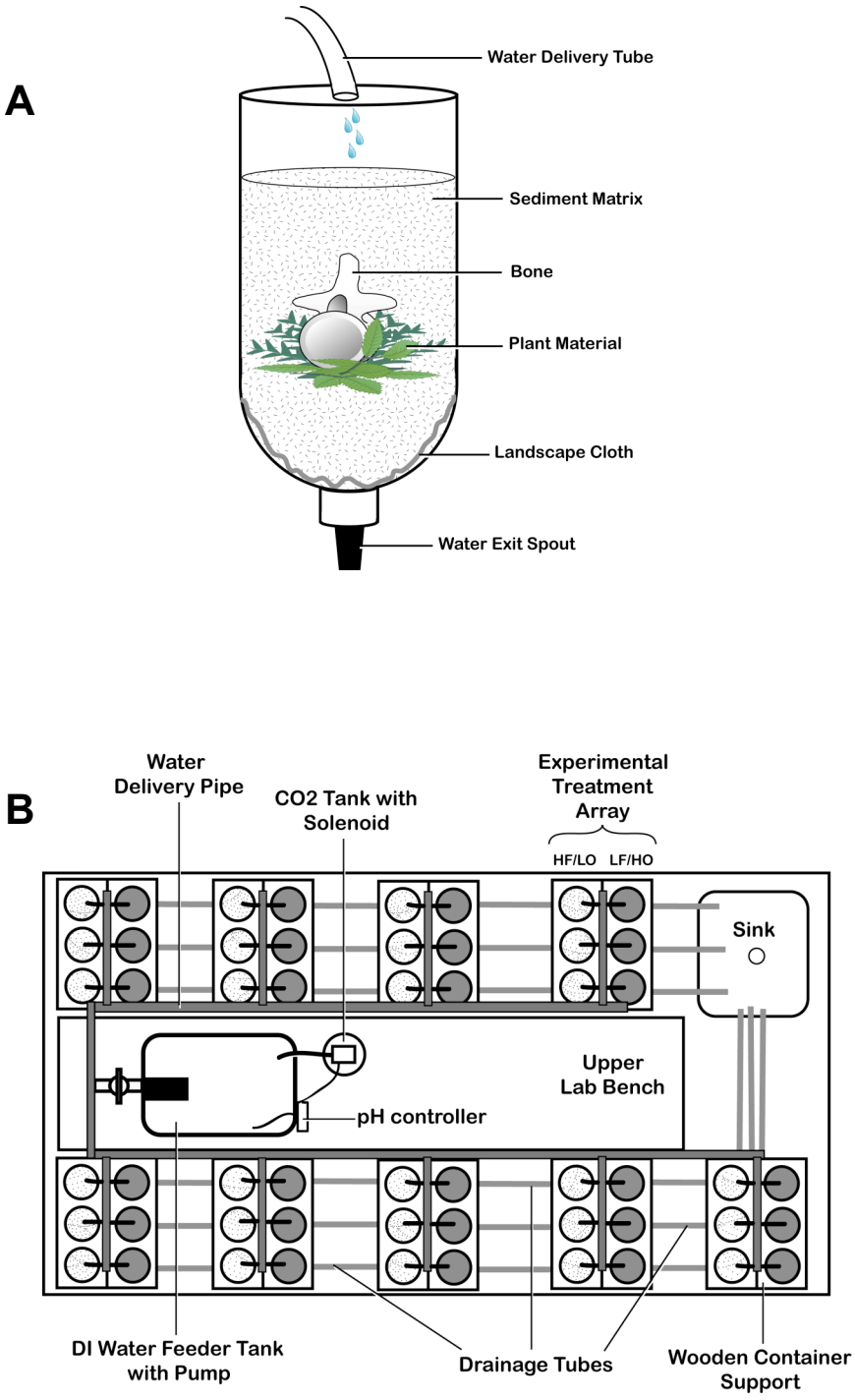


Figure 2.1: Diagram of experimental apparatus ("Taph-O-Matic"). A) Individual container showing placement of bone and plant material. Permeable landscape cloth prevents sediment loss. B) Full experimental design viewed from above. Deionized source water (not shown) empties into the feeder tank, where CO_2 is added to lower the pH. This water is then fed to individual containers through a PVC pipe system. Wastewater empties through tubing at the bottom of each container into a sink. Upper lab bench stands approximately 50 cm above lower level.

2.3.3 Experimental Period

Experimental matrix systems within each container were allowed to equilibrate with percolating water for one month before treatment began. Due to limited CT scanner availability, treatments including rabbit bones were buried up to one month after those including deer bones. The experimental period lasted for 13 months, from September 2005 to November 2006 for treatments including deer vertebrae and October 2005 to December 2006 for treatments including rabbit vertebrae, each identical amounts of time. Plant and sediment controls were interred from September 2005 to December 2006. Comparable taphonomic experiments have found diagenetic alteration within a similarly short time (e.g., Briggs and Kear 1993a, Brock et al. 1999). Once buried, bone and plant material was not removed or disturbed. After 13 months any remaining plant and bone material was removed from the container and a small sediment sample was taken for chemical analysis from near the bone/plant material. The containers were allowed to run for two additional months following bone/plant removal to follow any changes in the matrix.

2.3.4 Analyses

Porewater pH

Porewater pH within each container was measured weekly using a digital soil pH meter with automatic temperature compensation (Omega PHH-200 with Hanna Instruments pH probe). The probe was placed into a hole 12-14 cm. deep and varied in position between measurements. Temperature in each container was recorded, but found to follow changes in ambient room temperature and were not included in analyses.

Calcium Content of Porewater and Matrix

Water samples were collected monthly from the exit spout of each container to determine the dissolved calcium concentration leaving each container. All water samples were filtered using a 0.2 μm nylon syringe filter to remove bacteria and fine particles, then stored in glass vials under refrigeration until analysis. Calcium concentration in each sample was measured by Direct Current Plasma Atomic Emission Spectrometry (DCP-AES) using a Beckman Instruments argon plasma source with ARL SpectraSpan VB Emission Spectrometer located in the Geosciences Department at Stony Brook University. A standard measurement technique was employed. Before analysis a ~2 mL aliquot of each sample was taken and HCl added to ensure the calcium is fully dissolved. Each aliquot was then measured three times and these numbers averaged to obtain the calcium concentration (in ppm) for a sample.

Sediment samples were collected before and after the experiment and analyzed for chemical composition, including calcium content, in the lab of Dr. Cynthia Stiles at the University of Wisconsin–Madison. Sample preparation followed the protocol of Karanthanasis and Hayek (1996). Samples were oven-dried, ground, and passed through a 200 mesh sieve. A mixture of 8 g. sample and 2 g. cellulose binder were then pressed into a pellet for XRF. Total elemental concentrations were determined using X-ray fluorescence (XRF) on a Bruker AXS-model 3400 spectrometer (Bruker AXS Corp., Fitchburg, WI) (Karathanasis and Hayek 1996, Singer and Janitsky 1986). Loss on ignition at 1025ºC was determined on a sub-sample of each ground sample for entry into the XRF sample input system, to recalculate total elemental contents and account for compounds or elements not evaluated in the scans. An initial baseline measurement was

taken for comparison to the final experimental sample for chemical changes that could indicate internal conditions and potential diagenetic processes. The initial calcium value for each experimental matrix was calculated based on XRF-measured concentrations from each constituent and adjusted for the relative volumetric proportion using the following formula:

$$\frac{\left(\frac{\text{wt\%Ca} \times k \text{ mg kg}^{-1}}{1000 \text{ g kg}^{-1}}\right) \times \left(\rho_{\text{ sediment}} \text{ g cm}^{-3}\right) \times \left(\text{V}_{\text{sediment}} \text{ cm}^{3}\right)}{1000 \text{ mg g}^{-1}} = \text{g Ca}$$

Where wt%Ca is the measured XRF value, *k* is a conversion factor (7145 for CaO, 10,000 for Ca), ρ is the density of the sediment, and V is the volume of the sediment added to the experimental matrix for a single container. The amount of calcium present for that constituent in the experimental matrix is given in grams. The value from each constituent is added together to provide an approximation of the total amount of calcium present in the container at the beginning of the experiment. The initial amount of calcium calculated from this equation was 9.12 g calcium for LF/HO matrix and 27.8 g calcium for HF/LO matrix. Final calcium XRF values for each container at the end of the experiment were converted to grams Ca with the equation:

$$\frac{\left(\frac{\text{wt\%Ca} \times k \text{ mg kg}^{-1}}{1000 \text{ cm}^{3} \text{ kg}^{-1}}\right) \times 1500 \text{ cm}^{3}}{1000 \text{ mg g}^{-1}} = \text{ g Ca}$$

With all values same as above. 1500 cm^3 is the total volume of sediment added to a container. Calcium values given in grams are for comparison of before and after changes in matrix calcium, all other sediment calcium data refers to concentration values (ppm).

Matrix Hydraulic Conductivity

Following completion of the experiment, the sediment hydraulic conductivity in each container was measured with a handheld mini-disk infiltrometer (Decagon Devices, Inc.). Hydraulic conductivity is a dimensionless measure of the ease with which water flows through a porous medium in response to potential gradients, such as moisture, solute concentration, or gravity (Brady 1974), and is considered one of the most important hydraulic properties of a sediment due to its influence over water flow, solute transport, and diagenetic processes (Hedges, 2002, Zhang 1997). This property was measured for each treatment container to understand the connection between the physical properties of each sediment type and their influence over treatment effects.

Bone Mass and Density Loss

The pre- and post-treatment mass of each vertebra was measured on a digital balance to the nearest 0.01 g. after air drying for 1 hour. Bones were sealed and stored in a freezer until used in the experiment. At the end of the experiment all bones were visually inspected under a stereomicroscope and photographed for documenting differences in surface condition.

Many bones demonstrate very little overall volume change during decomposition (Hedges and Millard 1995); in these cases mass loss will reflect a change in the bulk

density of a bone. Mass loss alone is not enough to determine mineral density change, since a decrease in bone mass can be due to loss of the organic components with little effect on mineral density. Furthermore, bone tissue differs in internal surface area and reactivity (i.e., compact vs. spongy bone) (Bigi et al. 1997). Therefore density cannot be expected to change uniformly. To address this issue all vertebrae were subjected to X-ray computed tomography (CT) before and after burial using a GE Lightspeed 16 scanner at Stony Brook University Hospital. The internal densities of all vertebrae were then assessed using the program Microview (GE Healthcare). A complete description of this method is covered in Chapter 3.

Changes in internal density values can act as a proxy for loss of bone apatite (Lam et al. 1998, Lam et al. 2003). Bone mineral matrix is much denser than its organic counterpart and will show up as lighter values where X-rays are reflected. Mineral loss will show up as an increase in the shade of demineralized areas, corresponding to greater X-ray transmittance. The percent change between before and after measurements for each bone was calculated for both mass and density data. In the event that a bone was not recovered, it was considered a 100% change (i.e., a complete loss of mass and density).

SEM of Bone Surfaces

The surface morphology and chemical composition of selected bones from each sediment treatment were characterized using a high resolution Scanning Electron Microscope with Field Emission Gun filament (SFEG-SEM, model: LEO 1550) and outfitted with an Energy Dispersive Spectrometer (EDS, model: EDAX Phoenix) in the Materials Science And Engineering Department at Stony brook University. Samples were

fixed on aluminum plates with carbon tape and sputter-coated with 4-6 nm gold (Edwards 150B). SEM images were taken at a variety of scales with corresponding EDS measurements on elemental composition of the surface under the electron beam. Higher peaks in the EDS curve indicate qualitatively greater amounts of a given element in the sample area.

Plant Material

At the end of the experiment any remaining plant material was recovered from the container, visually inspected and photographed for physical decomposition, then sealed in plastic bags and stored under refrigeration. Surface features and composition of selected plant material were also examined under SEM-EDS.

2.3.5 Statistical Analyses

Box-Cox derived power transformations were applied to leached calcium, porewater pH, hydraulic conductivity, and sediment calcium data in order to satisfy the assumptions of parametric statistical tests. Percent change in bone mass and density data were both arcsin transformed for the same reason (Sokal and Rohlf 1995). Leached calcium and porewater pH data from each container were averaged over three separate 1-month time periods in order to test differences in these data related to changes over time. The time periods were identified following examination of experiment-wide porewater pH data.

Full factorial three-way analysis of variance (ANOVA) of matrix type, bone size, and plant type was applied to averaged data. Repeated measures ANOVA (RM-ANOVA)

was applied to porewater pH and leached calcium data because major changes were noted during the course of the experiment. Subsamples of these data were pooled into three discrete time periods, “Early”, “Middle”, and “Late”, corresponding to large changes in average porewater pH across treatments (see Results). For each time period four samples per replicate were chosen in leached calcium and ten samples per replicate were chosen for porewater pH. Three-way ANOVA was also performed separately on each time period. A t-test was performed on the regression slopes to assess interaction effects between treatments and data, with a significant difference between slopes indicating a differential response across treatments (interaction). Analyses were performed using JMP 7 (SAS Institute, Inc.) and SPSS 11.0 for Mac (SPSS, Inc.).

2.4 RESULTS

2.4.1 Changes Over the Experimental Period

Both porewater pH and leached calcium output were highly variable and changed over time as the experiment progressed. Porewater pH was sensitive to relatively small changes in the pH of deionized (DI) water feeding the system. This dependence resulted in three distinct time periods, each characterized by an increase or decrease in the average DI water pH entering the system: Early (August 2005-March 2006), Middle (March 2006-September 2006), and Late (September 2006-February 2007). In the Early period, from December 2005 to March 2006, average DI water pH fell below ~5.5 due to uncontrollable problems with the building DI system. Despite this, HF/LO treatments maintained a higher pH than LF/HO treatments, however the average pH value for all

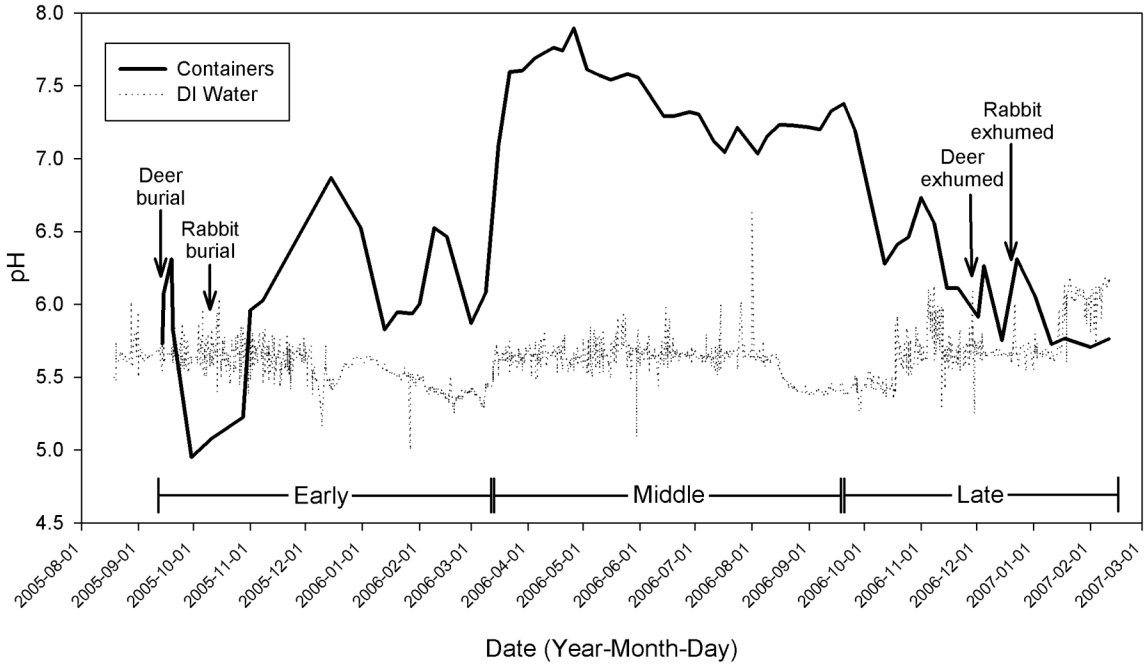


Figure 2.2. Average porewater pH for all containers and DI water feeder tank pH over the course of the experiment. Early, Middle, and Late periods of the experiment are indicated below. See text for explanation.

treatment replicates was relatively low (Figure 2.2). Leached calcium levels were correspondingly low across treatments. During the Middle period DI water pH returned to and was successfully maintained in the intended range of 5.6-5.7 and major pH differences between all treatments virtually disappeared. Leached calcium levels were among the highest observed in the experiment during the Middle period. Another decrease in DI water pH occurred six months later. This event preceded the Late period, during which lower average porewater pH values and lower leached calcium again prevailed. Individual patterns in porewater pH and leached calcium results among treatments are discussed below.

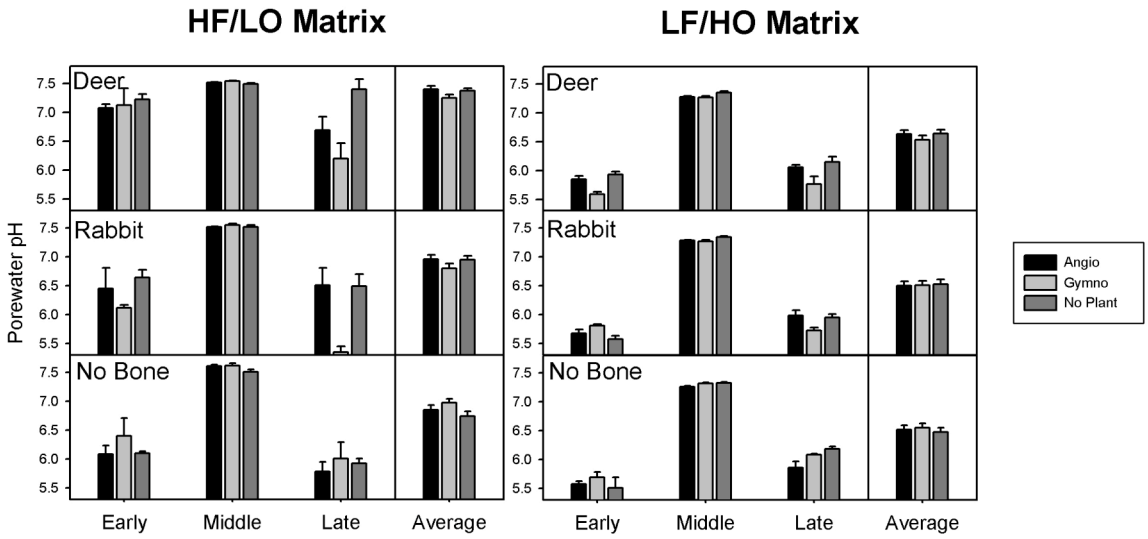


Figure 2.3: Average porewater pH over time for each treatment during the experiment, separated by sediment type. Angio=treatments including angiosperm leaves, Gymno=treatments including gymnosperm leaves, No Plant=bone and sediment controls. Error bars represent the standard error for each treatment. Note different Y-axis scales.

2.4.2 Matrix Treatments

Porewater pH

Porewater pH differed significantly within treatments between the three time periods (RM-ANOVA: $F_{2,72}$=943.088, p<0.001). Significant interactions with the treatment factors indicate changing conditions over time (Table 2.2A). Only matrix type remained a significant factor throughout the experiment, with LF/HO matrix (6.5-6.7) maintaining a consistently lower pH than HF/LO matrix (6.7-7.4) (RM-ANOVA: $F_{1,36}$=122.440, p<0.001). This difference remained during the Early, Middle, and Late periods (Figure 2.3), however the effect of other factors changed over time.

Early in the experiment (Table 2.2B), treatments with bone had significantly higher pH, with the effect greater in LF/HO the HF/LO matrix (ANOVA: $F_{2,36}$=11.474,

$p<0.001$). This pattern appears driven by treatments with deer bone. Plant controls and all treatments containing rabbit bone showed little difference in pH.

During the Middle period (Table 2.2C), pH differences between deer and rabbit bone treatments shrank but remained distinct from controls containing no bone (ANOVA: $F_{2,36}=3.802$, $p<0.05$). Plant effects appeared non-significant, however this may be due to an opposing interaction between matrix types (ANOVA: $F_{2,36}=12.277$, $p<0.001$). In HF/LO matrix both plant treatments had lower pH than no-plant controls; this pattern was reversed in LF/HO matrix.

Late in the experiment (Table 2.2D) bone remained significant with its effect depending on its combination with matrix type (ANOVA: $F_{2,36}=13.139$, $p<0.001$). Gymnosperm treatments were more acidic than angiosperm treatments in HF/LO matrix (0.2-0.5 pH units), which did not exist in LF/HO matrix treatments, signifying a plant × matrix interaction (ANOVA: $F_{4,36}=5.903$, $p<0.001$). Rabbit+plant treatments had a lower pH than deer+plant and control treatments, which created a significant bone × plant interaction effect (ANOVA: $F_{4,36}=5.903$, $p<0.01$).

Leached Calcium

Leached calcium results varied significantly between time periods (RM-ANOVA: $F_{2,72}=41.58$, $p< 0.001$), following a similar pattern of multiple interactions among factors (Table 2.3A). Across time periods leached calcium (Figure 2.4) was greater in LF/HO matrix (10-45 ppm) compared to HF/LO matrix (0.5-7 ppm) (RM-ANOVA: $F_{1,36}=480.31$, $p< 0.001$).

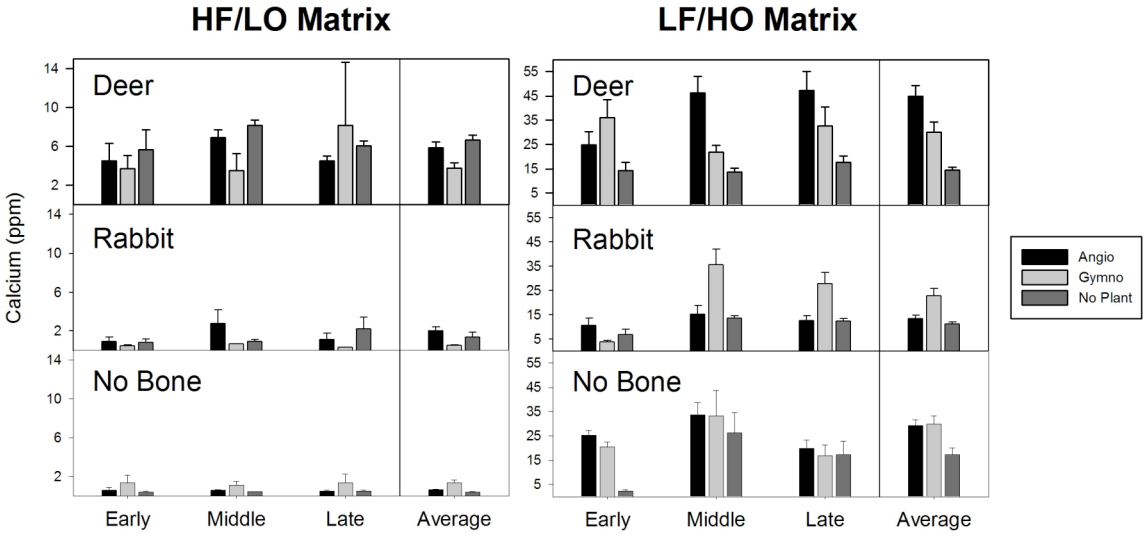


Figure 2.4: Average leached calcium over time for each treatment during the experiment, separated by sediment type. Angio=treatments including angiosperm leaves, Gymno=treatments including gymnosperm leaves, No Plant=bone and sediment controls. Error bars represent the standard error for each treatment. Note difference in Y-axis scales.

Early in the experiment (Table 2.3B) two significant interactions occurred between bone+plant and plant+matrix treatments. Deer treatments leached 30 to 50% more calcium than other treatments, with highest values occurring in plant treatments in LF/HO matrix (ANOVA: $F_{4,36}$=4.262, $p< 0.01$). Plant treatments in LF/HO matrix leached more calcium than HF/LO counterparts, even in the absence of bone (ANOVA: $F_{2,36}$=8.004, $p< 0.001$).

In the Middle period (Table 2.3C) a complex three-way interaction occurred between the three factors (ANOVA: $F_{4,36}$=3.978, $p< 0.01$). Note also that porewater pH remained around 7 during this period. Deer bone treatments continue to leach at least 20 to 50% more calcium than other treatments. Angiosperm treatments leached more calcium than gymnosperm or control treatments, except in LF/HO matrix where calcium levels in rabbit+angiosperm treatments were depressed below the other treatments, then

Table 2.2A: Summary table of repeated measures ANOVA for porewater pH.

Source	df	SS	MS	F	p
Between Subjects					
Matrix	1	3.032	3.032	122.440	0.000 ***
Bone	2	0.931	0.466	18.80	0.000 ***
Plant	2	0.253	0.126	5.100	0.011 *
Bone × Matrix	2	0.661	0.331	13.348	0.000 ***
Bone × Plant	4	0.388	0.097	3.922	0.010 **
Plant × Matrix	2	0.054	0.027	1.092	0.346 *ns*
Bone × Plant × Matrix	4	0.170	0.426	1.719	0.167 *ns*
Error	36	0.892	0.248		
Within Subjects					
Time	2	56.768	28.384	943.088	0.000 ***
Time × Bone	4	1.763	0.441	14.647	0.000 ***
Time × Plant	4	1.227	0.307	10.192	0.000 ***
Time × Matrix	2	2.798	1.399	46.487	0.000 ***
Time × Bone × Plant	8	0.746	0.093	3.098	0.005 **
Time × Bone × Matrix	4	1.293	0.323	10.743	0.000 ***
Time × Plant × Matrix	4	0.502	0.125	4.166	0.004 **
Time × Bone × Plant × Matrix	8	0.568	0.071	2.358	0.026 *
Error	72	2.167	0.030		

Table 2.2B: Summary table of three-way factorial ANOVA for porewater pH in the early period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	9.645	9.645	146.873	0.000 ***
Bone	2	2.844	1.422	21.655	0.000 ***
Plant	2	0.024	0.019	0.182	0.834 *ns*
Bone × Matrix	2	1.507	0.753	11.474	0.000 ***
Bone × Plant	4	0.318	0.079	1.211	0.323 *ns*
Plant × Matrix	2	0.029	0.015	0.225	0.800 *ns*
Bone × Plant × Matrix	4	0.411	0.103	1.564	0.205 *ns*
Error	36	2.364	0.066		

Table 2.2C: Summary table of three-way factorial ANOVA for porewater pH in the middle period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	1.006	1.006	532.175	0.000 ***
Bone	2	0.014	0.007	3.802	0.032 *
Plant	2	0.003	0.001	0.718	0.494 *ns*
Bone × Matrix	2	0.011	0.005	2.861	0.070 *ns*
Bone × Plant	4	0.013	0.003	1.730	0.165 *ns*
Plant × Matrix	2	0.046	0.023	12.277	0.000 ***
Bone × Plant × Matrix	4	0.008	0.002	1.017	0.412 *ns*
Error	36	0.068	0.002		

Table 2.2D: Summary table of three-way factorial ANOVA for porewater pH in the late period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	1.244	1.244	18.590	0.000 ***
Bone	2	1.698	0.849	12.678	0.000 ***
Plant	2	1.958	0.979	14.629	0.000 ***
Bone × Matrix	2	1.759	0.879	13.139	0.000 ***
Bone × Plant	4	1.580	0.395	5.903	0.001 **
Plant × Matrix	2	0.588	0.294	4.392	0.020 *
Bone × Plant × Matrix	4	0.660	0.165	2.466	0.062 *ns*
Error	36	2.409	0.069		

elevated in rabbit+gymnosperm treatments.

Late in the experiment the effect of matrix and bone treatments remained important (Table 2.3D), with a significant three-way interaction (ANOVA: $F_{4,36}$=3.204, p< 0.05). In HF/LO matrix deer+gymnosperm treatments leached more calcium, a reverse from the previous period, where the pattern in other treatments remained the same. In LF/HO matrix the pattern was similar to the Middle period, although with an overall decrease in callcium levels of rabbit and no-bone control treatments.

Changes Following Exhumation

Average values in porewater pH and leached calcium dropped following bone and plant exhumation (Figure 2.5). A repeated measures ANOVA showed conditions 2 months before and after exhumation were significantly different in porewater pH ($F_{1,36}$=100.73, p<0.001; Table 2.4) and leached calcium ($F_{1,36}$=9.22, p<0.01; Table 2.5). Response to exhumation differed between matrix types. HF/LO treatments showed a greater decrease in porewater pH ($F_{1,36}$=27.49, p<0.001) and leached calcium ($F_{1,36}$=8.31, p<0.01) than LF/HO treatments. Interaction effects show that changes were not uniform across treatments. Because porewater ph and calcium levels in sediment controls also changed, it is possible that changes after exhumation were the result of physically disrupting the biogeochemical conditions within the container and not due to removal of the bone and plant material.

Table 2.3A: Summary table of repeated measures ANOVA for leached calcium.
[1]Assumption of sphericity not met (Mauchly's test $\chi^2(2)=6.309$, $p<0.05$). Huynh-Feldt correction ($\varepsilon=1.00$) applied to within subjects tests.

Source	df	SS	MS	F	p
Between Subjects					
Matrix	1	29.906	29.906	480.31	0.000 ***
Bone	2	4.673	2.337	37.527	0.000 ***
Plant	2	0.684	0.342	5.490	0.008 **
Bone × Matrix	2	0.713	0.357	5.727	0.007 **
Bone × Plant	4	0.312	0.078	1.253	0.306 *ns*
Plant × Matrix	2	0.978	0.489	7.852	0.001 **
Bone × Plant × Matrix	4	0.624	0.156	2.505	0.059 *ns*
Error	36	2.242	0.062		
Within Subjects[1]					
Time	2	5.696	2.848	41.58	0.000 ***
Time × Bone	4	0.791	0.198	2.888	0.028 *
Time × Plant	4	0.370	0.093	1.352	0.259 *ns*
Time × Matrix	2	2.475	1.238	18.07	0.000 ***
Time × Bone × Plant	8	2.417	0.302	4.412	0.000 ***
Time × Bone × Matrix	4	1.207	0.302	4.407	0.003 **
Time × Plant × Matrix	4	0.584	0.146	2.132	0.086 *ns*
Time × Bone × Plant × Matrix	8	2.353	0.294	4.295	0.000 ***
Error	72	4.931	0.068		

Table 2.3B: Summary table of three-way factorial ANOVA for leached calcium in the early period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	17.573	17.573	175.004 ***	0.000 ***
Bone	2	6.178	3.089	30.762 ***	0.000 ***
Plant	2	1.274	0.623	6.209 **	0.005 **
Bone × Matrix	2	0.603	0.301	3.001 *ns*	0.062 *ns*
Bone × Plant	4	1.712	0.428	4.262 **	0.006 **
Plant × Matrix	2	1.608	0.804	8.004 ***	0.001 ***
Bone × Plant × Matrix	4	1.006	0.251	2.504 *ns*	0.059 *ns*
Error	36	3.615	0.100		

Table 2.3C: Summary table of three-way factorial ANOVA for leached calcium in the middle period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	38.826	38.826	337.049	0.000 ***
Bone	2	2.530	1.265	10.982	0.000 ***
Plant	2	0.995	0.498	4.321	0.021 *
Bone × Matrix	2	2.637	1.318	11.444	0.000 ***
Bone × Plant	4	1.163	0.291	2.525	0.058 *ns*
Plant × Matrix	2	1.077	0.539	4.676	0.016 *
Bone × Plant × Matrix	4	1.833	0.458	3.978	0.009 **
Error	36	4.147	0.115		

Table 2.3D: Summary table of three-way factorial ANOVA for leached calcium in the late period of the experiment.

Source	df	SS	MS	F	p
Matrix	1	35.794	35.794	330.928 ***	0.000 ***
Bone	2	6.103	3.051	28.211 ***	0.000 ***
Plant	2	0.179	0.089	0.827 *ns*	0.445 *ns*
Bone × Matrix	2	0.108	0.054	0.498 *ns*	0.612 *ns*
Bone × Plant	4	0.478	0.120	1.105 *ns*	0.369 *ns*
Plant × Matrix	2	0.833	0.416	3.849 *	0.031 *
Bone × Plant × Matrix	4	1.386	0.347	3.204 *	0.024 *
Error	36				

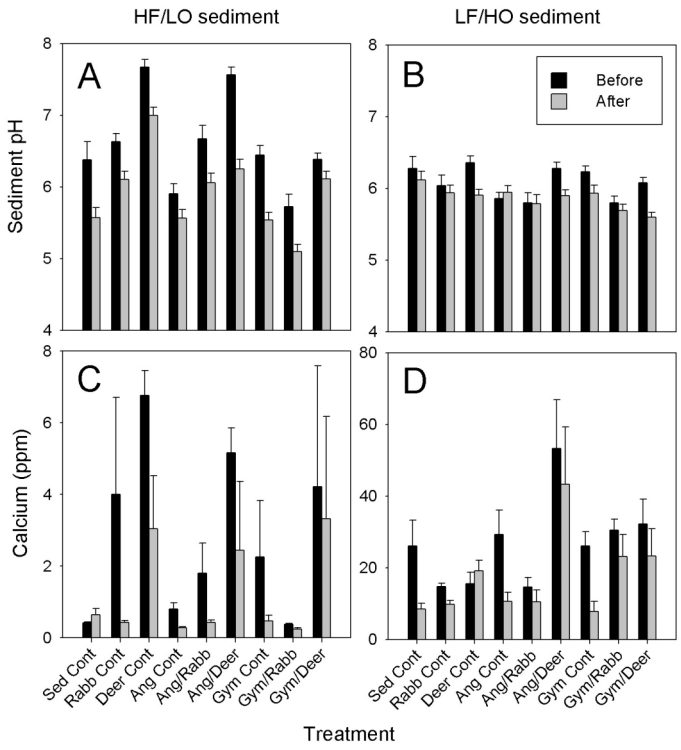


Figure 2.5. Change in average porewater pH (A,B) and leached calcium (C, D) values in the two months before and after bone and/or plant removal for HF/LO (A,C) and LF/HO (B,D) matrix. Treatment key: Sed=sediment, Cont=control, Rabb=rabbit, Deer=deer, Ang=angiosperm, Gym=gymnosperm.

Table 2.4: Summary table of repeated measures ANOVA for porewater pH before and after bone and plant exhumation.

Source	df	SS	MS	F	p
Between Subjects					
Matrix	1	2.212	2.212	18.899	0.000 ***
Bone	2	5.160	2.580	22.043	0.000 ***
Plant	2	3.622	1.811	15.471	0.000 ***
Bone × Matrix	2	4.314	2.157	18.427	0.000 ***
Bone × Plant	4	2.315	0.579	4.944	0.003 **
Plant × Matrix	2	1.141	0.571	4.874	0.013 *
Bone × Plant × Matrix	4	1.184	0.296	2.529	0.057 *ns*
Error	36	3250.767	90.299		
Within Subjects					
Time	1	5.313	5.313	100.727	0.000 ***
Time × Bone	2	0.331	0.166	3.140	0.055 *ns*
Time × Plant	2	0.002	0.001	0.028	0.972 *ns*
Time × Matrix	1	1.450	1.450	27.493	0.000 ***
Time × Bone × Plant	4	0.706	0.176	3.346	0.020 *
Time × Bone × Matrix	2	0.079	0.039	0.745	0.482 *ns*
Time × Plant × Matrix	2	0.137	0.068	1.296	0.286 *ns*
Time × Bone × Plant × Matrix	4	0.393	0.098	1.864	0.138 *ns*
Error	36	1.899	0.053		

Table 2.5: Summary table of repeated measures ANOVA for leached calcium before and after bone and plant exhumation.

Source	df	SS	MS	F	p
Between Subjects					
Matrix	1	10811.234	10811.234	119.727	0.000 ***
Bone	2	2372.808	1186.404	13.139	0.000 ***
Plant	2	634.324	317.162	3.512	0.040 *
Bone × Matrix	2	538.633	269.317	2.982	0.063 *ns*
Bone × Plant	4	1010.350	252.588	2.797	0.040 *
Plant × Matrix	2	718.119	359.059	3.976	0.028 *
Bone × Plant × Matrix	4	1387.125	346.781	3.840	0.011 *
Error	36	3250.767	90.299		
Within Subjects					
Time	1	567.594	567.594	9.218	0.004 **
Time × Bone	2	379.166	189.583	3.079	0.058 *ns*
Time × Plant	2	38.640	19.320	0.314	0.733 *ns*
Time × Matrix	1	511.668	511.668	8.310	0.007 **
Time × Bone × Plant	4	160.670	40.167	0.652	0.629 *ns*
Time × Bone × Matrix	2	258.171	129.085	2.096	0.138 *ns*
Time × Plant × Matrix	2	61.854	30.927	0.502	0.609 *ns*
Time × Bone × Plant × Matrix	4	81.258	20.314	0.330	0.856 *ns*
Error	36	2216.609	61.572		

Matrix Hydraulic Conductivity

Differences in hydraulic conductivity (Table 2.6) were largest between matrix types (ANOVA: $F_{1,36}$=459.54, p< 0.001), where average values ranged from 1×10^{-3}–2.5×10^{-2} in HF/LO matrix and 2.5×10^{-5}–3.5×10^{-4} in LF/HO matrix (Figure 2.6).

Significant interaction effects were encountered between bone and plant treatments ($F_{4,36}$=5.18, p< 0.01). Specifically, hydraulic conductivity was depressed most in deer+angiosperm treatments and to a lesser extent in rabbit+angiosperm treatments. Gymnosperm treatments maintained significantly higher values than angiosperm treatments, except when placed with deer bone in HF/LO matrix.

Linear regression of leached calcium against hydraulic conductivity suggested that leached calcium is negatively correlated with matrix hydraulic conductivity in each container (r^2=0.741, p<0.0001) with the points separated mainly by matrix type (Figure 2.7). A t-test for the similarity of slopes between matrix types was not significant (df=52,

t=0.69, p=0.493) and indicated no significant interaction effect between hydraulic conductivity and matrix type.

Sediment Calcium

Overall sediment calcium levels differed significantly between treatments (Figure 2.8). HF/LO matrix contained significantly greater amounts of calcium (9,700–11,900 ppm) than LF/HO matrix (7,200–8,100 ppm). Interaction effects occurred between all

Table 2.6: Summary table of three-way factorial ANOVA for sediment hydraulic conductivity.

Source	df	SS	MS	F	p
Matrix	1	0.00020264	0.00020264	459.54	0.000 ***
Bone	2	0.00000345	0.00000173	3.91	0.029 *
Plant	2	0.00001584	0.00000792	17.96	0.000 ***
Bone × Matrix	2	0.00000243	0.00000122	2.76	0.077 *ns*
Bone × Plant	4	0.00000913	0.00000228	5.175	0.002 **
Plant × Matrix	2	0.00000060	0.00000030	0.675	0.515 *ns*
Bone × Plant × Matrix	4	0.00000167	0.00000042	0.948	0.448 *ns*
Error	36	0.00001587	0.00000041		

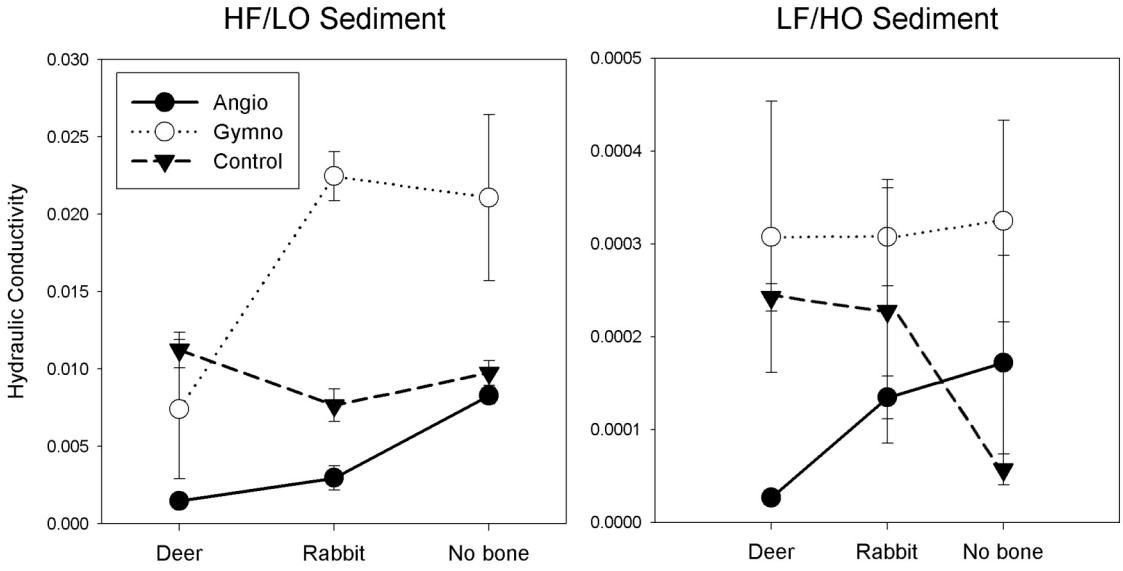


Figure 2.6: Average hydraulic conductivity for each treatment following completion of the experiment, separated by matrix type. Angio=angiosperm, Gymno=gymnosperm, Control=no plant. Note different y-axis scales.

three variables (ANOVA: 2.96, $p< 0.05$; Table 2.7). Calcium was dependent on the particular combination of bone and plant treatment. Sediment from gymnosperm treatments contained high calcium values except in the presence of rabbit bone. Angiosperm and control treatments demonstrated intermediate to low sediment calcium values, depending on the matrix type. In the context of initial sediment calcium values, LF/HO matrix contained an average 11.4 g, a net gain of 2 ±1 g calcium in each container over the starting level (9.12 g). HF/LO matrix averaged 15.5 g, a loss of 12 ±3 g calcium from each container over the initial value (27.8 g).

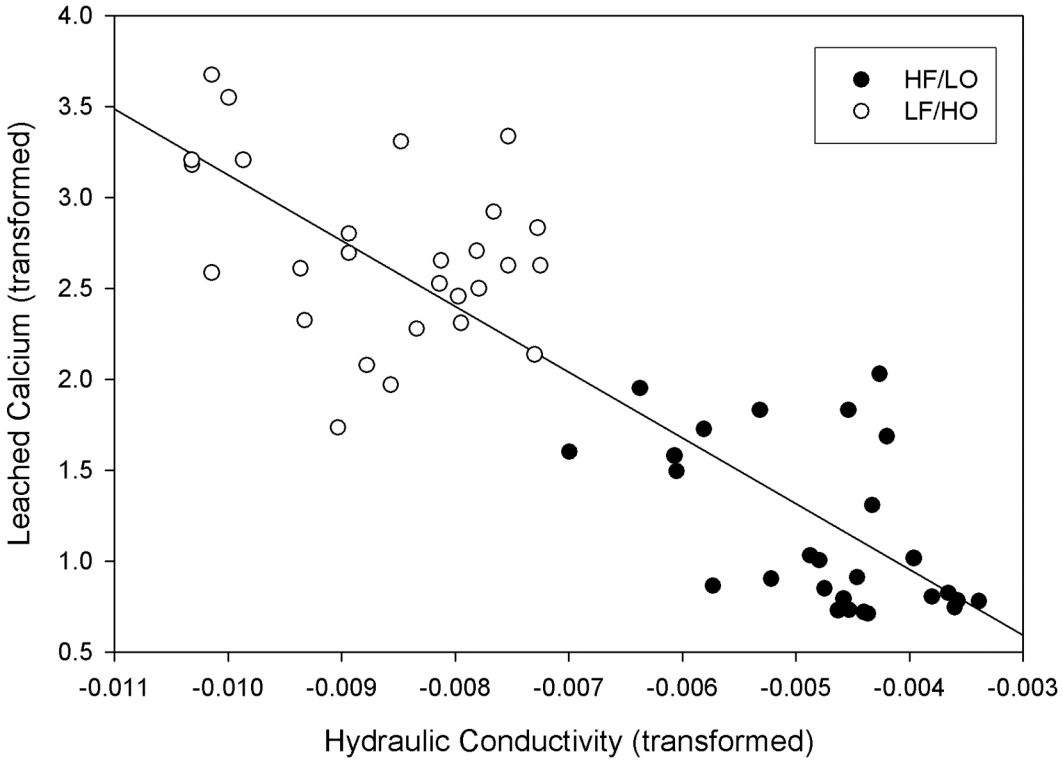


Figure 2.7: Regression of leached calcium on hydraulic conductivity, separated by bone type. All values have been power transformed. R^2=0.741, $p<0.0001$.

Table 2.7: Summary table of three-way factorial ANOVA for sediment calcium content.

Source	df	SS	MS	F	p
Matrix	1	99642954	99642954	864.98	0.000 ***
Bone	2	1048940	524470	4.55	0.017 **
Plant	2	1270576	635288	5.51	0.008 **
Bone × Matrix	2	95603	47802	0.42	0.663 *ns*
Bone × Plant	4	3323903	830976	7.21	0.0002 ***
Plant × Matrix	2	405569	202785	1.76	0.187 *ns*
Bone × Plant × Matrix	4	1362828	340707	2.96	0.033 *
Error	36	4147068	115196		
Total	53	111297441			

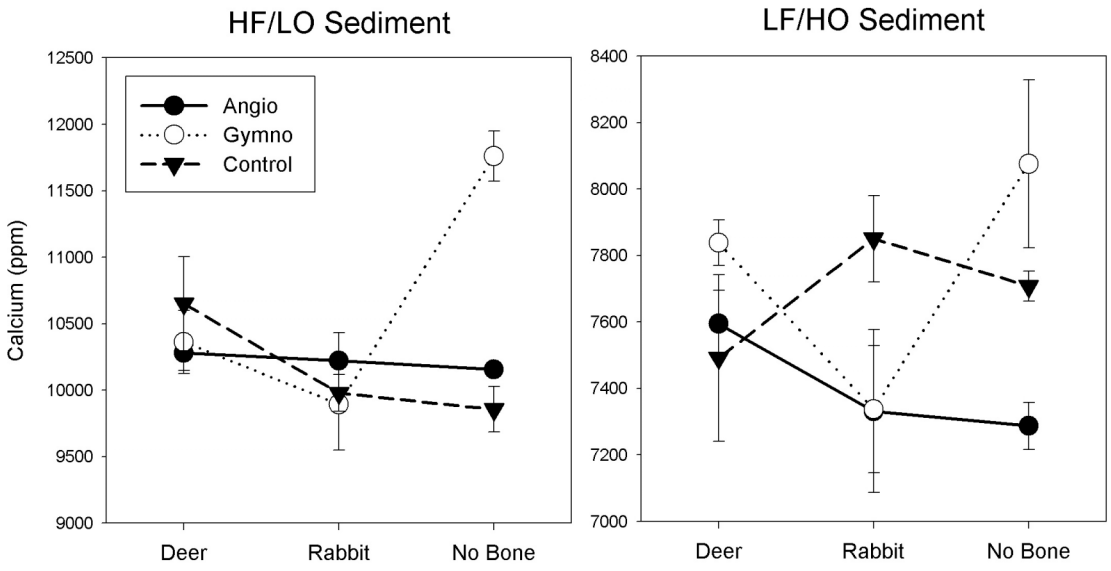


Figure 2.8: Average sediment calcium for each treatment following completion of the experiment, separated by matrix type. Legend follows Figure 2.6. Note different Y-axis scales.

Oxygen Levels in each Matrix Type

At the conclusion of the experiment the two sediment types differed markedly in appearance, providing a qualitative indication of redox conditions within the containers. All LF/HO matrix containers underwent a noticeable color change from light brown to gray-green, observable both externally and internally throughout the matrix (Figure 2.9A). Vivianite crystals found growing on many of the vertebrae (see next section) form only at low to medium Eh (-0.07 to -0.36) (McGowan and Prangnell 2006). Color change

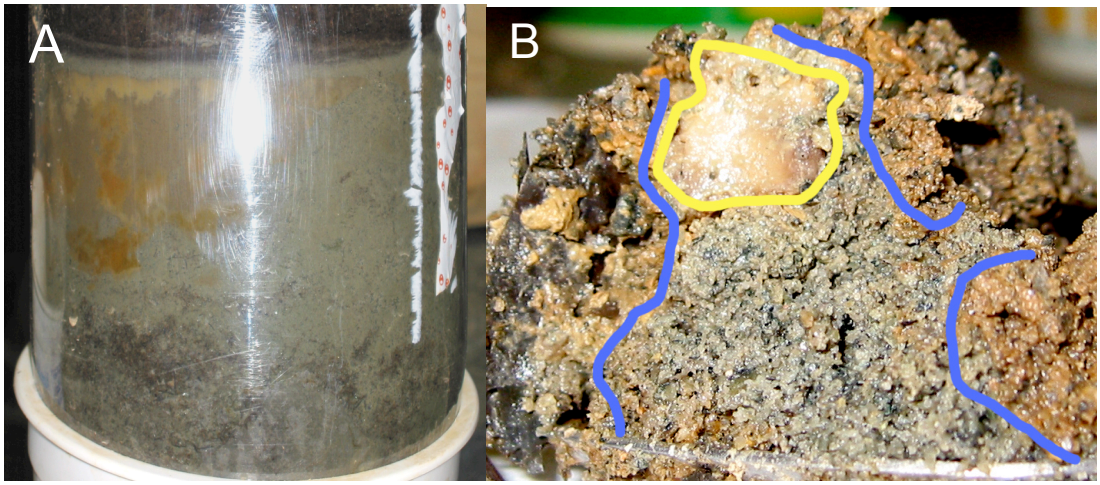


Figure 2.9: Color change in sediment indicating redox conditions. A) Drab gray-green color seen throughout LF/HO sediments. B) Similarly colored halo appearing only around bone in HF/LO sediments. Note lack of color change around plant material to the left. Remaining sediment retains original brown coloration. Yellow line=bone, blue line=halo.

and vivianite formation are known indicators of anoxia in saturated fine-grained, organic-rich sediments (Briggs and Kear 1993a, McGowan and Prangnell 2006, Sagemann et al. 1999, Schaetzl and Anderson 2005). A dense, dark fibrous layer that may represent decay products and/or the beginning stages of humus formation surrounded bone and plant remains in LF/HO matrix.

HF/LO matrix showed little evidence of color change. However, distinct gray-green anoxic haloes and trails running parallel to water flow were found around the rabbit and deer bones (Figure 2.9B). The trails probably represent the migration of decay products and associated bacteria out of the bone. This halo was less distinct in plant controls and absent in the matrix control containers. This result is not unusual, as is it well documented that the decomposition of fresh remains leads to localized anoxia even in well-aerated sediments (Briggs 1995, Briggs and Kear 1993a, Sagemann et al. 1999)

and is most likely the result of elevated bacterial activity in close proximity to the remains (Briggs et al. 2005, Kear et al. 1995).

2.4.2 Bone Treatments

Physical Condition and SEM-EDS

All bones showed evidence of chemical and physical alteration. Compared to an unaltered bone sample, SEM-EDS elemental profiles for surfaces of experimental bone showed no substantial change in elemental profile. Variation was observed in carbon and oxygen peak magnitudes, which were lower in some regions of a bone but followed no specific pattern between matrix treatments. Decreasing carbon may be a sign of organic matrix loss from the bone tissue.

The most obvious outwardly visible differences in bone condition occurred between bones interred in HF/LO versus LF/HO matrix types. Upon removal from HF/LO matrix, both deer and rabbit bones showed evidence of severe degradation. All bones appeared physically eroded with extensive surface damage, featuring a yellowish-white color, cracks, and deep pits that occasionally penetrated through the outermost compact layer of bone (Figure 2.10A, B). Erosion of bone tissue was most severe on those surfaces in the direct flow of water (i.e., spinous process, transverse processes, and zygapophyses). Rabbit bones presented the most extreme cases, where vertebral processes were partially or completely destroyed leaving only the centrum intact. In some cases, the rabbit vertebrae were completely destroyed. Deer bones demonstrated similar surface damage but most morphological features remained intact. SEM imaging of bone surfaces showed damage occurring at the tissue level, where isolated bundles of collagen

and apatite are separated by spaces (Figure 2.10C) in which possible nutrient canals or lacunae are exposed (Figure 2.10D).

Bones from LF/HO sediment on the other hand were recovered in good condition (Figure 2.11). Morphological features on all bones remained fully intact and the bones were stained a brown color, most likely the result of humic acids binding to proteins in the bone surface (Figure 2.11A, B) (van Klinken and Hedges 1995). The staining does not extend into the bone interior. In addition small (0.5-2 mm long), dark blue–purple

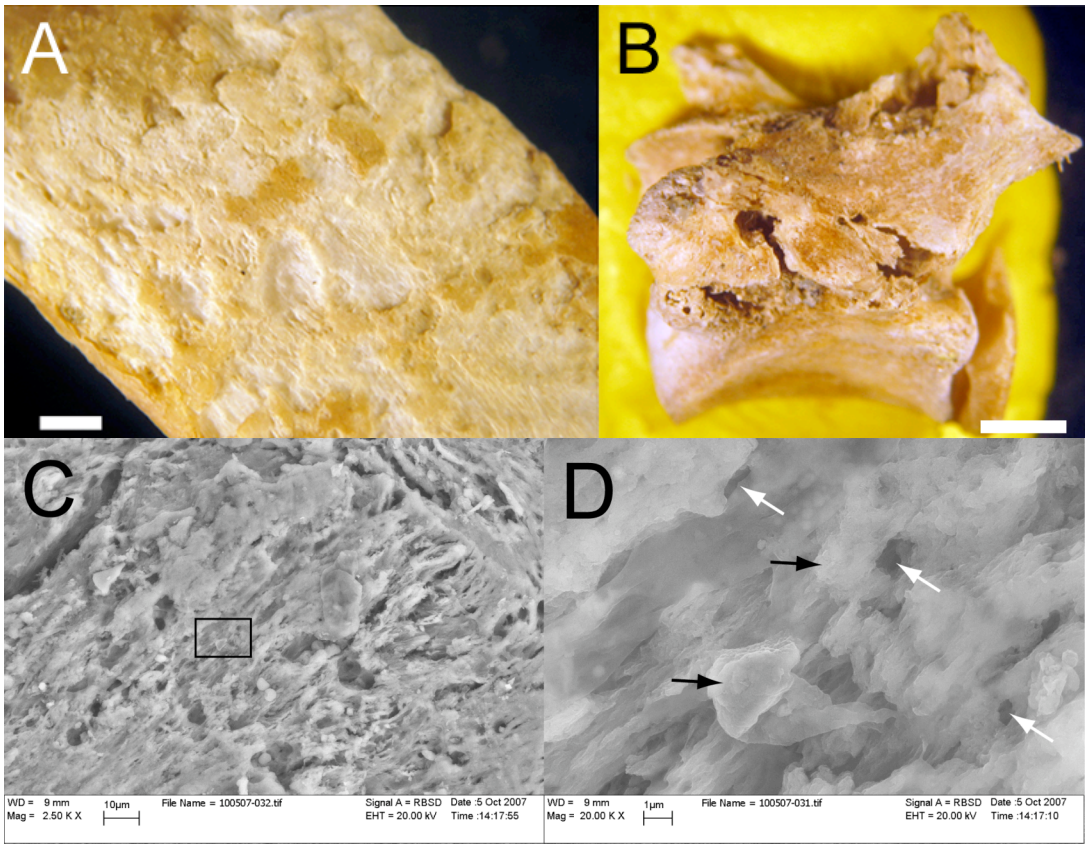


Figure 2.10: Physical condition of bones recovered from HF/LO matrix. A) Close up of deer transverse process surface showing erosion, pitting, and cracking of cortical layer. Scale bar=1 mm. B) Picture of whole rabbit thoracic vertebra, showing loss of spinous process, zygapophyses, and articular facets. Anterior to the left. Scale bar=5 mm. C) SEM image of bone surface. D) Magnification of boxed area in C, showing islands of eroded bone tissue (block arrows) and possible exposed canals (white arrows).

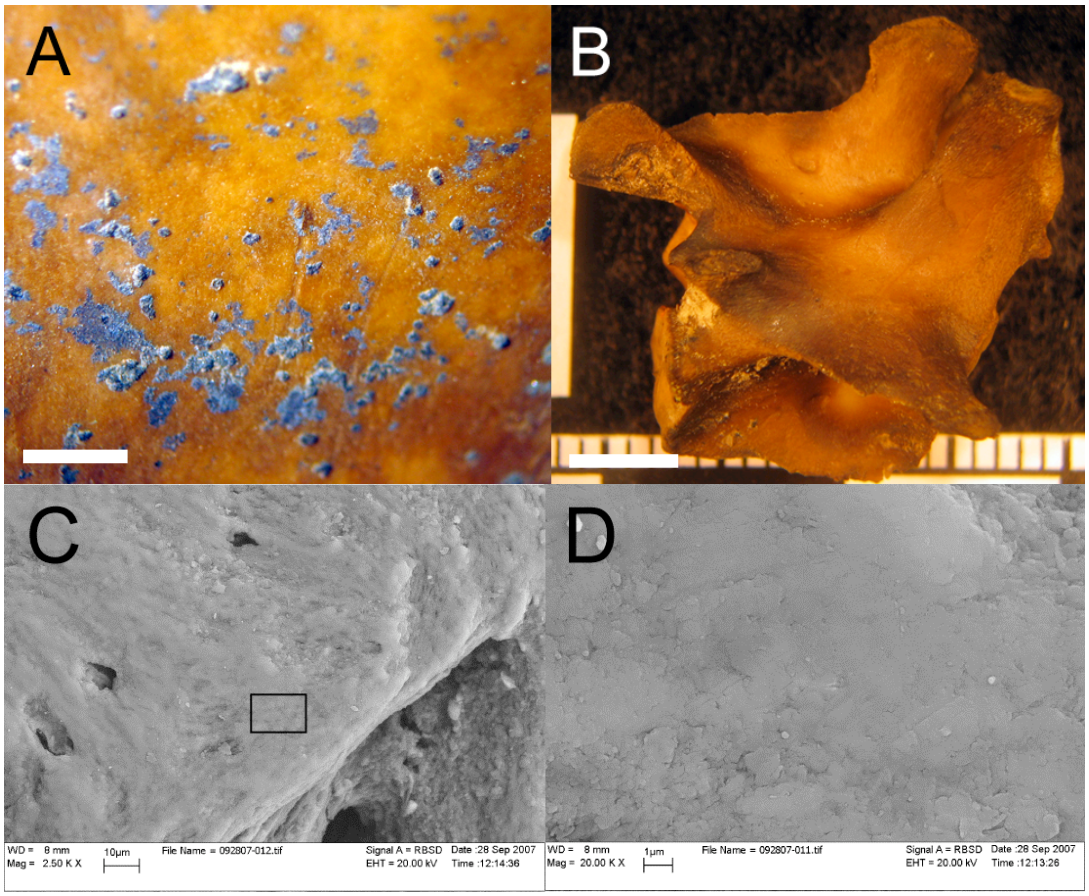


Figure 2.11: Physical condition of bones recovered from LF/HO matrix. A) Close up of deer centrum surface showing intact surface, brown staining, and mineral growth. Scale bar=1 mm. B) Picture of whole rabbit lumbar vertebra, showing retention of major morphological features. Anterior to the right. Scale bar=5 mm. C) SEM image of bone surface. D) Magnification of boxed area in C. Note intact surface features compared to Figure 2.10 C, D.

crystals were growing from the surface of every bone buried in LF/HO matrix (Figure 2.12). SEM images of the crystals show a range of growth habits, from large octahedral spires and rosettes to thin, platy sheets and amorphous mounds. The underside of the crystals in contact with the bone surface had needle-like shapes. EDS profiles of these crystals consistently showed peaks in Fe, P, and O suggesting that all are composed of an iron phosphate mineral. Both EDS profile and crystal shape closely match those of the hydrated iron phosphate mineral vivianite [$Fe_3(PO_4)_2 \cdot 8H_2O$]. If confirmed by further

crystallographic analysis, this is the first time vivianite growth on bone has been documented in the laboratory.

Bone Mass Loss

Bone mass loss clearly differed between treatments, with significant interaction effects (Figure 2.13 and Table 2.8). Rabbit bones in HF/LO matrix suffered greater proportional mass loss (75-100%) compared to those in LF/HO matrix (37-47%), while deer bone lost on average 27-47% g in both matrix types (ANOVA: $F_{1,24}$=60.171, p< 0.001). Overall mass loss in HF/LO matrix was higher in plant treatments than controls

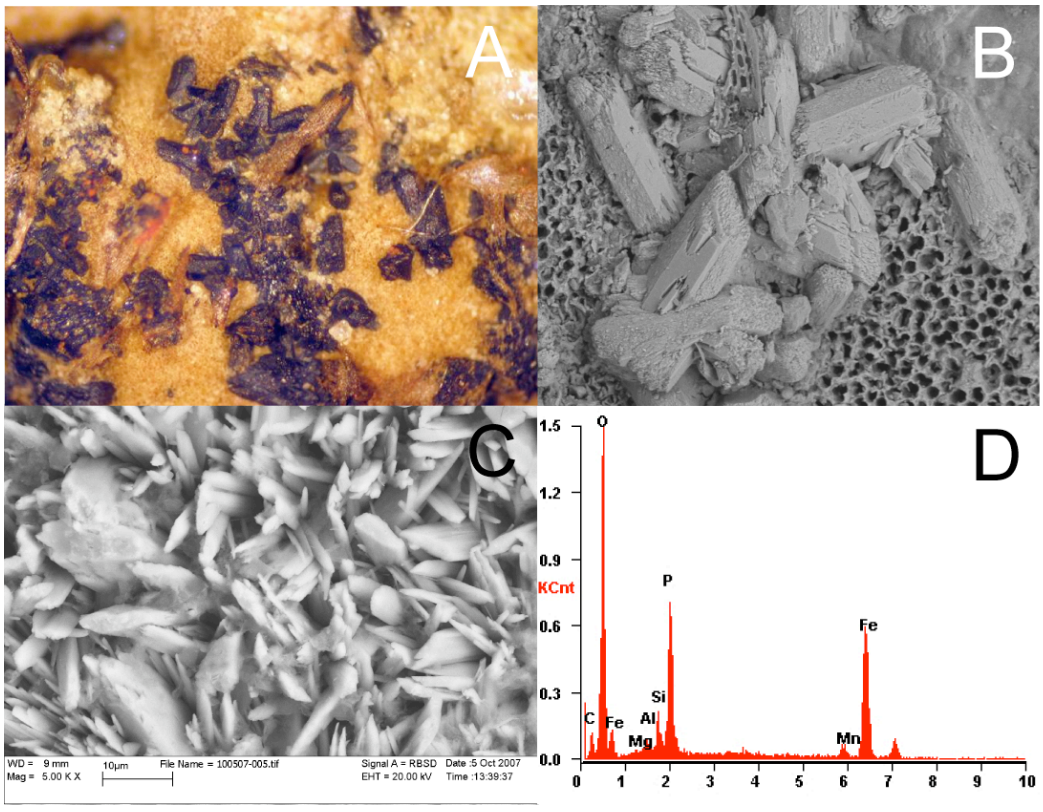


Figure 2.12: Vivianite crystals on bones from LF/HO sediment. A) Light microscope image. Photo contrast enhanced to show crystals. B) SEM image of crystals growing out of bone surface. C) SEM image of needle-shapes. D) EDS element profile of crystals in C.

but was reversed in LF/HO matrix, hence a significant interaction effect between matrix and plant treatments (ANOVA: $F_{2,24}$=7.459, p< 0.01). Mass loss in rabbit versus deer vertebrae depended on plant type (ANOVA: $F_{2,24}$=8.94, p< 0.01). Rabbit bones lost more mass in gymnosperm treatments, while treatments with deer bone lost more mass in the absence of any plant material with no difference between plant types.

Bone Density Loss

Bone density loss closely matched mass loss results, with significant interaction effects (Figure 2.14 and Table 2.9). Rabbit bones lost more density in HF/LO matrix (50-100%) than LF/HO matrix (20-50%), while there was little difference in deer bones across matrix types (10-30%) ($F_{1,24}$=9.859, p<0.01). The second interaction occurred

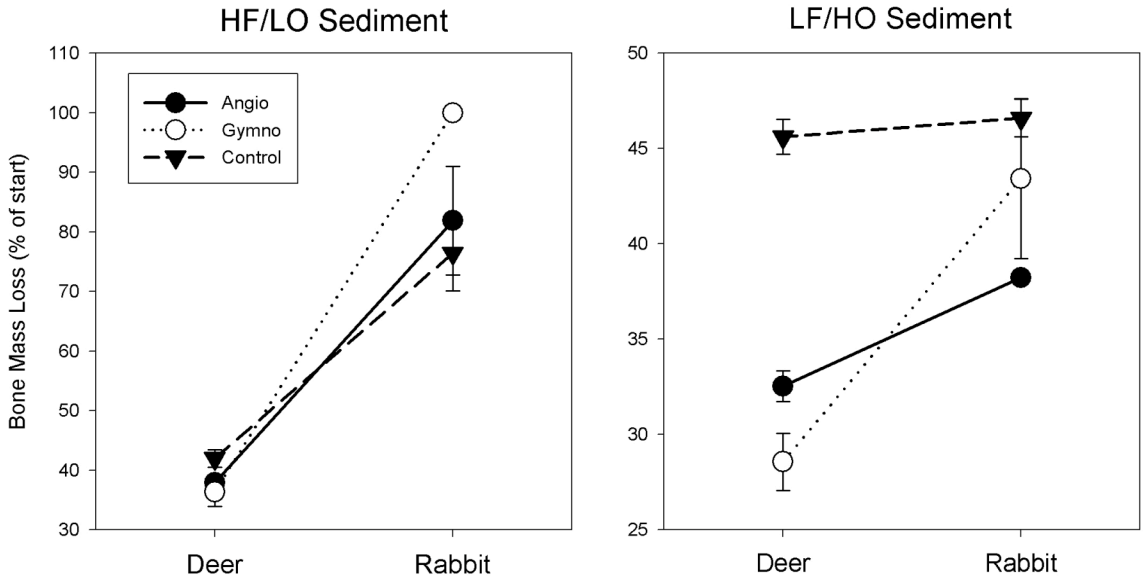


Figure 2.13: Averaged bone mass lost for each treatment following completion of the experiment, separated by sediment type. Note that all replicates of rabbit+gymnosperm and one replicate of rabbit+angiosperm were not recovered and were recorded as 100% mass lost. Legend follows Figure 2.6. Note different Y-axis scales.

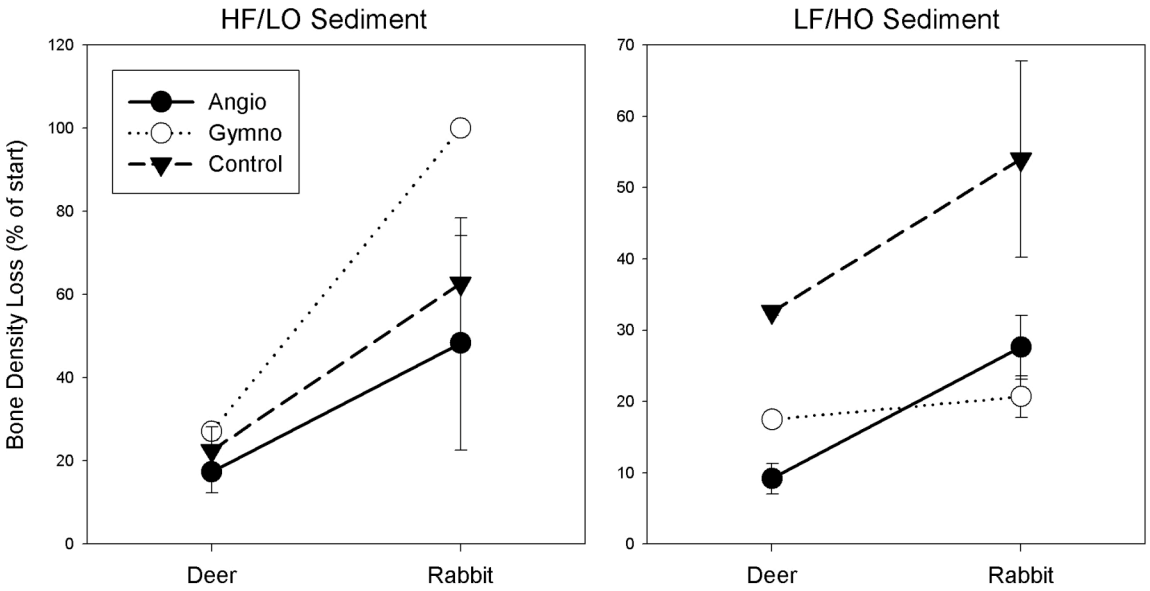


Figure 2.14: Averaged bone density loss for each treatment following completion of the experiment, separated by matrix type. Note that all replicates of rabbit+gymnosperm and one replicate of rabbit+angiosperm were not recovered and have been recorded as 100% density loss. Legend follows Figure 2.2. Note different Y-axis scales.

Table 2.8: Summary table of three-way factorial ANOVA for bone mass loss.

Source	df	SS	MS	F	p
Matrix	1	0.825792	0.825792	77.064	0.000 ***
Bone	1	1.056126	1.056126	98.560	0.000 ***
Plant	2	0.049940	0.024970	2.230	0.119 *ns*
Bone × Matrix	1	0.644769	0.644769	60.171	0.000 ***
Bone × Plant	2	0.191678	0.095839	8.944	0.001 **
Plant × Matrix	2	0.159846	0.079923	7.459	0.003 **
Bone × Plant × Matrix	2	0.065958	0.032979	3.078	0.065 *ns*
Error	24	0.257175	0.010716		

Table 2.9: Summary table of three-way factorial ANOVA for bone density change.

Source	df	SS	MS	F	p
Matrix	1	0.648302	0.648302	13.388	0.001 **
Bone	1	1.446198	1.446198	29.86	0.000 ***
Plant	2	0.334418	0.167209	3.453	0.048 *
Bone × Matrix	1	0.477446	0.477446	9.859	0.004 **
Bone × Plant	2	0.077130	0.038565	0.796	0.463 *ns*
Plant × Matrix	2	0.595715	0.297858	6.151	0.007 **
Bone × Plant × Matrix	2	0.309542	0.154771	3.196	0.059 *ns*
Error	24	1.1622164	0.048426		

between plant and matrix type ($F_{2,24}$=6.151, p< 0.01). Density loss in HF/LO matrix was higher under gymnosperm treatments but showed little difference between plant types in LF/HO matrix, while no-plant controls changed little across matrix types.

Relationship between Mass and Density Loss

Comparison of density change to mass loss shows a strong positive correlation (r^2=0.725, p<0.0001), with rabbit data covering a much wider spread than deer data (Figure 2.15). The t-test for similarity of slopes for this data separated by bone size found a marginally non-significant interaction with mass and density change (df=34, t=2.042, p=0.05). However, when the data are separated by sediment type, the t-test showed a significant difference (df=34, t=3.89, p=0.0004) demonstrating that each matrix type altered bone mass and density along different trajectories. The resulting regressions show a steep positive slope between density and mass loss for bones in HF/LO sediment (r^2=0.762, p<0.0001), while the slope of LF/HO sediment is less positive (r^2=0.257, p<0.05) (Figure 2.16). Further results as well as the relationship between density and mass loss are presented in Chapter 3.

2.4.3 Plant Treatments

Angiosperm and gymnosperm material from HF/LO matrix was more degraded than from the LF/HO matrix, lacking many discernable leaf characteristics. Although taxa with robust leaves and thick cuticles (Cycadales, Lauraceae, Arecaceae) appeared less degraded. Plant material from LF/HO matrix was in relatively good condition, with most leaf morphology reasonably intact and in some cases retaining original green

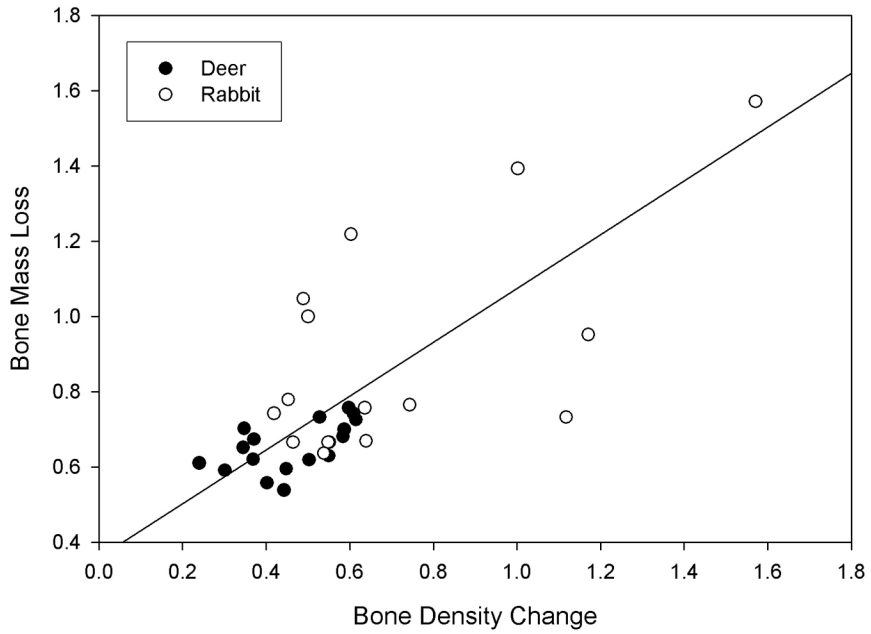


Figure 2.15: Regression of bone mass loss on density change, separated by bone type. All values have been arcsin transformed. y=0.361+0.714x (N=36, r^2=0.725, p<0.0001).

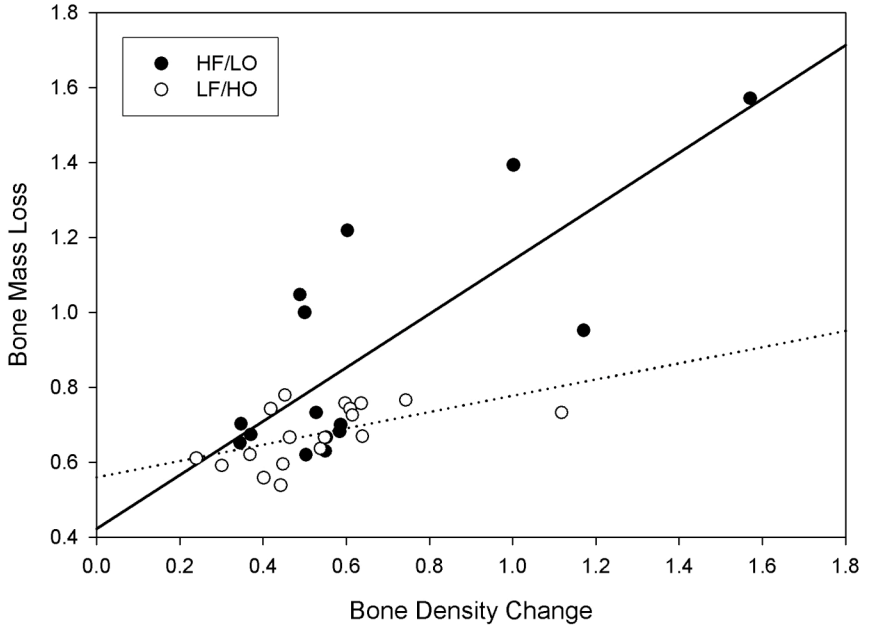


Figure 2.16: Regression of bone mass loss on density change, separated by matrix type. All values have been arcsin transformed. The following regression lines correspond to sediment type: Solid line is HF/LO matrix, y=0.423+0.716x (N=18, r^2=0.762, p=0.0001). Dotted line is LF/HO matrix, y=0.56+0.219x (N=18, r^2=0.257, p=0.019).

pigmentation. Secondary mineralization was again encountered. Small, clear crystals were found growing directly on the surfaces of *Sphagnum* organs adhering to the bone in LF/HO treatments. Gymnosperm and angiosperm material from both matrix treatments demonstrated similar mineral growths. EDS profiles showed that the mineral in both cases is likely silica dioxide (SiO_2). The growth of these crystals did not appear to be directly related to the presence of bone.

2.4.4 Variation Within Treatments

Variation between replicates was large within certain treatments. The standard deviation (SD) in porewater pH was similar in LF/HO and HF/LO replicates, with an average of 0.8 pH units (Figure 2.17A). In leached calcium data, HF/LO replicates had an average standard deviation of 1.6, while SD for LF/HO replicates averaged around 15 (Figure2.17B). The pattern was reversed for hydraulic conductivity, where HF/LO treatments had the greatest variation between replicates over their LF/HO counterparts (Figure 2.17C). Sediment calcium in HF/LO matrix treatments were slightly more variable than their LF/HO counterparts, with scores of 351 versus 260, respectively (Figure 2.17D). Overall, treatments containing bone+plant material tended to be the most variable across the data collected, with a few exceptions. Regardless of matrix type, the most consistently variable treatments across the four measurements given here include gymnosperm control, gymnosperm+rabbit, and gymnosperm+deer.

Summary of Test of Hypotheses

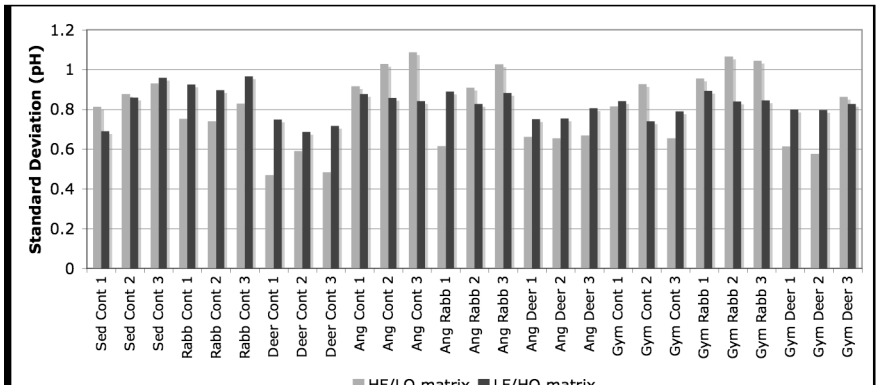
Bones interred in LF/HO matrix were well preserved, retaining a greater amount of mass and density and morphological features, compared to the severe damage or complete loss of bones from HF/LO matrix, supporting Hypothesis I. Bone preservation varied considerably according to the combination of plant, bone, and matrix type, and no clear pattern regarding the role of plant material or differences between plant groups can be made at this time, leading to the tentative rejection of Hypotheses II and III. The larger deer vertebrae lost a smaller proportion of their overall mass and density and were better preserved than the smaller rabbit vertebrae when buried under the same conditions, supporting Hypothesis IV.

2.5 DISCUSSION

2.5.1 Evolution of Conditions Over Time

Sediments are conditioned and altered by the interaction of climate, flora, and fauna present in the ecosystem. After a certain point these alterations cannot be reversed and play a role in shaping ecosystem dynamics long after the original circumstances creating those conditions has passed (Retallack 1990). Over shorter time spans, decomposition processes condition and alter the surrounding sedimentary matrix through the interaction of decay products and metabolic activities of microfauna, most notably bacteria. The strength and direction of these interactions is directed by sediment hydrology. Presented below is a possible scenario for the evolution of biogeochemical conditions in the containers during the course of the experiment.

A



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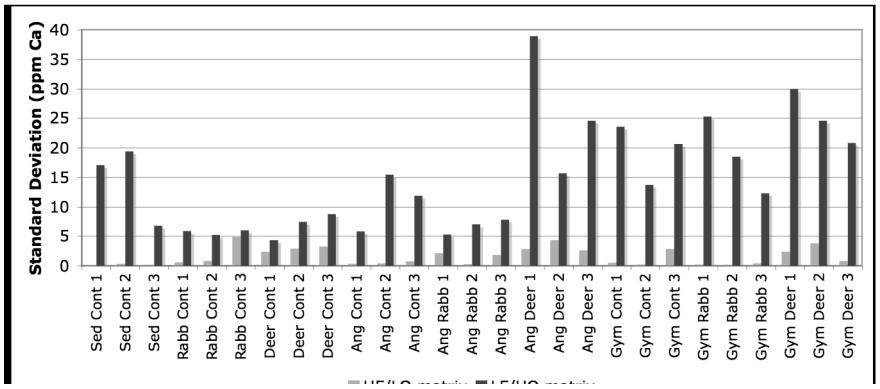

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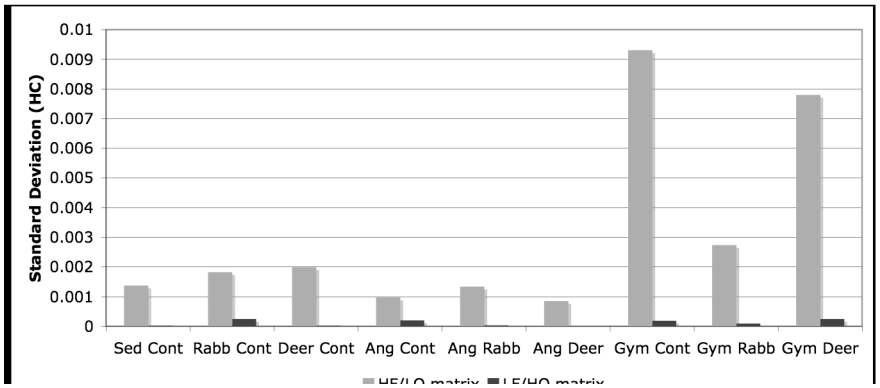

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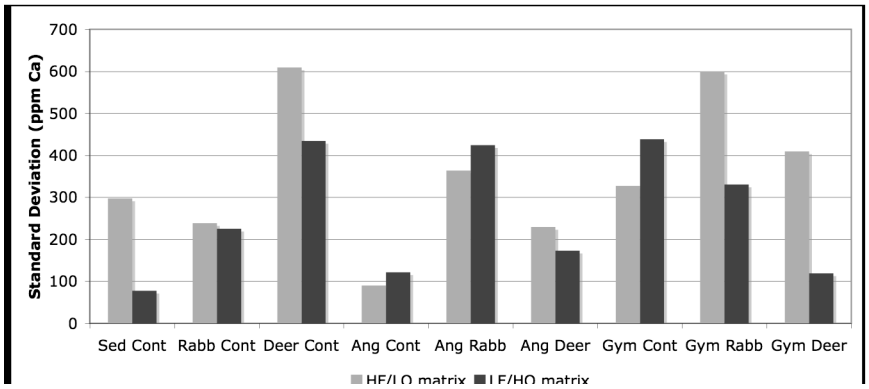

Figure 2.17: Standard deviation of replicates for each treatment. A and B represent multiple measurements taken from individual replicates during the experimental period when bone/plant material was interred. C and D represent single measurements taken on each replicate following the experiment. A) porewater pH, B) leached calcium, C) hydraulic conductivity, D) sediment calcium. Light bars represent HF/LO matrix and dark bars represent LF/HO matrix. Treatment key: Sed=sediment, Cont= control, Rabb=rabbit, Deer=deer, Ang= angiosperm, Gym= gymnosperm.

Porewater pH was mediated by incoming DI water pH, buffering capacity of the system, and metabolic activity of the microfauna. Early in the experiment, aerobic bacteria and fungi colonized available organic material, attacking first the most labile components (Berg and McClaugherty 2003, Dauwe et al. 2001, Hulthe et al. 1998). These groups multiplied rapidly, producing enzymes and organic acids that lowered porewater pH. Aerobic microfauna rapidly removed the majority of labile organic matter from plant material (Berg and McClaugherty 2003), and possibly the soft tissue adhering to the bone. Microbial action played some role in the degradation of organic molecules in bone tissue itself, however the degree to which it is responsible for bone destruction versus abiotic processes is still debated (Child 1995, Hedges et al. 1995, Jans et al. 2004, Piepenbrink 1986, Trueman and Martill 2002).

In the first stage exhaustion of labile organics and/or dissolved oxygen caused the aerobic microfauna population to crash around five months into the experiment with the onset of anoxia (Figure 2.2). Following this stage anaerobic bacteria proliferated, albeit more slowly due to a lower metabolic rate brought on by nutrient limitation and lower resource use efficiency (Berg and McClaugherty 2003, Dauwe et al. 2001, Hulthe et al. 1998). The most destructive agents, the fungi, were excluded due to being obligate aerobes. Onset of anoxia is independent of initial porewater oxygen infiltration rate, since both HF/LO and LF/HO treatments experienced some anoxia, even though oxygen penetration was much greater in the former. The anoxic zone remained localized around the bone in HF/LO matrix, while widespread anoxia predominated in LF/HO treatments due to the peat present throughout the sediment column. This observation agrees well with previous work in which intense bacterial activity created local anoxia regardless of

sediment pore oxygen levels (Briggs 1995, Briggs and Kear 1993a, b, Briggs et al. 2005, Kear et al. 1995, Sagemann et al. 1999).

In the next stage degradation of remaining organic matter continues for several more months. Porewater pH approaches neutral as the onset of reducing conditions consume H^+ ions from solution (Vepraskas and Faulkner 2001). The decrease in DI water pH eventually overcomes this process and acidic conditions return. Acidic conditions increased the energetic cost of anaerobic metabolism (Goodwin and Zeikus 1987, Messerli et al. 2005) and, combined with a decrease in metabolizable resources, lead to a decline in bacterial activity. Failure of the container pH values to increase to previous values following an increase in DI water pH around mid-October 2006 provides some support for this scenario. After this point sediment pH behaves independently of the incoming DI water pH.

Therefore, the context of burial is extremely important. Initial conditions at the time of burial play a vital role in determining the trajectory of diagenetic processes by determining the range of conditions that may occur next. This taphonomic succession explains why certain environments preserve certain types of organic remains better than others. As in ecological succession, taphonomic succession can act on vastly different timescales and may not be reversible within the normal range of environmental variation unless acted upon by extraordinary outside perturbation.

2.5.2 The Effect of Matrix Hydrology

Matrix type, HF/LO versus LF/HO, was clearly the most important determinant of bone preservation among all experimental treatments. The different hydrologic properties

of each matrix contributed to significant differences in pH, oxidation-reduction level, diffusion gradients, and flow rate, which in turn regulated the range of biogeochemical processes possible in the system, significantly impacting decomposition and diagenesis.

Hydraulic conductivity values within each of the two matrix types matched the range typically observed in unconsolidated sand (1×10^{-3} to 0.0) and soil (1×10^{-6} to 1×10^{-3}) systems (Bear 1988, p. 136). The open pore structure of coarse-grained HF/LO matrix provided a high vertical to horizontal ratio of water movement, which is a typical feature of sandy sediments. The fine grains and organic matter in LF/HO matrix slowed vertical flow and supported greater horizontal movement through the sediment (Brady, 1974).

The high hydraulic conductivity of HF/LO matrix is what likely made it so destructive. The low-pH DI water entering the system directly attacked bone apatite, creating strong diffusion gradients as decay products were rapidly transported away from the remains. Bone-derived calcium helped buffer the low pH, with the smaller rabbit vertebrae unable to buffer conditions as well as the much larger deer vertebrae. However, pH conditions remained $\leq$7, within the dissolution window for bone mineral (Berna et al. 2004). Anoxic conditions due to microbial activity remained localized due to: 1) high oxygen infiltration into pore spaces and removal of bacteria and decay products from the system; and 2) lack of abundant organic matter in the matrix, which restricted microbial activity to bone and plant material, the only available organic source in the system. Under these conditions the organic components and calcium compounds found in bone matrix and plant cells were readily removed from the remains leading to their rapid degradation over time.

Dissolved carbon dioxide was likely abundant in HF/LO matrix, derived from the DI water (see Methods), atmospheric CO_2, and bacterial decomposition of organic material (Wood and Petratis 1984). In terrestrial environments under near-neutral or higher pH, carbon dioxide combines with calcium to form calcite ($CaCO_3$), with precipitation dependent upon and/or enhanced by bacterial activity (Carpenter 2005, Daniel 2003, Ferris et al. 1994, Lian et al. 2006, Sposito 2008). It is also possible that precipitation was enhanced by bacterial decomposition of the soft tissue itself (Berner 1968, Sagemann et al. 1999). Calcite may be the mineral phase responsible for calcium stored in the sediment as measured by XRF analysis. Calcite deposition may have been aided by slowing flow near the exit spout, allowing $CaCO_3$ to build up in the pore spaces between sediment particles through bacterial activity. Sediment samples for XRF analysis were collected from around the bone and plant material farther above the exit spout and may have contributed to the apparent "loss" of calcium from the system.

Chemical conditions in LF/HO matrix were different due to the extremely low hydraulic conductivity and organic matter (peat) throughout the sediment column. Initially, organic acids (including those formed by humic compounds, decomposition of organic tissues, and bacteria) lowered porewater pH beyond the buffering capacity of even the largest bones, resulting in an average pH <6.0 across treatments and probably began an early mobilization of calcium. Organic acids may have also acted as ligands or colloids attracting Ca^{2+} ions present in bone apatite, shifting conditions towards greater apatite dissolution (Bengtsson et al. 2005, Goyne et al. 2006, McSween et al. 2003, Sneddon et al. 2006) and may have played a larger role than carbon dioxide–related chemistry. The low flow rate and high organic content also supported a more active

microbial community, which exhausted dissolved oxygen leading to widespread anoxic and reducing conditions (Falter and Sansone 2000, Forster et al. 1996). The onset of reducing conditions resulting from bacterial activity, in conjunction with an increase in DI water pH, likely contributed to higher average porewater pH in the Middle period of the experiment (Schaetzl and Anderson 2005, Vepraskas and Faulkner 2001).

The apparent increase in matrix-bound calcium in LF/HO matrix treatments may be due to heterogenous flow through the matrix, where the transport of calcium through the matrix was extremely slow of halted altogether. Slow flow may have led diffusion as the primary transport mechanism in some regions of the matrix. It is possible that mobilized calcium was removed from the system by water traveling out the side of sediment column and down the inner container wall, leading one to overestimate calcium mobilization in the system. Although evidence for ion mobiliziation in LF/HO matrix includes silicon, iron, and phosphate, as shown by the deposition of vivianite crystals on bone and amorphous silica dioxide on plant remains. Vivianite is known to form on bone and other decomposing organic material in waterlogged sediments under anoxic and reducing conditions (Eh -0.07 to -0.36), between pH 5.5 to 8.5, with high iron and low sulfide concentrations (Mann et al. 1998, McGowan and Prangnell 2006). Furthermore, laboratory experiments have shown that vivianite can be precipitated by metal reducing bacteria, especially in the presence of a humic acid analog (Fredrickson et al. 1998, Hansel et al. 2003, Zachara et al. 2002). Although it was not directly identified, the gray-green color change may be related to this process, since amorphous iron hydroxides [FeII, FeIII $(OH)_2$] also form under the same conditions and can be green in color (ibid, Hansen and Poulsen 1999).

The effect of biological vs. non-biological processes cannot be separated with the available data. Nonetheless, bacteria likely played an important role in altering matrix hydrology through creating extracellular polymers or filling pore spaces with bacterial bodies, both of which significantly decrease hydraulic conductivity (Vandevivere and Baveye 1992a, b). The metabolism of bacterial colonies may alter chemical conditions, such as oxygen availability and pH, which may help direct processes involved in decomposition. This appears to be a trait of aerobic bacteria and may not have been as prevalent in LF/HO treatments due to the prolonged anoxic conditions. Instead, the low hydraulic conductivity was mainly due to extremely small pore sizes and physical clogging with decay products, though the role of bacteria cannot be discounted.

2.5.3 The Effect of Bone Size

Bone size was found to play the second most significant role in decomposition dynamics within these experiments. Results suggest that bones differing in size by up to an order of magnitude will decay through the same fundamental process when placed under the same environmental conditions but differ in the rate of this process due to differences in the surface area to volume ratios (SA:V) of the bones. This agrees with previous observational (Andrews 1995, Lyman 1994, Nicholson 1998) and experimental (Von Endt and Ortner 1984) studies. Rabbit bones have a much higher SA:V than deer bones, particularly when comparing lumbar vertebrae, which have a smaller centrum relative to other vertebral components. The less volume contained in the centrum, the greater the available surface area for diagenetic reactions, making small bones more susceptible to decay.

Differences in decay may be explained by the fact that bones of large size (or low SA:V) have the capacity to resist decomposition and diagenetic processes better than smaller (high SA:V) bones (see also Chapter 3). In most cases deer treatments had higher pH values than those with rabbit or no bone. The pH values of the latter two treatments overlapped considerably. In HF/LO matrix deer bones lost proportionally less mass and mineral density than rabbit bones despite showing the same signs of severe degradation. Large bones can therefore suffer more tissue damage than small bones—without compromising structural integrity—by releasing decay products into the surrounding porewater, thus insulating themselves from rapid decay through changing the nearby biogeochemical environment. This may be accomplished through leached calcium buffering porewater surrounding the bone or decay products and/or bacteria clogging pore spaces, lowering hydraulic conductivity around the bone. The structural integrity of small bones may be compromised from loss of bone tissue before this point is reached.

Dynamics of Bone Decay

Not only does decomposition rate differ between bone sizes and environments, but also the suite of biogeochemical reactions available within an environment depends on the context. The rate of density loss in proportion to mass loss in HF/LO matrix is far higher than that observed under the LF/HO regime across treatments (Figure 2.16). This pattern is strongest in rabbit bones, again pointing to the importance of SA:V in mediating decomposition reactions. Density and mass loss results should be interpreted with some caution however due to the fact that the HF/LO regression line is driven

largely by rabbit bone data and may instead be related to weaknesses in the method used to measure bone density change (see Chapter 3 for a complete discussion).

Mass and density loss results suggest that bone density reduction and overall mass loss are not directly coupled. Each value measures separate, but related, aspects of bone alteration. Meunier and Boivin (1997) emphasize the dichotomy between methods used to distinguish the amount of bone tissue present (mass per unit volume) versus those used to measure the degree of bone tissue mineralization. Mass loss may be more closely tied to loss of the organic fraction, including the remaining tissue, fat, blood, collagen, and cement proteins (Weiner and Traub 1992). The organic fraction accounts for as much as 33% of total bone mass (Martini 2005). Many of these components are labile and particularly susceptible to hydrolytic and enzymatic breakdown from cell autolysis and microbial attack (Andrews 1995, Tappen 1995). CT imaging of bone density is most sensitive to changes in the mineral fraction (Genant et al. 2000, Genant and Jiang 2006) with dissolution the most likely mechanism of mineral loss under experimental conditions. The solubility of bone apatite increases linearly with decreasing pH, independent of temperature (Harouiya et al. 2007). Under burial conditions bone apatite is unstable below pH 7 (Berna et al. 2004).

Though discussed separately, both mineral density and tissue mass remain related (Meunier and Boivin 1997). Loss or gain of tissue will affect the amount of space available for apatite crystallites to occupy, while loss or gain of bone apatite will affect overall tissue mass because the mineral is significantly denser than the organic fraction. However, it must be remembered that bone mass can decrease without a change in

mineralization, and that bone mass can remain stable even when the level of bone tissue mineralization is in flux.

Under the near-neutral pH values and high flow rate of the HF/LO matrix, the mineral fraction would be stable but prone to recrystallization (Berna et al. 2004). Decomposition was controlled primarily by loss of the organic fraction leading to an overall decrease in bone mass. Collagen loss would further destabilize the mineral fraction, removing it from the bone and contributing to both density change and mass loss (Collins et al. 2002, Nicholson 1996). Tissue removal opens up additional pathways into the interior through nutrient canals, which could potentially accelerate decomposition over time, as more interior surfaces are open to alteration. In LF/HO matrix, humic compounds released from the peat bound to collagen with Maillard reactions, stabilizing them against microbial attack and further decomposition (Borsheim et al. 2001, van Klinken and Hedges 1995). Calcium was still removed from the bone interior, as shown by the small amount of density loss, but remained minor because fewer pathways in and out of the bone existed. These processes would have prevented large-scale loss of the organic fraction while continuing to allow mineral dissolution.

Further evidence of enhanced collagen loss in bones from HF/LO treatments was seen after bones were stored in air-tight containers under refrigeration following exhumation. Cold air acts as a desiccant and after several months of refrigeration, the bones demonstrated a small decrease in mass due to water loss, which had condensed in the containers. Small cracks and wrinkles appeared on bones that were not present at exhumation. Similar features appear on bones exposed for extended periods of time to ultraviolet (UV) radiation, but not on the side facing the substrate (Behrensmeyer 1978,

Trueman et al. 2004, Tuross et al. 1989). UV radiation has been shown to degrade Type I collagen by lowering its threshold denaturation temperature (Majewski et al. 2002). Degraded collagen weakens the bone matrix and becomes warped following water loss. A similar mechanism likely created the small cracks and wrinkling observed in the experimental bones. Bones from LF/HO treatments do not demonstrate this surface feature despite exposure to the same conditions, indicating more intact collagen is probably present.

Surface Degradation in High-Flow Sediments

Removal of the bone cortex under high flow regimes may lead to erroneous interpretations of extended surface exposure prior to burial. The extent and type of surface modifications observed following burial under high flow conditions, if the observer was unaware of the experimental treatment, could be possibly mistaken for degradation resulting from prolonged subaerial exposure and/or subaqueous transport. In this experiment, damage was worst on surfaces facing the flow of water. This becomes problematic for the taphonomic interpretation of fossil, sub-fossil, and archeological bone material, which relies on such features for reconstructing the postmortem history of recovered bones. In this case, the incorrect belief that surface features on these bones represent surface exposure and/or transport abrasion may lead to erroneous conclusions of an arid surface environment prior to burial or designating the remains as allochthonous and therefore not a member of the (reconstructed) community (Figure 2.18). This result may be more problematic for archeological specimens than fossil ones because most bones are destroyed prior to fossilization. Further work is necessary to determine whether

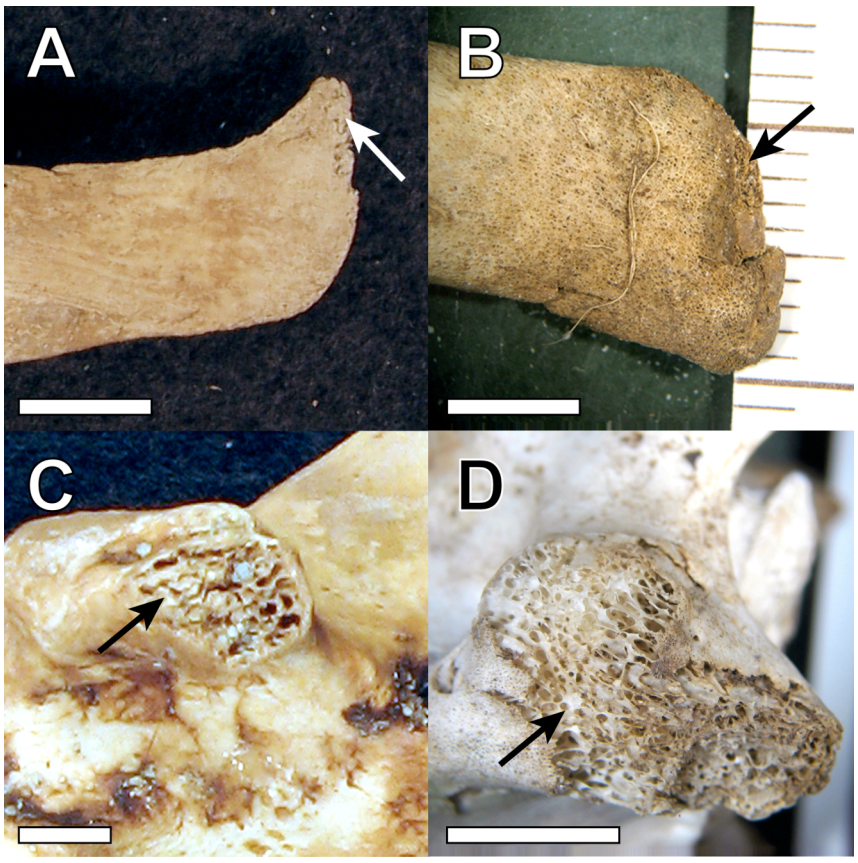

Figure 2.18: Comparison of external damage to deer bones from the experiment (A, C) with comparably-sized sheep bones naturally decayed on the ground surface for around one year (B, D). A) Distal end of transverse process of deer lumbar vertebra, superior view. B) Distal end of transverse process of domestic sheep (*Ovis aries*) lumbar vertebra, superior view. C) Transverse process of deer thoracic vertebra, left lateral view. D) Transverse process of sheep thoracic vertebra, left lateral view. Arrows point to damaged areas showing exposed trabecular tissue. All scale bars=0.5 cm. Images were contrast-enhanced and color-corrected to better show surface features, otherwise no additional alterations were made.

this phenomenon poses a legitimate hazard to taphonomic interpretations from coarse-grained sediments.

2.5.4 The Effect of Plant Material and Type

Based on the available data, there appears to be a strong pattern of interaction between plant and bone material in the burial environment, although it is not possible to determine the exact nature of the interaction at the current time. Nevertheless, I

hypothesize that this interaction is mediated by: 1) the relative mass of bone and plant material available, and 2) the kinds of products created during decay and their rate of release. An interaction between the decay products of the deer and plant material altered the environment sufficiently to slow the decomposition process. Some minimum amount of this decay product is necessary to slow decomposition, which was provided by the small mass of rabbit bone, but not before critical structural integrity was lost and the bone destroyed.

Plant material lowers hydraulic conductivity either as a physical mat, through the release of decay products, and/or encouragement of bacterial growth that blocks flow (Baveye et al. 1998, Vandevivere and Baveye 1992a, b). In most cases, angiosperms decreased and gymnosperms increased the hydraulic conductivity of the matrix compared to controls (Figure 2.6). The lowest hydraulic conductivity was achieved in fine sediment treatments with the greatest amount of available organic matter (i.e., deer and plant), suggesting an additive effect of organic decay products in depressing sediment hydraulic conductivity. Rabbit+plant treatments do not demonstrate as great a decrease due to lower overall organic mass.

Differences in hydraulic conductivity between angiosperm and gymnosperm treatments most likely reflect differences in initial composition and decay resistance. On average, gymnosperm litter is more resistant to decay than a comparable mass of angiosperm litter (Cornelissen et al. 2004, Enright 1999, Hobbie et al. 2006, Pereira et al. 1998) due in part to tissue lignin content, with higher amounts of lignin in the tissues associated with longer decay times (Aerts 1997, Berg and McClaugherty 2003, Cornelissen et al. 2004, Enriquez et al. 1993, Hobbie et al. 2006). Water soluble organics

released from the plant material may have played a role in clogging sediment pore spaces. Some decay products (calcium, organic acids, phenolics, and terpenoids) alter the biogeochemistry of the surrounding sediment and porewater (Gupta and Pancost 2004, Kainulainen and Holopainen 2002). Some of these compounds increase the solubility of different mineral species and/or facilitate their transport (Bengtsson et al. 2005, Goyne et al. 2006, Sneddon et al. 2006), while some (phenolics and terpenoids) have antimicrobial qualities that interfere with decomposition, mineralization, and humification (Kainulainen and Holopainen 2002, and references therein). The distribution of secondary compounds in plants varies depending on climate and plant functional group (Aerts 1997, Berg and McClaugherty 2003, Cornelissen et al. 2004).

One characteristic for which generalized data exist is foliar calcium content. Gymnosperms on average contain less calcium in their leaves than angiosperms (Hobbie et al. 2006, Reich et al. 2005). The decay-resistant gymnosperm material released calcium more slowly leaving less calcium available to interact with the burial environment, which may explain the lower pH and leached calcium values observed from gymnosperm treatments. It is not known why gymnosperm controls demonstrated higher sediment calcium values compared to other treatments. It is possible that gymnosperm decomposition in this setting was more accelerated due to the absence of bone or that decay products were less effective at mobilizing sedimentary calcium compared to other treatments, leading to local precipitation. Higher hydraulic conductivity (Figure 2.6) and sediment calcium values (Figure 2.8) in the gymnosperm controls may be understood as accelerated decomposition of the plant material in the absence of bone.

2.5.5 Limitations of the Current Study

Several limitations of the current study deserve attention. Certain simplifications were made to the design in order to maintain tighter control over experimental conditions, which may limit the direct applicability of these data to completely natural systems.

1. The use of deionized (DI) water is different from many natural systems, which contain some dissolved species, which could alter subsequent chemical reactions.
2. The matrix was kept completely saturated with water, whereas many burial environments are undersaturated (Brady 1974, Schaetzl and Anderson 2005). These results are most applicable to sediments beneath the water table and may not be well suited for explaining diagenesis of remains in the vadose zone of terrestrial sediments.
3. Use of only fresh vertebrae in the experiment excludes many other taphonomic scenarios commonly encountered by vertebrate remains. The effect of surface exposure or presence of soft tissue on bone diagenesis has yet to be studied. Furthermore, the decay products of multiple bones buried together may alter the surrounding sediment in ways not encountered by this experiment.
4. Bones from other parts of the body and other taxa may demonstrate different alteration features due to variation in density, size, and internal (histological) architecture (Enlow and Brown 1956, 1957, 1958).
5. Although this experiment used leaves from a range of plant functional groups and environments, had different species, plant organs, and functional groups been used, even those from the same family, results may have differed.

6. If two sets of remains experienced similar types and amounts of early diagenesis in similar environments, subsequent differences in history between the sedimentary beds due to the effects of deep burial, uplift, and erosion may alter the fossils or leave none at all.
7. Future experiments should aim for much larger sample sizes in order to provide the greatest statistical rigor possible (Denys 2002).

2.6 CONCLUSIONS

2.6.1 Implications for Vertebrate Taphonomy

This experiment support previous experimental, observational, and theoretical work citing the overwhelming influence of sediment hydrology on organic decomposition (Falter and Sansone 2000, Forster et al. 1996, Gastaldo and Demko 2005, Hedges and Millard 1995, Hulthe et al. 1998, Pike et al. 2001, Reiche et al. 2003). Indeed, this pattern is observed across such a wide range of terrestrial and aquatic environments that it may be considered a common factor driving decomposition of all organic remains. Sediment hydrology either directly controls or indirectly influences the factors controlling bone degradation, including pH, diffusion gradients, oxidation-reduction conditions, and (micro)faunal assemblage and activity level. These factors in turn can alter local hydraulic conditions, further changing decomposition dynamics.

Bone size is a critically important determinant of preservation due to differences in the surface area-to-volume ratio of large versus small bones but remains secondary to hydrology. Under similar environmental conditions bones lose material at the same rate,

however smaller bones have a lower threshold for critical loss of structural integrity. Larger bones maintain a higher threshold, allowing them to effectively buffer surrounding conditions, at least over the short-term. Therefore, under conditions in which diagenesis proceeds very slowly, the effect of bone size on preservation becomes negligible.

Some disagreement exists regarding which fraction of the bone matrix is removed first, the collagen scaffold or apatite crystallites. The results of this experiment agree with those who assert that each fraction degrades at different rates, and the extent of alteration to a fraction varies with environment (Fernández-Jalvo et al. 2002, Hedges 2002, Hedges and Millard 1995, Hedges et al. 1995). Further work is necessary to understand how each component degrades under different environmental conditions and the extent to which this affects fossilization potential, not only of bone in general, but bones of different size.

Plant material may play a more important role in bone preservation than previously realized, with the record of its contribution lost due to decay prior to fossilization. Importantly, the contribution of plant-derived calcium to the burial environment and its impact on bone mineral solubility, sediment pH, and subsequent permineralization has yet to be discussed in the taphonomic literature. In addition changes in the above-ground plant community may have important impacts on below-ground bone preservation. The assumed antagonistic relationship between the preservation of plant and bone material in the burial environment may need revision, although more work is needed to further test this hypothesis.

The preservation of bone and other organic remains will vary depending on how the previous set of conditions altered the remains and/or the burial environment. Even

under ideal environmental conditions like rapid burial and low hydraulic flow, certain alterations to the remains are necessary in order to provide the long-term stability necessary for diagenetic processes to transform the remains into a fossil. Optimal conditions, from the point of view of subsurface processes, include the following:

- Low hydraulic conductivity;
- The presence of humic acids that stabilize collagen in the bone matrix and mobilize metal cations;
- Large quantities of decay products that slow flow, decreasing the diffusion gradient surrounding remains; and
- Anoxia, which shifts the microfaunal community to mainly anaerobic bacteria with lower metabolism and helps promote early mineral formation.

A critical link between surface and subsurface patterns still remains tentative, but the results of this experiment suggest the following environments contain many of the attributes given above and may be best for preserving bone over the interval between burial and fossilization:

- Environments where remains continue in constant contact with water but under low hydraulic flow, for example fine-grained point bar deposits opposite the cut bank of a meandering river where lateral migration of porewater into the surrounding water table is reduced (Peyrard et al. 2008).
- Environments with a very shallow water table and lower biological productivity where remains would quickly move out of the vadose zone, such as overbank deposits and proximal floodplains.

- Other environments with little to no water flow and fine sediment deposition, as found in strongly meandering or braided rivers, oxbows, and eutrophic ponds or lakes.

2.6.2 Impact on Future Taphonomic Studies

This experiment is one of the first to explicitly test taphonomic hypotheses about the decay and diagenesis of fresh bone material under different post-burial environmental conditions in a controlled laboratory setting. This work is among the first to empirically examine the relationship between sediment hydrology and bone diagenesis by constructing matrices with different physical and chemical properties. This approach provides critical information about the mechanisms behind bone preservation. Individual researchers have used small-scale, short-term laboratory experiments to study specific processes, however the narrow focus of this work makes it difficult to predict how the biogeochemical processes observed in the experiment play out in real environments due to the complex conditions found in natural burial environments. On the other hand, results from experiments conducted under natural conditions can lead to contradicting results because of complexity and site-specific characteristics. In many cases taphonomic experiments suffer from poor experimental design and repeatability, severely limiting their application to the understanding of bone diagenesis (Denys 2002). An intermediate approach, such as the one used here, combines rigorous experimental methods with quasi-natural systems of varying complexity, providing a more efficient route for testing taphonomic hypotheses.

The methods used to track physical and chemical changes in the bone, plant, and burial environment are likewise comparable to those taken during field studies, making direct comparison between the two possible. Water chemistry, pH, dissolved ions, hydraulic conductivity, and even bone mass loss are all measurable under field conditions. This study is unique in its use of computed tomography (CT) techniques to quantify changes in bone density, examining changes to both the organic and inorganic fractions of the bone, where previous studies tended to focus on alterations to either fraction individually. These methods are by no means exhaustive but nevertheless do provide a strong indication of the important mechanisms driving bone decomposition. Further refinement of both the experimental design and methodology should help to improve future data and provide a more comprehensive understanding of the processes involved in decomposition.

The interdisciplinary approach of this project generates knowledge useful to a wide range of fields, including paleontology, anthropology, archeology, paleobotany, taphonomy, ecology, and forensics. The use of novel, non-invasive diagnostic methods, such as DCP-AES, provides an unprecedented look at patterns of decay *in situ*. Few studies have attempted to monitor conditions in this way, leaving our knowledge of the chemical changes within and surrounding a bone woefully incomplete. Future work should look to measure chemical changes, both within and immediately external to, an interred bone. Expanding this method to other vertebrate taxa will allow for comparisons of decay in similar environments, providing further insight into the formation of fossil assemblages. Methods developed here are broadly applicable to different clades,

environments, and paleoecosystems, and could be used to test specific diagenetic hypotheses related to fossilization.

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Chapter 3–Quantification of Taphonomic Alteration to Mammalian Vertebrae using Computer-aided Tomographic (CT) Imaging and Bulk Density Measures

ABSTRACT

Bone density is known to play an important role in element survival at the surface. Following burial density is also thought to play some role in diagenesis, however our knowledge of its role in subsurface taphonomic processes remains incomplete. Multiple methods have been used to quantify bone density, each with their own drawbacks. Medical-grade computed tomographic (CT) scanning offers an accessible and low-cost alternative when used with appropriate software. This study was part of a larger controlled laboratory experiment testing the role of sediment hydrology, bone size, and plant type on bone decay and diagenesis. The project outlined here quantified changes to bone density using mineral density (BMD) derived from CT scan data and bulk density (BD) from mass loss and volume data. BMD chiefly measures loss of bone apatite from the tissue while BD tracks more general changes in the organic component. Results show that both measures react in a similar fashion, however may be altered along different trajectories depending on external conditions. Differences between large and small bones indicate that the rate of bone diagenesis is a nonlinear function of bone size. Therefore multiple measures, which account for alteration to both the mineral and organic fractions, are necessary to understanding bone diagenesis under different subsurface conditions and environments.

3.1 INTRODUCTION

Accurately reconstructing an ancient community requires an assessment of the taphonomic history to determine the role that biotic and abiotic factors played in altering the community composition in forming the death assemblage (Behrensmeyer et al. 2000, Lyman 1994, Martin 1999). Even under the best conditions preservation is an episodic and context-dependent event that varies between environments and seasons. This has led to use of two complementary approaches in studying decomposition patterns, focusing on: 1) the impact of environmental conditions on bone preservation; and 2) the role that bone structural differences play in preservation and assemblage formation. Elements of each approach are found in many taphonomic studies, especially when comparing fossil assemblages thought to have formed under similar environmental conditions, or when examining potential paleoecological differences between assemblages from different environmentals (Andrews 1995, Behrensmeyer 1975, Behrensmeyer 1978, Behrensmeyer et al. 2003, Brain 1969, Davis and Briggs 1998, Fernández-Jalvo et al. 2002, Henderson 1987, Ioannidou 2003, Lam et al. 1998, Lyman 1994, Munoz-Duran and Van Valkenburgh 2006, Nicholson 1998, Nielsen-Marsh et al. 2007, Sept 1994, Smith et al. 2007, Smith et al. 1988, Smith and Swart 2002, Tappen 1994, Von Endt and Ortner 1984).

Bone density, specifically apatite mineral density, has been applied to vertebrate assemblages across disciplines, and is used by archeologists, paleoanthropologists, and paleontologists interested in the role of density-mediated attrition in shaping the faunal profiles of terrestrial sedimentary deposits (Broughton et al. 2007, Dirrigl 2001, Faith and

Behrensmeyer 2006, Ioannidou 2003, Lam and Pearson 2005, Lyman 1994, Symmons 2005).

Rigorous quantification of bone density took place with the pioneering work of Lyman (1984), who used photon densitometry to measure bone mineral density to show a strong positive relationship between the mineral density of an element and its representation in archeological deposits. The reliability of these measurements has recently been called into question, although not the importance of mineral density in surface taphonomic processes (Lam et al. 1998, Lam and Pearson 2005, 2003). Density has also been implicated in the transport potential of bones under aqueous conditions, where low-density bones are more likely to be transported and suffer damage than high-density bones (Behrensmeyer 1975, Behrensmeyer 1982, Coard 1999, Coard and Dennell 1995, Martin 1999). While the role of mineral density in surface taphonomic processes has received considerable attention, less work has gone into understanding the role of bone density in subsurface diagenetic processes. The hierarchical organization of the mineral and collagen in bone tissue provides multiple levels at which the internal structure can interact with and influence diagenetic processes and determine preservation (Collins et al. 2002, Hedges 2002, Pfretzschner 2006, Pike et al. 2001, Trueman et al. 2002, Weiner et al. 1989).

At the gross level bone density can be considered in two ways: bulk density and mineral density. Bulk density (BD) includes the organization of fibrils, spaces, and vascular canals. Bone mass acts as a reasonable proxy for BD if bone volume does not change appreciably. Bone mineral density (BMD) represents the total amount of apatite present in the collagen fibrils only. The two values are related, since BD is influenced by

the total amount of the much denser mineral apatite, however changes in BMD have been observed without a concomitant change in bone mass (Meunier and Boivin 1997). This distinction is drawn because a bone may be highly mineralized but still maintain a low bulk density. For example, avian bones have a relatively thin but highly mineralized cortex surrounding an extensively pneumatized interior, making some avian bones susceptible to certain types of taphonomic alteration (crushing), over others (microbial attack and dissolution) (Behrensmeyer et al. 2003, Broughton et al. 2007, Cruz 2007, Davis 1997, Davis and Briggs 1998, Dirrigl 2001, Nicholson 1996).

More importantly, the separate nature of BMD and BD suggests that each should respond differently to diagenetic processes. Therefore both represent a valuable indicator of bone alteration. Nielsen-Marsh and Hedges (1999) found that diagenetically altered bones undergo an increase in the largest (>10μm) and decrease in the smallest (<2 nm) pore sizes. Loss of the smallest pores may be related to collagen loss and/or recrystallization of apatite filling vacant pore spaces, while an increase in larger pores indicates bone mineral loss (Hedges 2002). In the early stages of diagenesis it is expected then that, in the absence of authigenic mineral formation, collagen loss should have a measurable effect on overall bone mass but not mineral density, though after a certain point this will increase porosity and enhance mineral loss, recrystallization, and authigenic mineral formation (Hedges 2002, Reiche et al. 2003).

Given the established connection between the proportions of the organic versus inorganic fractions of a bone and its bulk and mineral density, and the impact changes in these values have on diagenesis, it is imperative to our understanding of bone preservation to track changes in these values across a range of environmental conditions.

Several studies on the interaction between post-burial conditions, bone density, and diagenetic alteration have been carried out in natural environments (Fernández-Jalvo et al. 2002, Hedges et al. 1995, Liebig et al. 2007, Nicholson 1996, Nicholson 1998, Pfretzschner 2004, Reiche et al. 2003). Few such studies have been carried out under laboratory experimental conditions.

This project utilized X-ray computed tomographic (CT) imaging to directly observe changes to internal density values of bones undergoing decay and diagenesis. Comparison of scans taken before and after the experiment were used to assess the role of sediment hydrology, bone size, and fresh plant material on the mode and rate of bone decomposition (see Chapter 2). Changes in CT-derived density estimates were compared with bulk density estimates for each treatment to provide information on possible pathways of decomposition and diagenesis.

3.2 MATERIALS AND METHODS

3.2.1 Description of Experiment

A 14-month controlled laboratory experiment was designed to examine the connection between post-burial environment and decomposition of mammalian vertebrae. Two different sediment types were used: a High Flow/Low Organic (HF/LO) matrix composed of sand and silt, and a Low Flow/High Organic (LF/HO) matrix composed of peat, silt, and sand. The effect of plant material on bone decay was examined using collections of gymnosperm or angiosperm leaves. Variables were combined in a full factorial experimental design, which resulted in 18 treatments (including controls) with

three replicates of each treatment to create a total of 54 experimental containers. Each container was serviced by a pH-controlled deionized water delivery system. Bones were left undisturbed for the entire experimental period and exhumed at the end. See Chapter 2 for the full details of the experiment.

3.2.2 Deer and Rabbit Bones

Vertebrae came from farm-raised adult rabbit (*Oryctolagus cuniculus*) and white-tailed deer (*Odocoileus virginianus*), purchased from a local butcher and donated from a deer farm, respectively. Cervical and thoracic vertebrae were chosen because they share a similar morphology and are often preserved as fossils. All vertebrae were mechanically separated and cleaned of flesh before use. The starting and ending mass of each bone was measured on a digital scale to the nearest 0.01 g. Bones were allowed to air dry for 1 hour before weighing. Bone volume was calculated using water displacement in a graduated cylinder to the nearest milliliter. Final bone volume was not measured since most bones do not change volume significantly during decay (Hedges and Millard 1995) and graduated cylinders were not precise enough to measure small changes. Bones were stored in a freezer until buried for the experiment.

3.2.3 CT Image Acquisition

Medical CT was used to generate digital images of vertebrae before and after burial using a GE Lightspeed 16 medical CT scanner located at Stony Brook University Hospital (Stony Brook, New York) with the following parameters: tube voltage, 120kV; tube current, 70 mA; and scan time, 1.0 s. A slice thickness of 0.625 mm was used during

image data acquisition. All vertebrae were scanned in air to maximize contrast, sealed in plastic containers and held in place on the ventral surface of the centrum with clay. Containers were placed directly upon a plastic reference standard containing 5 tubes with fluid of known density. Time constraints and limited machine access necessitated the inclusion of multiple rabbit vertebrae in a single scan; therefore pixel resolution in these specimens is relatively poor. All deer vertebrae were scanned individually. Image reconstructions were made using a bone reconstruction algorithm (Bone Plus) in order to maximize the contrast between air spaces, pores, and bone tissue.

3.2.4 Bone Density Analysis

Changes in internal density values, as revealed by x-ray absorbance, can act as a proxy for bone apatite loss from the organic matrix with mineral loss indicated by darker shades. The internal densities of all vertebrae were assessed using the free software GE Microview (version 2.1.2), which allows 3D analysis of digital CT image data. A great advantage of this software is the ability to reorient the major axes easily to correct for variations in bone orientation during the CT scan. Complete digital CT image series were imported into Microview and reoriented so that the spinous process was parallel with the sagittal plane (y axis), the dorsal surface of the vertebral body was parallel to the frontal plane (x axis), and the long axis of the vertebral body was parallel with the z axis (Figure 3.1). This arrangement ensured a consistent orientation, which was necessary for comparative analysis.

The greater density and lower vascularity of the cortical bone leads to very low rates of alteration compared to trabecular bone, which has a much higher surface area

(Child 1995, Hedges 2002, Nicholson 1998, Nielsen-Marsh and Hedges 1999, Pfretzschner 2004). In order to observe density change within the relatively short timeframe of the experiment, only trabecular bone was examined. First, a cylindrical region of interest (ROI) was created in Microview. This ROI had a length half that of the centrum and a diameter that maximized the volume of trabecular bone while excluding the cortical layer (Figure 3.2). For each vertebra, a ROI of the same size and placement was used for before and after scan image sequences, providing measurements of the same volume. It was not possible to use the same sized ROI between all bones because of differences in centrum size and shape. For deer vertebrae, the maximum difference in ROI diameter was 4.3 mm and maximum difference in length was 6 mm. The maximum difference in rabbit ROI diameter was 1.2 mm and maximum difference in length was 7.2 mm.

Change in the distribution of pixel gray values in the ROI was calculated as a proxy for bone density using the "BMD Analysis" function. Actual bone mineral density could not be calculated because the scans are at too coarse a resolution for the algorithms to make an accurate estimate (i.e., each pixel can include both airspace and bone). All measurements therefore are reported in gray scale values, also known as Hounsfield Units (HU). Relative measures similar to the method used here have been used successfully in other studies concerned with measuring differences in BMD (Karlson and Patel 2006). The percent change between initial and final density measurements for each bone was calculated using the following equation:

$$\left(\frac{A_i - A_f}{A_i}\right) \times 100 = \%\ \text{change}$$

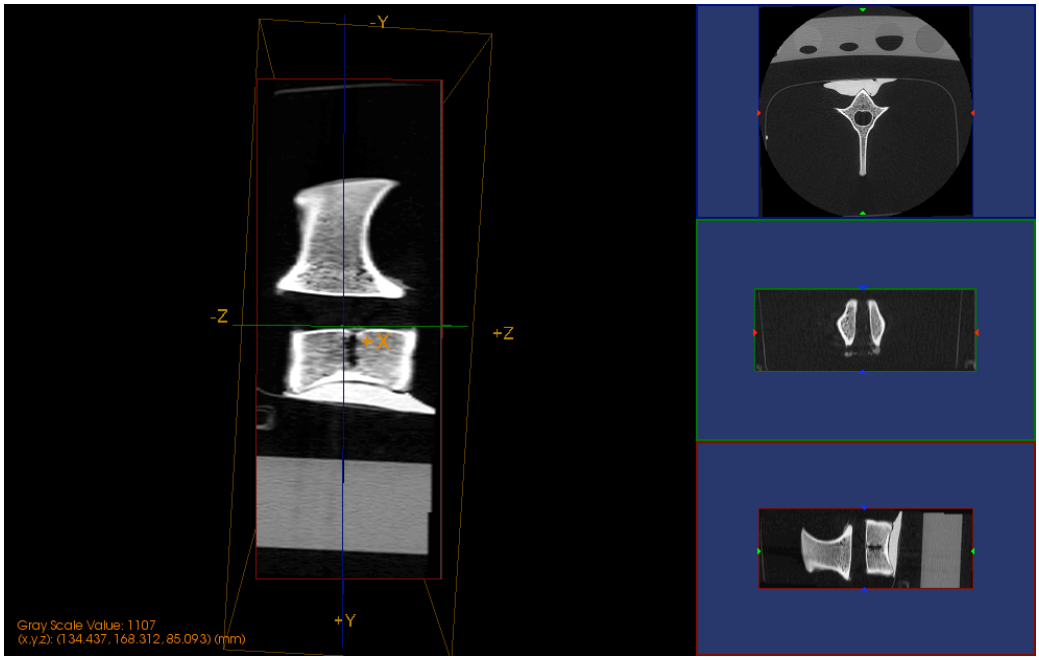

Figure 3.1: Screen capture of Microview program showing reorientation sequence of digital CT image data to lie precisely along X, Y, and Z axes (see text for details). Left image is 3-dimensional combination of axes, with positions of colored boxes/lines denoting their associated axis on the right: blue (upper right), Z axis; green (middle right), X axis; red (lower right), Y axis.

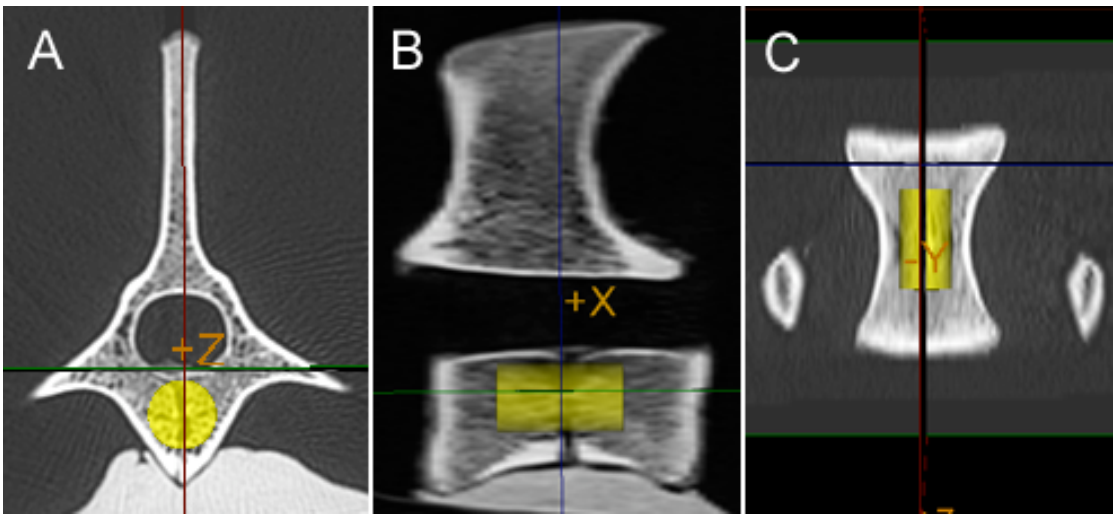

Figure 3.2: Screen captures of Microview program showing position of ROI (yellow cylinder) in vertebral centrum. Views: A) anterior, B) lateral, and C) dorsal. Note diameter of cylinder depends on centrum size and shape.

where A_i is the initial average gray scale value and A_f is the final average gray scale value. In the event that a bone was not recovered, it was scored as a 100% change (i.e., a complete loss of density). These values were also compared to the percent mass loss data from each bone (see Chapter 2 for details). Initial and final bone mass data were divided by the initial volume measurement to calculate the bulk density of each vertebra, recorded as g/cm^3.

3.2.5 Statistical Analyses

Initial density measurements were Box-Cox transformed prior to statistical analysis with JMP 7 (SAS Institute, Inc.). Differences between initial density measurements based on vertebral size (rabbit vs. deer) and type (thoracic vs. lumbar) were examined using two-way analysis of variance (ANOVA). All experimental bone density loss (percent change) data were first arcsin transformed. Differences between the amount of density lost based on vertebral size and type were examined using two-way ANOVA. The overall effect of experimental treatments on bone mineral and bulk density was examined with a three-way ANOVA. Linear regression was applied to percent change data for BMD and BD to examine the relationship between each measure.

3.3 RESULTS

Measures of bone mineral density (BMD) and bulk density (BD) demonstrate similar patterns, though with a few key differences. Each bone showed an overall decrease in measured BMD or BD, with the degree of change influenced by experimental

treatment, described below (Tables 3.1 and 3.2). BMD data show a decrease in the average gray scale value (increase in radiotransparency) for the same volume of bone studied. A decrease in bone mass was responsible for change in BD. On average BD estimated a higher percent density change than BMD. Despite this BMD and BD are closely correlated (r^2=0.736, p<0.001; Figure 3.3).

3.3.1 Initial Density Estimates

Plots of initial BMD and BD show a wide range of overlapping values between bone size and vertebral type, confirming the results of previously published estimates (Lyman 1984, Lyman 1994, Pavao and Stahl 1999). However, results of ANOVA demonstrated significant differences between deer and rabbit bone densities. BMD

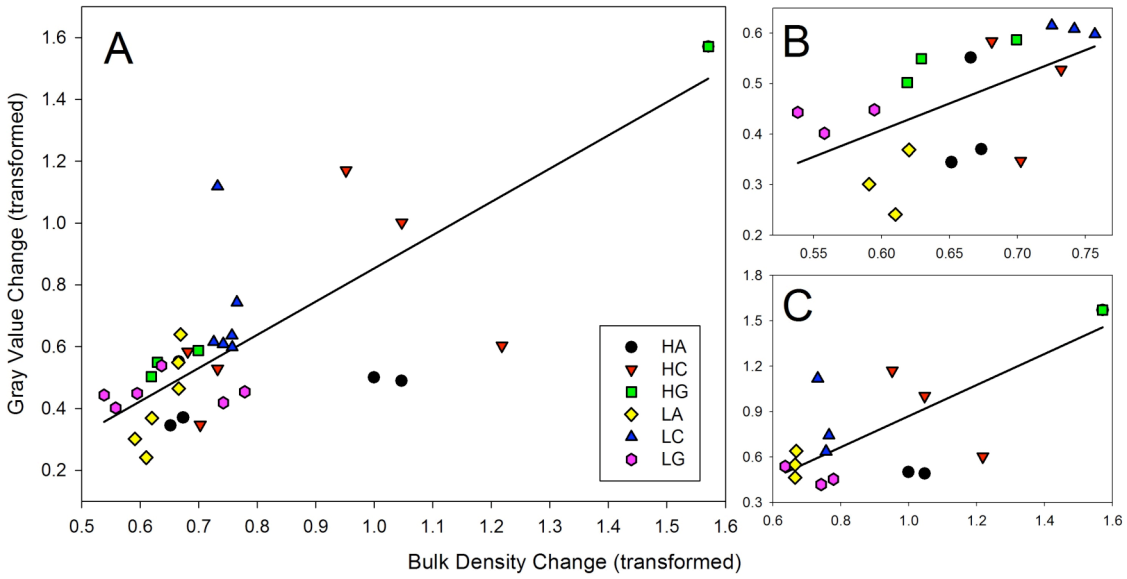

Figure 3.3: Percent bone mineral density change (gray value change) as a function of bulk density change separated by experimental treatment. Treatments follow Table 3.1. All data arcsin transformed. A) Combined bone data; y=1.075x-0.221 (r^2=0.736, p<0.001). B) Deer vertebrae only; y=1.056x-0.225 (r^2=0.286, p=0.013). C) Rabbit vertebrae only; y=1.028x-0.158 (r^2=0.647, p<0.001).

Table 3.1: Bone mineral density (BMD) change data for individual *Odocoileus* and *Oryctolagus* vertebrae. Standard deviation (SD) calculated by the Microview program given in parentheses. Treatments are as follows: H=high flow/low organic matrix, L=low flow/high organic matrix, A=angiosperm material, G=gymnosperm material, C=control treatment without plant material. †=Bone was highly degraded, missing spinous process, lamina, zygapophyses, and/or transverse processes; centrum remains more or less intact. *=Highly degraded as previous, but with interior of centrum partly missing.

Bone	Type	Treat-ment	ROI Diameter (mm)	ROI Length (mm)	Average Gray Value (SD)		Percent Change
					Initial	Final	
DT1	Deer thoracic	LC	13	14	1196.5 (241.6)	817.9 (229.4)	31.7
DT2	Deer thoracic	LC	13	14	1209.0 (267.6)	813.1 (204.6)	32.7
DT3	Deer thoracic	LC	11	14	1179.3 (256.9)	786.8 (221.3)	33.3
DT4	Deer thoracic	HC	11	14	1179.5 (259.8)	880.0 (293.7)	25.4
DT5	Deer thoracic	HC	10	14	1138.3 (248.2)	792.1 (243.7)	30.4
DT6	Deer thoracic	HC	10	14	1155.5 (259.4)	1021.4 (366.3)	11.6
DT7	Deer thoracic	HA	10	14	1051.3 (247.9)	913.2 (302.3)	13.1
DT8	Deer thoracic	HA	9.5	14	1064.4 (248.0)	942.6 (293.5)	11.4
DT9	Deer thoracic	HA	9	14	1148.4 (303.1)	833.1 (259.6)	27.5
DT10	Deer thoracic	LA	8.7	15.8	1044.5 (271.5)	908.5 (307.3)	13
DT11	Deer thoracic	LA	9.5	15	1141.2 (306.0)	1076.7 (371.6)	5.7
DT12	Deer thoracic	LA	10	15	1147.3 (334.5)	1046.3 (366.3)	8.8
DL1	Deer lumbar	LG	9.6	17	1202 (370.7)	976.6 (366.2)	18.8
DL2	Deer lumbar	LG	9.4	17	1174.1 (368.0)	994.6 (400.3)	15.3
DL3	Deer lumbar	LG	9.7	17	1185.2 (362.3)	967.7 (348.9)	18.4
DL4	Deer lumbar	HG	9.5	18	1229.5 (353.2)	893.7 (351.4)	27.3
DL5	Deer lumbar	HG	10	18	1213.6 (364.7)	931.6 (370.6)	23.2
DL6	Deer lumbar	HG	10	20	1152.5 (370.6)	769 (427.3)	30.7
RT1	Rabbit thoracic	HG	1.2	4	1075.7 (268.3)	—	100
RT2	Rabbit thoracic	HG	1.5	3	954.3 (398.6)	—	100
RT3	Rabbit thoracic	HG	1.8	3.5	903.9 (363.8)	—	100
RT4	Rabbit thoracic	LG	1.8	3.5	1036.8 (238.3)	865.3 (340.5)	16.5
RT5	Rabbit thoracic	LG	2.3	3.3	937.3 (326.0)	757.6 (388.7)	19.2
RT6	Rabbit thoracic	LG	2.1	3.9	1120.8 (414.2)	826.4 (480.8)	26.3
RT7	Rabbit thoracic	HA	2	4.7	994.8 (473.1)	—	100
RT8	Rabbit thoracic	HA	2.4	5.3	1014 (228.7)	790.2 (466.8)	22.1
RT9	Rabbit thoracic	HA	2.3	6.5	1012.9 (422.6)	780.0 (455.2)†	23
RT10	Rabbit thoracic	LA	1.4	5	1198.5 (486.9)	772.4 (441.1)	35.6
RT11	Rabbit thoracic	LA	1.2	6	1202.4 (315.8)	875.4 (251.6)	27.2
RT12	Rabbit thoracic	LA	1.2	6.7	815.6 (203.0)	652.0 (222.8)	20.1
RL1	Rabbit lumbar	HC	1.8	7.4	905.7 (375.9)	614.5 (442.2)*	32.2
RL2	Rabbit lumbar	HC	1.8	10.2	817.0 (471.4)	237.0 (303.2)*	71
RL3	Rabbit lumbar	HC	1.2	7	727.7 (442.9)	110.4 (168.9)	84.8
RL4	Rabbit lumbar	LC	1.8	8.4	854.2 (443.7)	462.9 (489.5)	45.8
RL5	Rabbit lumbar	LC	1.6	9.6	960.9 (377.0)	621.8 (349.2)	35.3
RL6	Rabbit lumbar	LC	1.8	8.6	988.2 (404.6)	189.1 (269.4)	80.9

Table 3.2: Bone bulk density (BD) change data for individual *Odocoileus* and *Oryctolagus* vertebrae. Treatments and symbols follow those given in Table 3.1.

Bone	Treat-ment	Bone Mass (g)		Volume (cm^3)	Bulk Density (g/cm^3)		Percent change
		Initial	Final		Initial	Final	
DT1	LC	37.55	19.84	27	1.39	0.73	47.2
DT2	LC	32.05	17.42	20	1.60	0.87	45.6
DT3	LC	28.74	16.09	20	1.44	0.80	44.0
DT4	HC	25.67	14.20	19	1.35	0.75	44.7
DT5	HC	23.86	14.40	19	1.26	0.76	39.6
DT6	HC	22.98	13.39	19	1.21	0.70	41.7
DT7	HA	21.09	12.89	18	1.17	0.72	38.9
DT8	HA	18.68	11.81	13	1.44	0.91	36.8
DT9	HA	18.69	11.56	13	1.44	0.89	38.1
DT10	LA	18.89	12.51	10	1.89	1.25	33.8
DT11	LA	19.92	13.38	10	1.99	1.34	32.8
DT12	LA	22.66	15.63	10	2.27	1.56	31.0
DL1	LG	27.43	18.82	20	1.37	0.94	31.4
DL2	LG	32.53	23.41	20	1.63	1.17	28.0
DL3	LG	35.12	25.89	23	1.53	1.13	26.3
DL4	HG	38.83	25.38	30	1.29	0.85	34.6
DL5	HG	40.80	27.07	36	1.13	0.75	33.7
DL6	HG	42.46	24.87	37	1.15	0.67	41.4
RT1	HG	0.63	—	0.5	1.26	—	100
RT2	HG	0.63	—	0.5	1.26	—	100
RT3	HG	0.58	—	0.5	1.16	—	100
RT4	LG	0.60	0.33	0.5	1.20	0.65	45.7
RT5	LG	0.58	0.29	0.5	1.16	0.59	49.3
RT6	LG	0.64	0.41	0.5	1.28	0.83	35.3
RT7	HA	0.73	—	0.5	1.46	—	100
RT8	HA	0.79	0.20	0.5	1.58	0.40	74.9
RT9	HA	1.07	0.31	0.5	2.14	0.63†	70.7
RT10	LA	0.96	0.59	1	0.96	0.59	38.4
RT11	LA	1.00	0.62	1	1.00	0.62	38.1
RT12	LA	1.19	0.74	1	1.19	0.74	38.2
RL1	HC	1.55	0.19	1.5	1.03	0.12*	88.1
RL2	HC	2.23	0.56	1.5	1.49	0.37*	75.0
RL3	HC	1.95	0.66	2	0.98	0.33	66.3
RL4	LC	2.37	1.23	2	1.19	0.62	48.0
RL5	LC	2.78	1.47	2	1.39	0.74	47.1
RL6	LC	2.63	1.46	2	1.32	0.73	44.7

Table 3.3: Summary table for two-way analysis of variance results in initial bone mineral density (BMD) data.

Source	df	SS	F	p
Vertebral type	1	11044.72	1.6631	0.2064 *ns*
Bone size	1	354872.54	53.4356	0.0000 ***
Vertebral type × Bone size	1	74793.70	11.2622	0.0021 **
Error	32	212516.15		

Table 3.4: Summary table for two-way analysis of variance results in initial bone bulk density (BD) data.

Source	df	SS	F	p
Vertebral type	1	0.07342426	1.1784	0.2858 *ns*
Bone size	1	0.27284129	4.3789	0.0444 *
Vertebral type × Bone size	1	0.01353514	0.2172	0.6443 *ns*
Error	32	1.9938506		

showed a greater degree of difference between the vertebrae due to size and vertebral type (Table 3.3 and Figure 3.4A). Deer vertebrae had significantly higher initial gray values than their rabbit counterparts although deer lumbar were denser than deer thoracics, while rabbit thoracics were denser than rabbit lumbars, leading to a bone size × vertebral type interaction (ANOVA: $F_{1,32}=11.26$, $p<0.01$). BD data for bone size and vertebral type overlapped to an even greater degree (Table 3.4 and Figure 3.4B). Initial

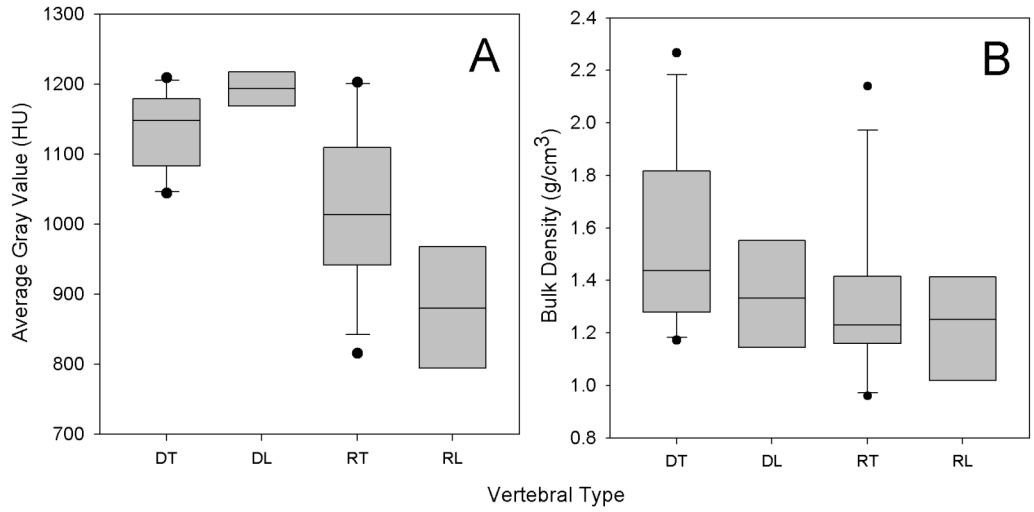

Figure 3.4: Initial density estimates for *Odocoileus* and *Oryctolagus* thoracic and lumbar vertebrae used in the experiment: A) Average gray scale value (bone mineral density), B) Bulk density. D=deer, R=rabbit, T=thoracic, L=lumbar. N=12 for thoracic boxes and N=6 for lumbar boxes.

Table 3.5: Summary table for three-way analysis of variance results for bone mineral density response to experimental treatment.

Source	df	SS	F	p
Matrix	1	0.6471429	13.3665	0.0013 **
Bone	1	1.4468303	29.8838	0.0000 ***
Plant	2	0.3343455	3.4529	0.0481 *
Bone × Plant	2	0.0768677	0.7938	0.4636 *ns*
Bone × Matrix	1	0.4779363	9.8716	0.0044 **
Plant × Matrix	2	0.5953649	6.1485	0.0070 **
Bone × Plant × Matrix	2	0.3098080	3.1995	0.0586 *ns*
Error	24	1.1619647		

Table 3.6: Summary table for three-way analysis of variance results for bone bulk density response to experimental treatment.

Source	df	SS	F	p
Matrix	1	0.8257916	77.0642	0.0000 ***
Bone	1	1.0561263	98.5595	0.0000 ***
Plant	2	0.0499402	2.3302	0.1189 *ns*
Bone × Plant	2	0.1916780	8.9439	0.0013 **
Bone × Matrix	1	0.6447686	60.1709	0.0000 ***
Plant × Matrix	2	0.1598464	7.4586	0.0030 **
Bone × Plant × Matrix	2	0.0659582	3.0777	0.0646 *ns*
Error	24	0.2571750		

BD values were significantly higher in deer vertebrae compared to rabbit vertebrae (ANOVA: $F_{1,32}=4.38$, $p<0.05$) but showed no difference between types.

3.3.2 Bone Size and Matrix Type

Rabbit and deer bones differed significantly in their response to each matrix type (Tables 3.5 and 3.6). HF/LO matrix had a differential effect on rabbit bones for both BMD (ANOVA: $F_{1,24}=9.87$, $p<0.01$) and BD (ANOVA: $F_{1,24}=60.17$, $p<0.001$), whereas rabbit bones in the LF/HO matrix were largely unaffected. Deer vertebrae also showed little or no difference in BMD and BD between matrix types (Figure 3.5). Density loss was similar between all deer and rabbit vertebrae from the LF/HO matrix, with only rabbit vertebrae from HF/LO matrix losing significantly more mineral.

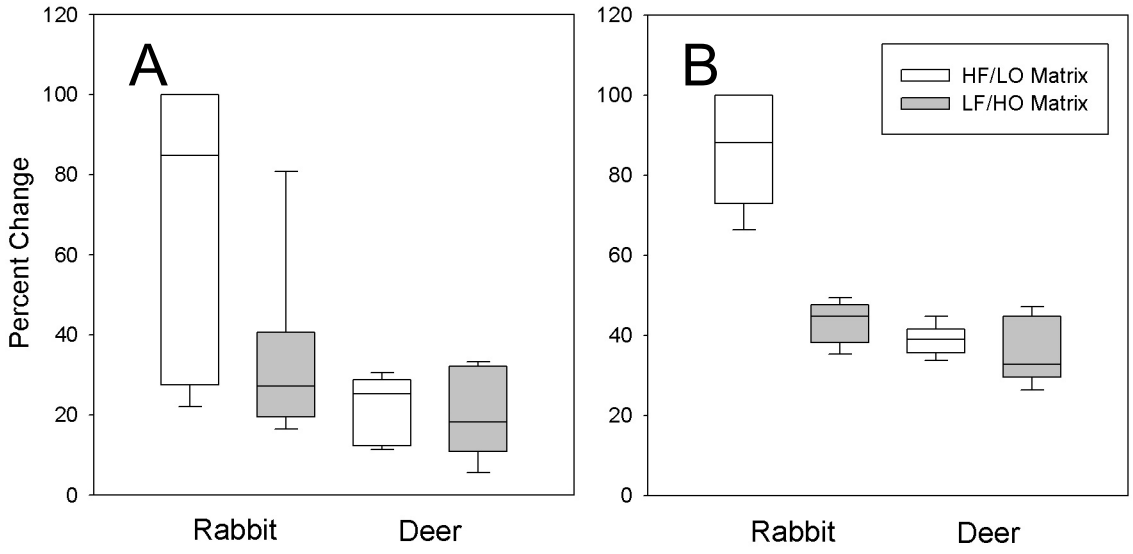

Figure 3.5: Percent change between initial and final density values for different-sized vertebrae: A) Average gray scale value (bone mineral density), B) Bulk density. N=9 for each box. HF/LO=high flow/low organic, LF/HO=low flow/high organic.

A total of four rabbit bones (RT1-3 and RT7) were not recovered after sifting through the matrix and assumed destroyed. Three other rabbit bones (RT9, RL1, and RL2) were highly degraded. In some cases the centrum was also partly destroyed, resulting in a large effect on the density estimates for these specimens. These lost and highly degraded vertebrae were all buried in HF/LO matrix. See Chapter 2 for a detailed description of bone condition following removal from the sedimentary matrix.

Linear regression of BMD on BD by bone size (Figure 3.3 B and C) shows a stronger positive relationship in rabbit vertebrae (r^2=0.647, p<0.001) than deer vertebrae (r^2=0.286, p=0.013). The slope of the deer regression was slightly steeper than that of the rabbit however a t-test for heterogeneous slopes was not significant (t=0.0667, p=0.947). This difference may be driven by the four unrecovered rabbit vertebrae, which could have a disproportionate influence on the line fit equation. Without these four vertebrae, the line becomes nearly horizontal.

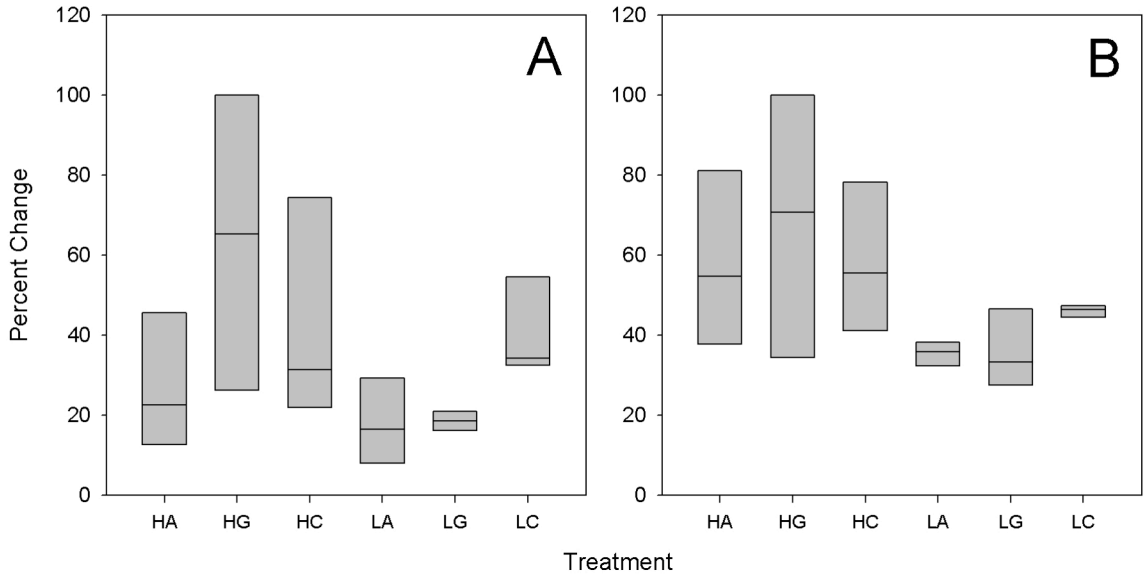

Figure 3.6: Percent change between initial and final density estimates separated by experimental treatment: A) Average gray scale value (bone mineral density), B) Bulk density. N=6 for all boxes. Treatment abbreviations follow those from Table 3.1.

3.3.3 Plant and Control Treatments

The interaction of plant treatment and matrix type resulted in major differences in decomposition (Figure 3.6; Tables 3.5 and 3.6). Bones placed in treatments with HF/LO matrix and gymnosperm material showed greater density decreases than bones in angiosperm or control treatments, indicating that gymnosperm material had a direct influence on density loss. In LF/HO treatments, bones placed with any plant material, whether angiosperm or gymnosperm, lost on average less density than control treatments. This pattern was significant for both BMD (ANOVA: $F_{2,24}$=6.15, $p<0.01$) and BD (ANOVA: $F_{2,24}$=7.46, $p<0.01$). BD data also demonstrated an interaction between bone and plant treatments (ANOVA: $F_{2,24}$=8.94, $p<0.01$) that was not reflected in BMD. Rabbit vertebrae lost more density with gymnosperm material than angiosperm or control treatments. On the other hand, the presence of any plant material suppressed density loss in deer bones below that of control treatments.

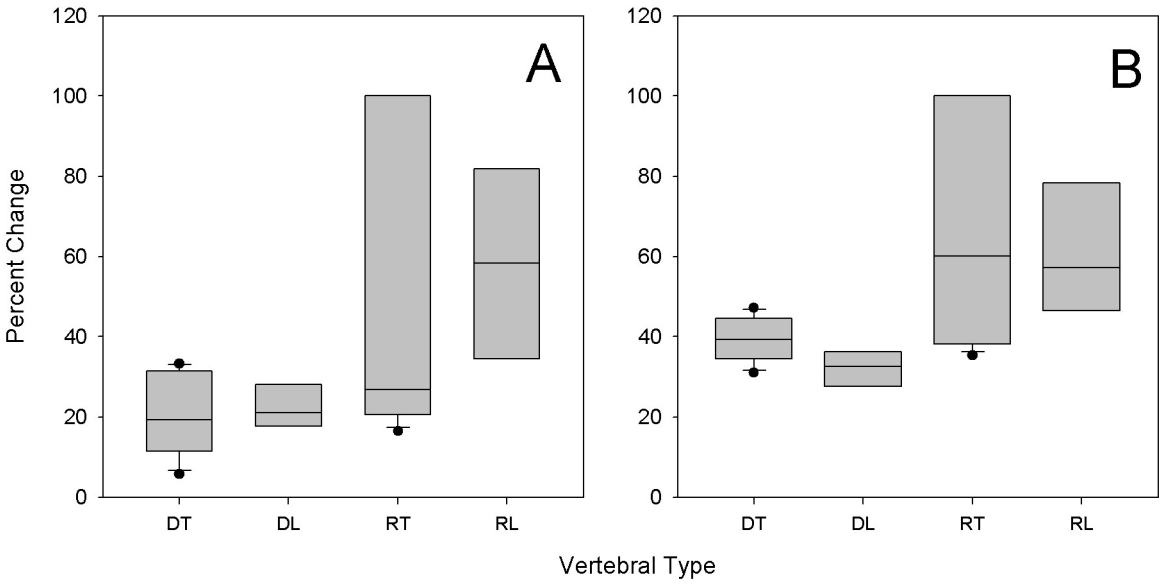

Figure 3.7: Percent change between initial and final density estimates for vertebral types: A) Average gray scale value (bone mineral density), B) Bulk density. Bone abbreviations follow those in Figure 3.3. N=12 for thoracic and N=6 for lumbar.

Table 3.7: Summary table for two-way analysis of variance results for percent change in bone mineral density (BMD) following the experiment.

Source	df	SS	F	p
Vertebral type	1	0.0053169	0.0473	0.8292 *ns*
Bone size	1	1.2687339	11.2852	0.0020 **
Vertebral type × Bone size	1	0.0005295	0.0047	0.9457 *ns*
Error	32	3.5975836		

Table 3.8: Summary table for two-way analysis of variance results for percent change in bone bulk density (BD) following the experiment.

Source	df	SS	F	p
Vertebral type	1	0.08132424	1.2348	0.2748 *ns*
Bone size	1	0.88846039	13.4896	0.0009 ***
Vertebral type × Bone size	1	0.00623672	0.0947	0.7603 *ns*
Error	32	2.1075971		

3.3.4 Vertebral Type

Thoracic and lumbar vertebrae within each bone size class (rabbit and deer) showed no significant differences with respect to treatment (Figure 3.7; Tables 3.7 and 3.8). However, the range of percent change from initial to final values in rabbit vertebrae was far greater than those of deer regardless of vertebral type. The values for rabbit vertebrae, especially rabbit thoracic vertebrae, were much greater in BMD than BD estimates. The median BMD value for rabbit thoracic vertebrae is much closer to the median of both deer vertebral types, the upper limit being set by the four unrecovered rabbit vertebrae. This pattern is not present in BD rabbit thoracic data, where the median value is much closer to that of rabbit lumbar vertebrae. If the four lost bones were to be removed from Figure 3.6, then the range covered by rabbit thoracic vertebrae would be diminished leaving rabbit lumbar as having undergone the greatest amount of change in BMD and roughly coequal change with rabbit thoracic vertebrae in BD.

3.4 DISCUSSION

Both bone mineral density (BMD) and bulk density (BD) decreased under the experimental conditions, demonstrating that each measure records a distinct aspect of bone diagenesis. BD appears more sensitive to loss of soft tissue and collagen content of a bone, as these components account for a third or more of total bone mass and are more labile than the mineral fraction. Many soft tissues will begin to break down following death due to cell autolysis, creating byproducts that are readily removed by water and/or metabolized by bacteria or fungi (Andrews 1995, Carter et al. 2007, Dent et al. 2004).

BMD is most sensitive to alteration of the mineral fraction and may only undergo significant change following perturbation of the organic fraction. This is supported by the overall greater mass loss and mineral density change encountered in HF/LO matrix treatments and the generally poor condition of the recovered bone (see section 2.4.2). Alteration to bone in LF/HO matrix treatments is more restricted in both measures resulting in bones that are well preserved. This data appears to confirm the interdependence of the organic and inorganic fractions as implied by previous studies (Collins et al. 2002, Hedges 2002, Pfretzschner 2006). Early in decomposition each fraction behaves more or less independently until a critical amount of one fraction is degraded or removed, after which point alteration of both fractions becomes more closely coupled due to their intimate association in the bone matrix. This threshold coupling is likely initiated through continued loss of the organic fraction, in particular collagen. Bones from LF/HO treatments probably remained intact despite lower average porewater pH because of low hydraulic conductivity and stabilization of collagen on the bone surface through humic crosslinking (Nicholson 1998, van Klinken and Hedges 1995).

At the near-neutral pH conditions present in HF/LO treatments bone apatite is normally insoluble but prone to *in situ* recrystallization (Berna et al. 2004, Nielsen-Marsh and Hedges 1997). Therefore the greater mass loss and density change observed in these bones are most likely the result of oxidative decomposition of soft tissue and collagen. Loss of collagen then exposed the recrystallizing apatite, facilitating its removal (Hedges 2002). Further quantitative analyses would be necessary to determine the extent of alteration and confirm the above observations.

Digital CT image data is useful in delineating changes in the content of mineral apatite in the bone matrix. However other factors may affect the resulting data. The pixel resolution of digital CT image data is a primary concern. Under the conditions used to scan the bones, deer vertebra scans have a higher pixel resolution than do rabbit vertebra scans by virtue of the former's larger size. In both cases each pixel represents some average of mineral, air, and water content. The higher resolution of deer scans may provide more accurate estimates of internal mineral density because each pixel represents a smaller area of bone matrix. On the other hand, if we assume that the general pore structure and size of cancellous bone between mammals is more or less similar, then the difference in resolution may not be an issue. Imaging methods that allow one to distinguish bone tissue from pore space, such as quantitative micro-CT, are likely to provide more accurate assessments of changes to BMD within and between specimens.

The morphology of the bones themselves affects decomposition rates. Even though the same number of each vertebral type (thoracic vs. lumbar) from each species was used, differences in the geometry of the centra may have contributed to the variation encountered in treatment response. Lumbar vertebrae, chiefly in the rabbit, have relatively small and laterally compressed centra compared to thoracic vertebrae. This makes them less cylindrical and raises the surface area to volume ratio (SA:V), potentially exposing more of the interior to diagenetic alteration. This may explain the differential response of lumbar vertebrae to treatment, where they appeared to lose more mass and density than thoracic vertebrae. This may also explain the wide variance seen in some treatments, particularly the matrix control (HC and LC) and gymnosperm treatments (HG and LG), each of which used lumbar vertebrae.

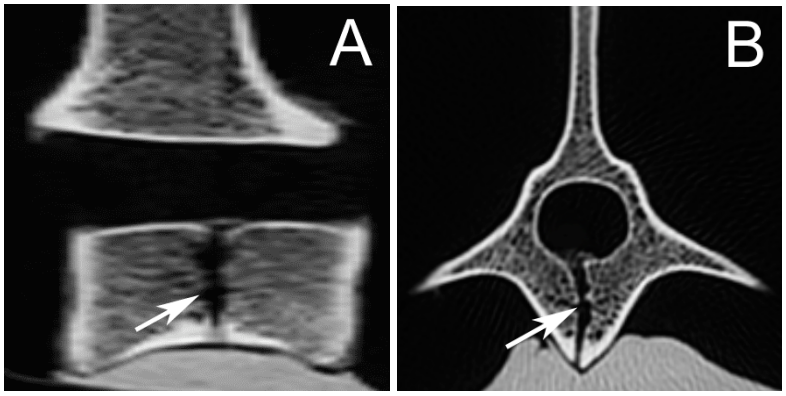

Figure 3.8: Location and extent of vascular foramina in a deer vertebral body (white arrows). Position of foramina is similar in rabbit vertebrae. A) right lateral view in midsagittal plane, B) anterior view in transverse plane.

Bone diagenesis may have been accelerated by the presence of vascular foramina in the vertebral centra, which provide a ready entry point for water into the bone tissue interior (Figure 3.8). This may have led to the greater overall mass and density loss observed in the rabbit bones, since a greater internal and external surface area of the centrum was exposed to diagenetic factors. The degree of foramen development appeared to be greater in lumbar vertebrae than thoracic vertebrae, and was greatest in rabbit lumbars. Because all the vertebrae contain vascular foramina, they are not considered to have played a disproportionate role in the response of individual bones to experimental treatment. Nonetheless, future taphonomic work should take into account bone porosity when designing actualistic experiments like the one performed here.

Highly vascular bone, such as the Haversian bone found in mammals, is highly mineralized yet also contains a vast network of osteonal canals and canaliculi for the transport of materials to the cells maintaining and remodeling bone matrix. These channels provide many pathways for the ready movement of water and bacteria. Compared to other bones from within the same individual or from a different taxon, more

vascular bones should decay faster, even if the bones have the same mineral density (Hedges 2002). This potential bias alone speaks to the need for any measurement of the capacity of a bone to be altered to include BD because it implicitly includes the porosity or vascularity of the bone in its estimation (Lyman 1994). Indeed both BD and BMD are necessary for a full understanding of bone diagenesis, in which case the approach widely used by Lyman and others (Dirrigl et al. 2004, Ioannidou 2003, Lyman 1984, Lyman et al. 1992, Symmons 2004) and that recently championed by Lam et al (Lam et al. 1998, Lam and Pearson 2005, 2003) are each valid and complementary to studying the role of bone density in diagenesis.

The significance of different initial densities in deer and rabbit bones is difficult to determine because so few comparative resources exist. Lyman (1994) provides *Odocoileus* density values of 0.29-0.30 g/cm^3 for lumbar and 0.24-0.27 g/cm^3 for thoracic vertebrae. A density of 0.35 g/cm^3 is available for *Oryctolagus* lumbar vertebrae only (Pavao and Stahl 1999). Not only are the density patterns contrary to results of the current study, the values are likely underestimates and the method used differs from this study, precluding a direct comparison (Lam et al. 1998, Lam et al. 2003). More importantly perhaps, the density values within each analysis are of a similar magnitude with different degrees of overlap. Therefore differences between vertebral types are considered to be relatively minor compared to the role of SA:V ratio in driving the experimental results.

Another line of evidence supporting the role of SA:V ratio lies in the different regression equations for the deer and rabbit vertebrae. Though the slopes of each line are not significantly different, their slight differences and the wider dispersion of deer data about the regression line suggests that decomposition follows a nonlinear response with

increasing size. The positive allometric scaling of the vertebrate skeleton leads to a proportionally greater cross-sectional area in the bones of large animals (Christiansen 2002). This scaling has a further impact on trabecular architecture, increasing the number, size, and connectedness of trabecular bone and thus substantially increasing the internal surface area of larger bones (Doube et al. 2009, Swartz et al. 1998). This relationship should lead to a nonlinear pattern in bone diagenesis when comparing bones from species across a wide size spectrum. Bone that lacks a substantial trabecular component may react more linearly over a similar size range. Very little, if any, work has been done to test this.

The combination of plant type, matrix type, and bone size all had a measurable effect on bone density loss. Overall, plant material reduced density loss across treatments, except for rabbit+gymnosperm treatments in HF/LO matrix, where decomposition was actually enhanced to the point of complete bone loss. The reduction of density loss was strongest in the presence of LF/HO matrix and plant material. A complete discussion of the effect of plant material and potential mechanisms by which it slows degradation are covered in Chapter 2.

3.5 CONCLUSIONS

This research is the first to connect changes in bone density with differences in external conditions present in the post-burial environment, complementing previous work that documents the importance of density in surface taphonomic processes. Bone density plays an important role in the decomposition process, though the relationship between

this trait and bone survivability is nonlinear and in many cases may be mediated by other aspects of bone morphology.

An important contribution of this study is the recognition of the need for multiple measures of internal bone tissue organization in order to understand its response to, and relationship with, different diagenetic processes. Therefore the bulk density (BD), which includes the porosity and soft-tissue content of a bone, and mineral density (BMD), which measures the degree of mineral formation in the bone matrix, of a bone each are necessary in predictive and diagnostic studies of bone diagenesis. Density change is quantifiable through measuring mass loss (volume remains relatively constant, with a few exceptions) and the relative intensity of CT image data taken from inside a bone. Used together, these measures provide a relatively easy and low-cost way to monitor the diagenetic status of a bone.

The method outlined here using comparative CT images to study 3-dimensional changes to bone matrix properties is more readily accessible and less expensive than more intrusive methods such as mercury intrusion porosimetry, although it will require the identification of appropriate baselines for use in archeological or forensic contexts where “initial” values for the bones are unknown. This method is readily applicable to experimental studies similar to the one described here. Despite some of its shortcomings, this type of semi-quantitative CT image analysis has great potential as a taphonomic tool that so far has been underutilized. Further work should help elucidate the connection between certain environmental parameters and aspects of diagenesis over time.

ACKNOWLEDGEMENTS

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Chapter 4–Multivariate Analysis of Vertebrate Taphonomic Indicators in the Late Jurassic Morrison Formation, U.S.A.

ABSTRACT

The Morrison Formation of the western United States is one of the best-studied terrestrial fossil assemblages from the Late Jurassic period, yielding a rich assemblage of vertebrates, invertebrates, and plants. Vertebrate remains occur in a wide array of depositional environments, including fluvial, floodplain, crevasse splay, alluvial fan, lacustrine, and pond settings under a semi-arid climate. The great taxonomic and environmental variation present in the Morrison Fm. provides an excellent opportunity to examine large-scale patterns of fossil distribution and preservation, comparing environmental and taphonomic variables with results of taphonomic experiments. The current study applied multiple regression, correlation, and principal components analysis to a database of 984 vertebrate fossil occurrences from the Morrison Fm. downloaded from the Paleobiology Database. Preservation quality was positively correlated with sediment grain size (proxy for hydrology), while it was negatively correlated with reducing conditions and surface exposure. Body size does not appear to play a direct role in preservation but instead mediates taphonomic processes, and appeared most important at the extremes. In addition, the number of fossil occurrences increased and preservation quality improved in proximity to moisture sources in the Morrison basin. Furthermore, preservation patterns were strongly influenced by paleoenvironment and the ecology of the animals. This study shows the importance of both surface and subsurface processes for vertebrate fossil preservation in the Morrison Fm.

4.1 INTRODUCTION

The Late Jurassic Morrison Formation represents the remains of a great floodplain basin deposited from between 155 and 148 million years ago (Kowallis et al. 1998, Turner and Peterson 2004). Outcrops of the formation extend across the United States (Figure 4.1) including Montana, Wyoming, South Dakota, Colorado, Utah, New Mexico, and Arizona (Foster 2003). The Morrison Fm. is underlain by marine beds of Middle to Late Jurassic age and overlain by Lower Cretaceous–aged beds including the Cloverly, Cedar Mountain, and Lakota Formations (Foster 2003, Turner and Peterson 2004). The prevailing climate during Morrison deposition was arid to semi-arid, with strongly seasonal precipitation, which resulted in broad, open expanses of low-lying vegetation interspersed with smaller areas of standing forest, roughly analogous to an African savannah ecosystem (Demko et al. 2004, Dodson et al. 1980, Dunagan 2000, Foster 2003).

The Morrison Fm. represents an ideal opportunity for testing taphonomic patterns of vertebrate fossil preservation and distribution, as it has been intensively studied for over 100 years, with thousands of individual vertebrate remains collected from over 200 described localities. The diverse fauna is best known for its dinosaurs, which include nearly fifty described species. Other vertebrate fauna include mammals, pterosaurs, fish, frogs, salamanders, turtles, lizards, snakes, and crocodilians (Dodson et al. 1980, Foster 2003, Turner and Peterson 2004). The formation is also environmentally diverse and includes deposits from lacustrine, fluvial, floodplain, wetland, alluvial, and eolian

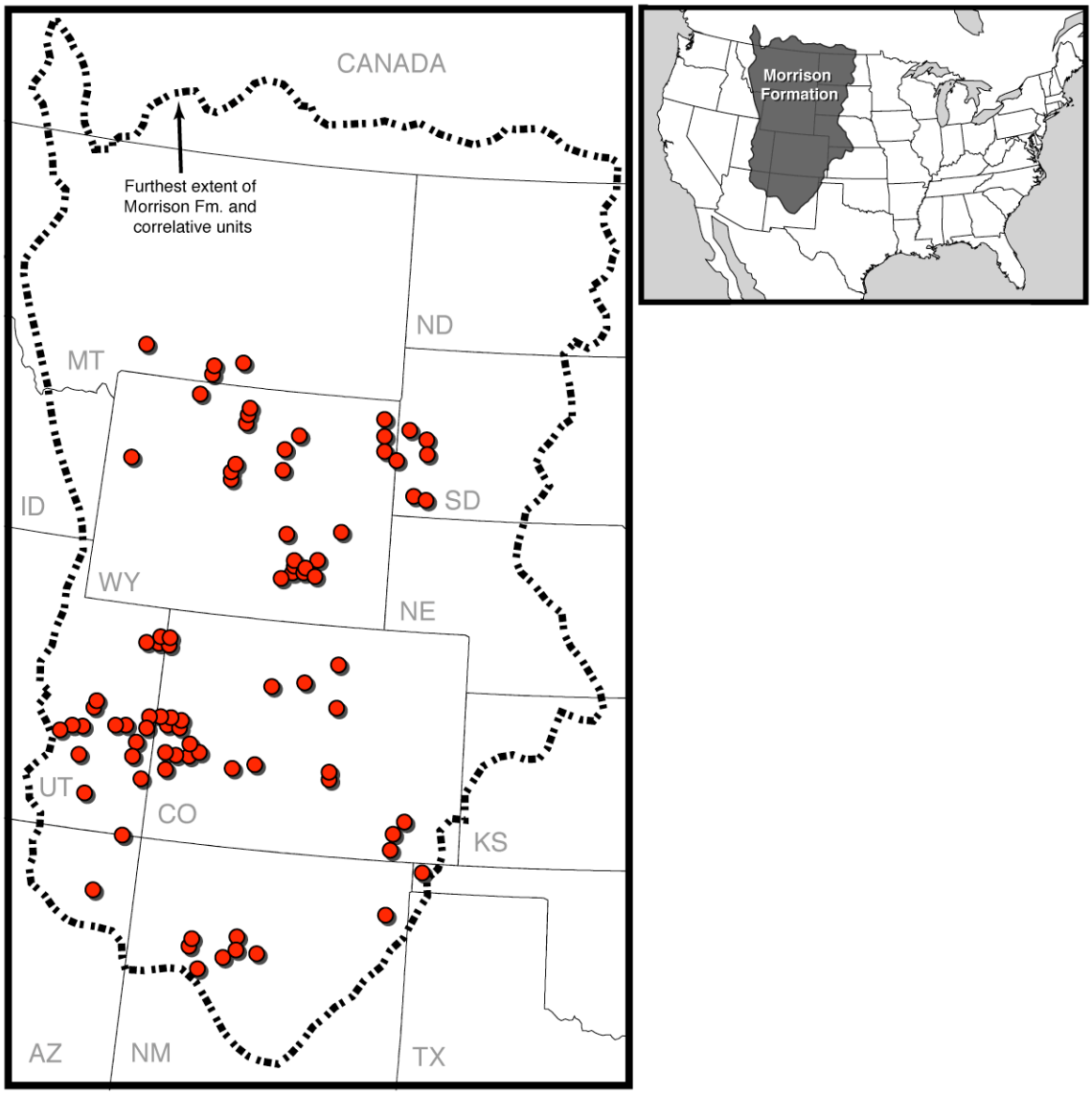

Figure 4.1: Location and extent of Morrison Fm. (small map) and location of vertebrate fossil occurrences used in this study. Occurrences plotted on a paleogeographic map rotated to 150 mya (large map). Present state boundaries marked in gray. Map adapted from Turner and Peterson (2004).

environments (Demko et al. 2004, Dunagan and Turner 2004, Peterson 1994, Turner and Peterson 2004).

Recent work has assembled a comprehensive picture of environmental distribution in the Morrison Fm. over space and time (Turner et al. 2004). Most important among these are two spatial gradients: the first is a south to north, arid to temperate climate gradient present in North America during the Late Jurassic (Rees et al. 2000, Turner and Peterson 2004); the second is an east to west precipitation/drainage gradient driven by mountain uplift to the west, which increased sediment moisture levels and sediment transport towards the east (Turner and Peterson 2004). These conditions combined to create a greater proportion of lakes and wetlands to the north and center of the depositional basin, where rivers entering from the broad alluvial plains emptied into the basin and supported a higher water table than to the south or west (Dunagan and Turner 2004). Paleosols (fossil soils) indicate that continued mountain uplift throughout Morrison deposition increased the strength of this moisture gradient in the basin, but general climatic conditions remained unchanged (Demko et al. 2004). Much of the fossil data is available to researchers via the Paleobiology Database (http://www.paleodb.org), thus providing a readily usable source for examining vertebrate preservation throughout the Morrison Fm.

4.1.1 Vertebrate Taphonomy at Large Scales

The fossil record recovered from the Morrison Fm. depends on the fidelity of taphonomic processes in preserving the original biological patterns present during deposition. Furthermore, a large-scale study of vertebrate taphonomy is necessary for

understanding the role of terrestrial taphonomic processes on preservation and ultimately the accuracy of paleobiological patterns present in the Morrison Fm. (see Chapter 5).

Studies in terrestrial taphonomy usually focus on either surface (including consumption, trampling, weathering, and transport) or subsurface processes (including sediment compaction, dissolution, microbial digestion, and recrystallization). Many surface processes acting on terrestrial vertebrates have been studied in seasonal, semi-arid environments similar to the Morrison Fm. (Cutler et al. 1999, Trueman et al. 2004) but the role of subsurface processes has received far less attention. This is especially important in view of potential differences between surface and subsurface taphonomic processes in affecting preservation quality and biological fidelity (Fernández-Jalvo et al. 2002). The taphonomic effects of differences in surface/subsurface environment, body characteristics, and ecology have been documented as major contributors to large-scale bias among marine invertebrates under different environmental conditions (Best 2008, Kidwell et al. 2005, Smith and Nelson 2003, Valentine et al. 2006) but the role of these factors in vertebrate preservation has yet to be considered.

The study of vertebrate taphonomy in the Morrison Fm. has a long history (Bader et al. 2009, Brezinski and Kollar 2008, Dodson et al. 1980, Engelmann et al. 2004, Engelmann and Fiorillo 2000, Foster 2003, Jennings and Hasiotis 2006, Myers and Storrs 2007), however these studies focus more on the taphonomy of a particular locality and/or paleoecological implications than the effect of different taphonomic pathways on fossil preservation. Several studied have identified important associations between lithofacies, vertebrate fossil distribution, and preservation quality although no large-scale study to date has studied these observed patterns of association under a statistical, hypothesis-

driven framework to examine common taphonomic patterns across different environments.

The Morrison Fm. offers a wide diversity of taxa, body sizes, preservation modes, and depositional environments, a long temporal range, as well as moisture gradients across latitude and longitude that can be used to investigate how surface and subsurface taphonomic processes may have influenced vertebrate fossil preservation and preservation quality, and thus our perception of the composition of the Morrison fauna. This study will statistically analyze a collection of vertebrate fossil occurrences from the Morrison Fm. using a combination of multiple regression, correlation, and principal components methods to examine relationships between variables and their effect on preservation quality. These results will be used to assess potential sources of taphonomic bias at three times (153, 150, 148 mya) and two spatial gradients (south-north, east-west).

4.1.2 Hypotheses

A number of subsurface factors have been shown to be crucial for bone preservation including sediment hydrology and moisture levels, redox conditions, body size, and sediment organic content (Fernández-Jalvo et al. 2002, Hedges 2002, Nicholson 1998, Chapter 2). Based on these factors the following hypotheses will be tested with the Morrison Fm. data:

Hypothesis I

H1: Fine-grained sediments will contain a greater proportion of fossil occurrences than coarse-grained sediments.

H0: There will be no measurable dependence of fossil occurrence upon sediment grain size.

Predictions and Additional Notes: Sediment hydrology is known to play a large role in bone preservation (Hedges and Millard 1995, Pike et al. 2001). If grain size is an accurate proxy, low-flow (fine) sediments will preserve more fossils than high-flow (coarse) sediments.

Hypothesis II

H1: Overall quality of preservation will be better in fine-grained sediments than it will be in coarse-grained sediments.

H0: There will be no relationship between preservation quality and sediment grain size.

Predictions and Additional Notes: Coarser sediment will be associated with lower preservation quality due to the destructive nature of high-flow conditions. This also assumes that most bones are buried in relatively good condition, having survived surface degradation processes.

Hypothesis III

H1: A greater range of body sizes will be represented in fine-grained sediments, while the bones of larger taxa will dominate coarse-grained sediments.

H0: There will be an even distribution of body sizes across sediment grain size categories.

Predictions and Additional Notes: Large bones are far more resistant to degradation across environments, but small bones are more sensitive to external conditions and easily removed from the record (Badgley et al. 1995, Clyde et al. 2005, Fiorillo et al. 2000).

Therefore, fine-grained sediments will contain a more even distribution of body sizes, while coarse-grained sediments will contain a greater proportion of large remains.

Hypothesis IV

H1: The number of fossil occurrences and preservation quality will be positively correlated with latitude and longitude.

H0: Physical location in the Morrison basin will have no bearing on the number of fossil occurrences or preservation quality.

Predictions and Additional Notes: A consistently high water table is an essential element of the preservation process (Fiorillo et al. 2000, Reiche et al. 2003, Turner and Peterson 2004). The number of fossil occurrences and quality of preservation should improve as proximity to moisture sources increases, including latitude (south to north) and longitude (east to west).

4.2 MATERIALS AND METHODS

4.2.1 The Paleobiology Database

All data used in this study were downloaded from the Paleobiology Database (PBDB), which is an open-access resource on the Internet. All content is collaboratively managed by dozens of contributors. Thousands of fossil occurrences from around the world are stored in the database, with more added on a regular basis (over 810,000 as of July 2009). Each occurrence is tied to at least one published book, journal article, or conference abstract.

4.2.2 Data Description and Treatment

Data were downloaded as an occurrence list from the PBDB website on July 17, 2008. All occurrences listed under the working group "vertebrate" were downloaded using the following search parameters: Time span = Late Jurassic, Taxon = Vertebrata, Stratigraphic unit = Morrison, Environments = terrestrial, and Continents = North America. All available options for Time, Geography, Stratigraphy, Lithology, Taphonomy, and Occurrence fields were also checked. Minimal lumping options for taxonomic identity or geographic location were chosen. All other options remained unaltered. Individual occurrences occupy data rows, while columns contain data associated with each fossil occurrence.

In total 984 fossil occurrences and their attendant data were available for analysis. Five columns were discarded from the dataset due to an abundance of blank entries or were otherwise uninformative. Some data columns, such as sediment grain size, were altered from their original PBDB entry by scoring and binning them, while others were combined to form composite data focused on the taphonomic characteristics of each occurrence (see below).

Data columns were scored as ordinal or nominal data with ordination being the preferred method. Ordination was carried out as a presence/absence score of a variable or as a discrete, increasing scale. Resulting data columns, categories used in scoring the data, and sample sizes are given in Table 4.1. Missing data were marked as unknown. The sample size for each data column varies due to missing PBDB data. The following is a description of each data column and its scoring method (nominal or ordinal).

Taxonomic Identity—This information was unaltered. Because of varying completeness between specimens, each occurrence was assigned to a higher-level taxon: Amphibia, Mammalia, Dinosauria, Testudines, Crurotarsan archosaur, Pterosauria, Sphenodontia, Squamata/other diapsids, and Osteichthyes. No distinction is made in the database between bony skeletal remains and teeth. The taxonomic identity of the fossil is the primary unit of the dataset; therefore common metrics like minimum number of elements (MNE) or minimum number of individuals (MNI) were not available.

Body Size—Each taxon was assigned a body mass in kilograms following estimates made by Foster (2003) and others (ibid), converted to a $\log_{10}$ scale and placed in one of six body size bins (ordinal variable, zero to five). In most cases, body sizes were assigned to genera with two exceptions: 1) when there were significant body size differences documented between congeneric species, or 2) the taxon belongs to a clade from which known specimens in the formation fall within a narrow size range (i.e., Mammalia, Amphibia, Squamata, Spenodontia, and Osteichthyes). In the latter case some suprageneric taxa were assigned a representative body size. All fossils were assumed to come from adult individuals unless otherwise noted as embryonic or juvenile. The mass of juvenile remains was based on the size fraction of the juvenile element compared to a corresponding adult specimen. Embryonic remains were placed in the smallest size category. This should not have a large effect on results due to there being only seven non-adult specimens identified in the current dataset.

Paleocoordinates—Paleolatitude and longitude data were downloaded unaltered. Many of the fossil occurrences come from the same excavation sites (localities) and therefore have the same coordinates (Figure 4.1). Paleocoordinates were grouped into

two-degree bins encompassing the furthest extent of all occurrences in the dataset. This created six bins for paleolatitude (south-north, one to six) and five bins for paleolongitude (east-west, one to five), scored as ordinal variables.

Member—These data remained unaltered and was scored as a nominal variable. Member refers to the major stratigraphic unit of the Morrison in which a fossil was found. Occurrences were assigned to one of three members: Brushy Basin, Salt Wash, or Tidwell. Remaining occurrences lacking member data were scored as Unknown.

Age—Used mid-range age data estimate of 148, 150, or 153 mya and scored as nominal variables. Given ages do not directly correspond to the named members. Stratigraphic units of the Morrison Fm. are not necessarily coeval, and may have been deposited at different times; in general the northern parts of the Morrison Fm. contain younger sediments (Turner and Peterson 2004). For these reasons age assignments in the database may not be entirely accurate.

Sediment Color—Four colors are included in the analysis: gray, green, red, and brown, and scored as ordinal data for presence/absence. Sediment color is a well-known indicator of redox conditions in both modern and lithified sediments (Retallack 1990, Schaetzl and Anderson 2005) with color depending on the oxidation state of iron minerals present in the matrix. Red and brown colors are associated with oxidizing conditions and presence of Fe^{III} minerals (such as hematite). Gray and green colors occur under reducing conditions and precipitate Fe^{II} minerals (such as iron hydroxide) (Vepraskas and Faulkner 2001, Zachara et al. 2002).

Sediment Grain Size—The lithology description included in the database was used to create an ordinal grain size scale from one to nine of increasing grain size. A one

(very fine) was applied to claystone, marl, shale, limestone, and siliciclastic, two (very fine–fine) to mudstone, three (fine) to siltstone, five (medium) to sandstone, seven to coarse sandstone, and nine to conglomerate. Categories four, six, and eight represent intermediate grain sizes (e.g., six=medium-coarse).

Surface Exposure—Taphonomically relevant but patchy data columns were combined into a single metric providing an estimate of the amount of surface exposure at the sediment-air and/or sediment-water interface, scored as an ordinal variable with three levels. The types of degradation and accumulation observed at the surface are largely independent of body size or taxon and more related to the properties of individual skeletal elements and amount soft tissue on the body (Aslan and Behrensmeyer 1996, Boaz and Behrensmeyer 1976, Coard 1999, Coard and Dennell 1995, Elder and Smith 1988, Faith and Behrensmeyer 2006, Trueman et al. 2004). Occurrences with mostly articulated bodies, few disarticulated remains, and little fragmentation were given a low exposure level. At a moderate exposure level, more disarticulated than articulated remains are present and occasional fragmentation, insect borings, tooth marks and bioerosion are encountered. Extended exposure was assigned to occurrences dominated by disarticulated remains, frequent fragmentation, and surface modifications (tooth marks, bioerosion, etc.).

Preservation Quality—These data remained unaltered from the original. Each occurrence was rated on an ordinal scale as poor, medium, good, or excellent. The criteria used to assign this designation are unknown but are assumed to incorporate some measure of completeness and surface texture.

Table 4.1: Data columns and categories used in this study. Descriptions and rationale for each set of data is given in the text. *=column altered from original PBDB entry. †=composite data column based on original entries.

Data Column	N	Categories
Taxonomic Designation	984	Am = Amphibia Ma = Mammalia Di = Dinosauria Te = Testudinata Ar = Crurotarsan archosaur Pt = Pterosauria Sp = Sphenodontia Sq = Squamate/other diapsid Os = Osteichthyes
Body Size* $\log_{10}$ scale (based on Foster 2003)	875	0 = <1 kg 1 = 1-10 kg 2 = 10-100 kg 3 = 100-1000 kg 4 = 1000-10,000 kg 5 = >10,000 kg
Paleolatitude Bin	984	6 = 40-42˚ 5 = 38-40˚ 4 = 36-38˚ 3 = 34-36˚ 2 = 32-34˚ 1 = 30-32˚
Paleolongitude Bin	984	1 = ˉ48-ˉ50˚ 2 = ˉ50-ˉ52˚ 3 = ˉ52-ˉ54˚ 4 = ˉ54-ˉ56˚ 5 = ˉ56-ˉ58˚
Age	984	148, 150, 153 million years ago
Member	984	Bb = Brushy Basin, Sw = Salt Wash, Tw = Tidwell, U = Unknown
Sediment Color*	516	gray, green, brown, red
Sediment Grain Size*†	779	1 = very fine 2 = very fine-fine 3 = fine 4 = fine-medium 5 = medium 6 = medium-coarse 7 = coarse 8 = coarse-conglomerate 9 = conglomerate
Paleoenvironment	984	FC = fluvial channel FCF = coarse channel fill F= fluvial indeterminate FL = fluvial-lacustrine L = lacustrine P = pond CS = crevasse splay LV = levee AF = alluvial fan TFD = dry floodplain TFW = wet floodplain T = terrestrial indeterminate
Surface Exposure†	829	1 = Low 2 = Moderate 3 = Extended
Preservation Quality	676	1 = Poor 2 = Medium 3 = Good 4 = Excellent

Paleoenvironment—These data were downloaded unaltered, and scored as nominal categories: Fluvial Channel, Coarse Channel Fill, Fluvial Indeterminate, Fluvial-Lacustrine, Lacustrine, Pond, Terrestrial Indeterminate, Wet Floodplain, Dry Floodplain, Levee, Crevasse Splay, and Alluvial Fan. Two categories included in the downloaded

dataset, Channel Lag and "Floodplain", were folded into the Fluvial Channel and Terrestrial Indeterminate categories, respectively, because each was observed in less than ten occurrences. Paleoenvironment categories are based on Behrensmeyer and Hook (1992).

4.2.3 Data Analysis

Dependent variables for this study included the preservation quality assigned to a fossil occurrence and the number of occurrences associated with a particular variable. The predominance of categorical variables in the dataset and unknown nature of relationships between them necessitated use of nonparametric and nonlinear statistical methods. Analyses were carried out in JMP 7 (SAS) and SPSS 11 for Mac (SPSS, Inc.)

A Kruskal-Wallis test was used to compare the distribution of body sizes across sediment grain size categories. The relationship between all ordinal variables was assessed using a categorical multiple regression analysis (CATREG in SPSS). Categories are first assigned numerical values through optimal scaling, and then a multiple linear regression is performed using the quantified data (Meulman 2009). An ordinal quantification for each variable was chosen that preserved the original order of the categories. Occurrences with missing data were excluded from the analysis.

Other potentially important relationships between variables necessary for testing the above hypotheses were assessed using a Spearman rho correlation. This test was performed on body size against sediment grain size, surface exposure, sediment color, paleolatitude, and paleolongitude as well as for sediment grain size against the same

variables, except body size. A Bonferroni correction for multiple comparisons was applied to each analysis.

Finally, a nonlinear principal components analysis (CATPCA in SPSS) was used to further examine relationships between the variables, especially with regards to time, member, and paleoenvironment. CATPCA uses the same optimal scaling process described above and depends on the number of components chosen and the quantification applied to each variable (Linting et al. 2007, Meulman et al. 2004). All variables were quantified as ordinal to aid interpretation, however this method still allows differential spacing between categories, making it more flexible than standard PCA in dealing with nonlinear relationships. Sediment colors were excluded because at least three categories are required for analysis. Paleocoordinate data were excluded because PCA is generally inappropriate for direct gradient analysis (Minchin 1987, Shi 1993). Age, member, and paleoenvironment data were included as multiple nominal supplementary variables, which were not used in creating the model. Such an approach allows one to examine the behavior of multiple nominal categories within the model without affecting the model itself (Meulman et al. 2004).

4.3 RESULTS

4.3.1 Distribution of Occurrences

The frequencies of vertebrate fossil occurrences for the categories of each variable are shown in Figure 4.2. Note that sample sizes vary due to missing data. A majority of occurrences (757) are 150 my in age, followed by 153 mya (199), and 148 my

(28) (Figure 4.2A). Most occurrences are part of the Brushy Basin Mbr. (642), while the next largest group has an unknown affiliation (275), followed by the Salt Wash Mbr. (66), with a single occurrence from the Tidwell Mbr. (Figure 4.2B).

Taxonomically, a majority of occurrences belong to dinosaurs (632), followed by mammals (117), followed by lower numbers of crurotarsan archosaurs (65), testudines (53), osteichthyan fish (37), squamates/other diapsids (25), sphenodonts (22), amphibians (19), and pterosaurs (14) (Figure 4.2 C). Paleoenvironments (Figure 4.2D) were similarly dominated by occurrences from Terrestrial Indeterminate deposits (245), followed by Fluvial Channel (157), Wet Floodplain (150), and Pond (148). The remaining deposits had fewer than 100 occurrences: Fluvial-Lacustrine (92), Coarse Channel Fill (42), Crevasse Splay (40), Lacustrine (35), Dry Floodplain (24), Alluvial Fan (20), Fluvial Indeterminate (19), and Levee (12).

Across paleolatitude bins, Figure 4.2E shows the greatest number of occurrences is centered around the center of the range (34-36˚=314; 36-38˚=416; 38-40˚=259), then drops off sharply towards the upper and lower margins (30-32˚=22; 32-34˚=62; 40-42˚=61). Figure 4.2F shows paleolongitude following a similar pattern, centered around ˉ52-ˉ54˚ (473) and declining to the east and west (ˉ48-ˉ50˚=13; ˉ50-ˉ52˚=195; ˉ54-ˉ56˚=259; ˉ56-ˉ58˚=44). These results support the predictions of Hypothesis IV.

Hypothesis I was tested by comparing the number of fossil occurrences within each sediment grain size bin. The greatest number of occurrences come from the finest sediments (very fine=109, very fine-fine=318, fine=70), with far fewer in intermediate (fine-medium=80, medium=102, medium-coarse=45) or coarse-grained (coarse=25,

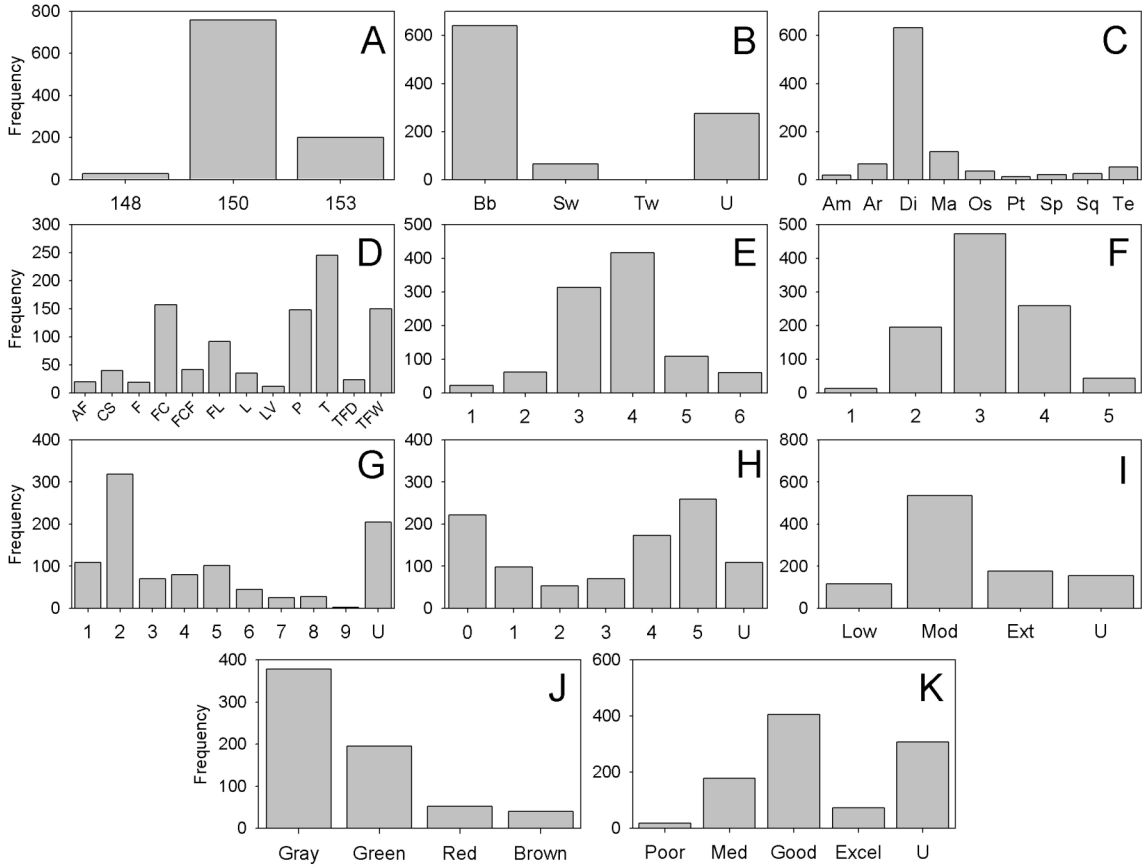

Figure 4.2: Frequencies of fossil occurrences for variables in the dataset. A) Age in million years. B) Member. C) Taxonomic identity. D) Paleoenvironments. E) Paleolatitude. F) Paleolongitude. G) Sediment grain size. H) Body size. I) Surface Exposure, Mod=moderate, Ext=extensive. J) Sediment color. K) Preservation quality, Med=medium, Excel=excellent. X-axis labels follow Table 4.1. U=unknown value.

coarse-conglomerate=28, conglomerate=2) categories (Figure 4.2G). All fossil-bearing layers have an average grain size below fine-medium, supporting predictions of greater fossil occurrences in fine-grained sediments made in Hypothesis I. Figure 4.2J shows that gray was the dominant sediment color associated with fossil occurrences (378), followed by green (196), then red, (53) and brown (40).

The greatest number of occurrences come from the very largest and smallest size categories and the fewest from intermediate sizes (Figure 4.2H). Animals >10,000 kg were most abundant (259), followed closely by animals <1 kg (222), 1000-10,000 kg

(173), 1-10 kg (98), 100-1000 kg (70), and finally 10-100 kg (53). Hypothesis II was tested using a Kruskal-Wallis test, in which a significant difference in body size was found across sediment grain sizes (Chi-square=62.05, df=7, $p<0.0001$). Post-hoc Mann-Whitney U tests showed that this result was driven mainly by the very fine–fine category, which contained a much greater proportion of fossils <1 kg and a lower proportion of fossils 1000-10,000 and >10,000 kg. In all other grain size categories the greatest proportion of occurrences come from very large animals and a lower proportion from smaller body sizes, however the lowest proportion is still made of intermediate body sizes. This result provides at best equivocal support for the predictions of Hypothesis III, which expected a relatively even distribution of body sizes in fine-grained sediment and overrepresentation in coarser sediments.

Most occurrences exhibited a moderate amount of surface exposure (535), followed by those with extensive exposure (177), and low exposure (117) (Figure 4.2I). A large majority of occurrences were preserved in good condition (406), then medium condition (179), and very few with an excellent (73) or poor (18) status (Figure 4.2K).

4.3.2 Categorical Multiple Regression

Hypotheses II and IV were tested using this method. Because complete data for all variables are required, only about half of the occurrences (510) could be used for analysis. Results, including total and partial correlations, are given in Table 4.2. The model fit was reasonably good, explaining 65% of the variance in the data. Collinearity between variables did not surpass ±0.45. Coarse grain sizes and higher paleolongitudes had the strongest correlations with preservation quality, 0.572 ($p<0.001$) and 0.449

($p<0.001$), respectively. Larger body sizes were slightly correlated with better preservation (0.228, $p<0.01$), however a reversed sign in the partial coefficient suggests that the effect of body size is dependent on other variables in the model. The low effect of paleolatitude (0.005, $p<0.001$) is similarly affected by other variables, especially paleolongitude.

Green sediment color was most correlated with lower preservation quality (-0.584, $p<0.001$), whereas gray color had very little effect (-0.040, $p<0.001$) even in the absence of other variables. Both red and brown colors had no significant effect on preservation quality. Surface exposure had a relatively minor effect (-0.025, $p<0.001$) on preservation quality. Besides red and brown colors, further removal of variables led to a poorer fit of the model. The positive correlation between sediment grain size and preservation quality runs counter to the predictions of Hypothesis II, which expected preservation quality to increase in association with finer-grained sediments. A greater number of fossil occurrences and their overall preservation quality increases to the north and west, supporting the predictions of Hypothesis IV, albeit with a weak relationship between paleolongitude and preservation quality.

4.3.3 Spearman Rho Correlations

This method was used to test Hypothesis III and assess additional important relationships among the variables. Table 4.3 shows the relationships between body size and environmental variables in the dataset. Sediment grain size was the only variable to demonstrate a positive correlation with body size (0.155, $p<0.001$), which supports predictions of Hypothesis III, though the relationship is weak. Green (-0.299, $p<0.001$)

Table 4.2: Results of Nonlinear Multiple Regression for preservation quality.

Variable	Correlations		df	F	p value
	Total	Partial			
Body Size	.228	-.100	2	4.948	.007
Paleolatitude	.005	.348	4	67.974	.000
Paleolongitude	.449	.542	2	205.982	.000
Grain Size	.572	.346	1	67.063	.000
Gray	-.040	.194	1	19.323	.000
Green	-.584	-.607	1	287.771	.000
Brown	.153	-.006	1	.016	.898
Red	.075	.055	1	1.493	.222
Surface Exposure	-.025	-.228	2	27.202	.000

Table 4.3: Relationship of Body Size with Environmental Variables

Variable	Spearman rho	p value[a]
Sediment Grain Size	0.155	<0.0001 *
Surface Exposure	-0.161	<0.0001 *
Paleolatitude	-0.066	0.0498 *ns*
Paleolongitude	-0.145	<0.0001 *
Gray	-0.242	<0.0001 *
Green	-0.299	<0.0001 *
Red	0.004	0.9278 *ns*
Brown	0.019	0.6279 *ns*

[a] Bonferroni correction for α=0.05 for 8 measures is 0.006; * indicates a significant result at this level, *ns* is nonsignificant.

Table 4.4: Relationship of Sediment Grain Size with Environmental Variables

Variable	Spearman rho	p value[a]
Surface Exposure	-0.172	<0.0001 *
Paleolatitude	-0.1126	0.0016 *
Paleolongitude	0.138	0.0001 *
Gray	-0.299	<0.0001 *
Green	-0.229	<0.0001 *
Red	0.193	<0.0001 *
Brown	0.124	0.0005 *

[a] Bonferroni correction for α=0.05 for 7 measures is 0.007; * indicates a significant result at this level, *ns* is nonsignificant.

and gray (-0.242, $p<0.001$) sediment colors tended to be more prevalent at smaller body sizes, but still represent a weak relationship. Smaller body sizes tend to have greater levels of surface exposure than larger body sizes (-0.161, $p<0.001$), however the correlation is not strong. Similarly, smaller body sizes are slightly more prevalent as one moves westward through the basin (-0.145, $p<0.001$). Variation in body size with paleolatitude and red and brown sediment colors was not significant.

Table 4.4 shows the relationship between sediment grain size with other environmental variables. Red (0.193, $p<0.001$) and brown (0.124, $p<0.001$) sediment colors were found more often with coarse-grained sediments while gray (-0.299, $p<0.001$) and green -0.229, $p<0.001$) colors were more common among fine-grained sediments. Indications of greater surface exposure are present in fine-grained sediments, though it is not a strong relationship (-0.172, $p<0.001$). Sediment grain size showed a moderate decrease towards the north of the Morrison basin (-0.113, $p<0.01$), while grain size was somewhat finer to the east (0.138, $p<0.001$).

4.3.4 Nonlinear Principal Components Analysis

A model using two components and composed of the variables sediment grain size, surface exposure, body size, and preservation quality provided a very good fit of the data, explaining 82% of the variance (Cronbach's alpha=0.927). Using a less restrictive nominal quantification on the variables only marginally improved the fit, however the ordinal quantification is preferred here for ease of interpretation.

Examining the quantification plots for each variable (see Appendix F) reveals important information about its behavior in the model (Linting et al. 2007, Meulman et

al. 2004). The largely flat lengths along the quantification plots for body size, surface exposure, and preservation quality indicate nonlinear relationships among categories in the model. On the other hand, an ordinal transformation for sediment grain size offers a good fit and demonstrates distinct differences between occurrences in fine, medium, and coarse-grained sediments.

Each variable is represented in the component plot by a vector (Figure 4.3). Component length represents the correlation of the variable and component, and the angle between vectors represents the correlation between variables (Linting et al. 2007, Meulman et al. 2004, Shi 1993). Preservation quality, sediment grain size, and surface exposure load heavily on Component 1, which explains about 46% of the variance in the model. Preservation quality and sediment grain size are positively correlated, agreeing with the Spearman rho result. Surface exposure was negatively correlated with both variables. Body size loads strongest on Component 2, which explains 36% of the variance. The orthogonal position of body size relative to the other variables suggests that its correlation structure is independent from the other variables, playing a separate role in preservation. This result affirms the multiple regression analysis, which showed a very weak relationship between body size and preservation quality.

Supplementary plots are useful for examining relationships among the categories of multiple nominal variables, which appear as the centroid of the occurrences in a category (Meulman et al. 2004). Centroids close to the origin are poorly differentiated by the model, while those furthest away indicate stronger relationships with particular components. Centroids representing the times 153 and 150 mya remain relatively close to the origin, suggesting they contain a wide variety of taphonomic modes (Figure 4.4).

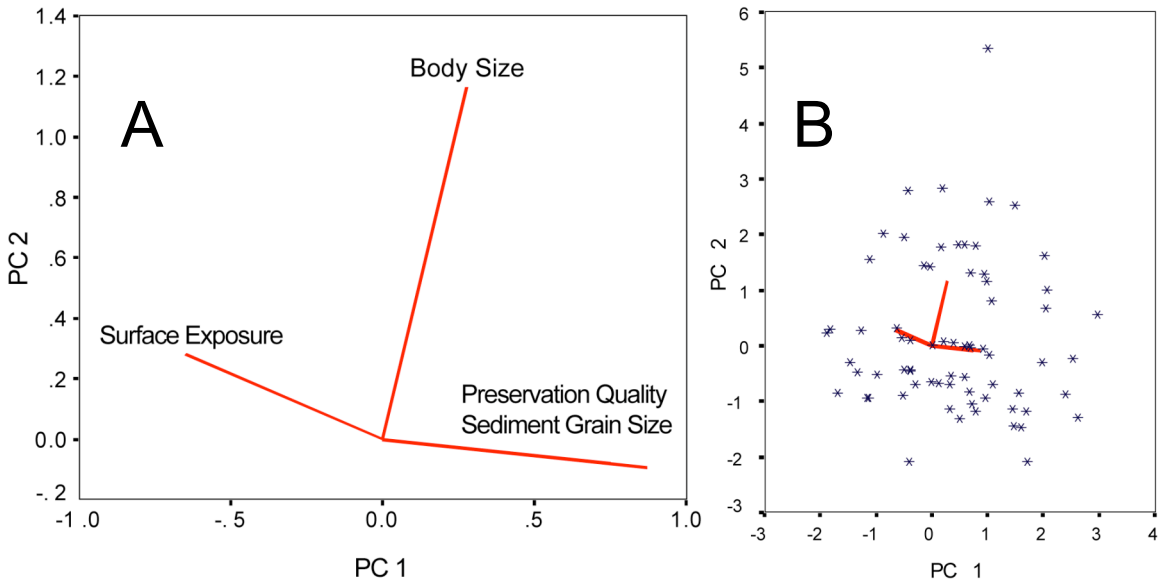

Figure 4.3: Non-linear Principal Components Analysis of Morrison Fm. occurrence data using the variables body size, sediment grain size, preservation quality, and surface exposure. A) component loadings only. B) Occurrences (blue stars) plotted in component space with component vectors.

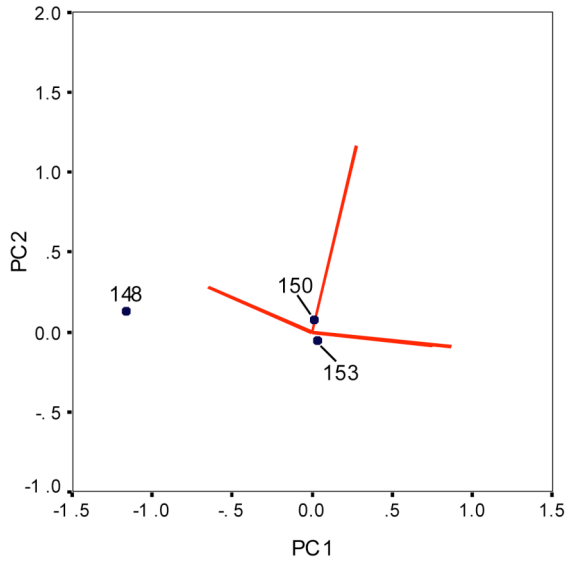

Figure 4.4: Position of group centroids for mid-age range (in million years).

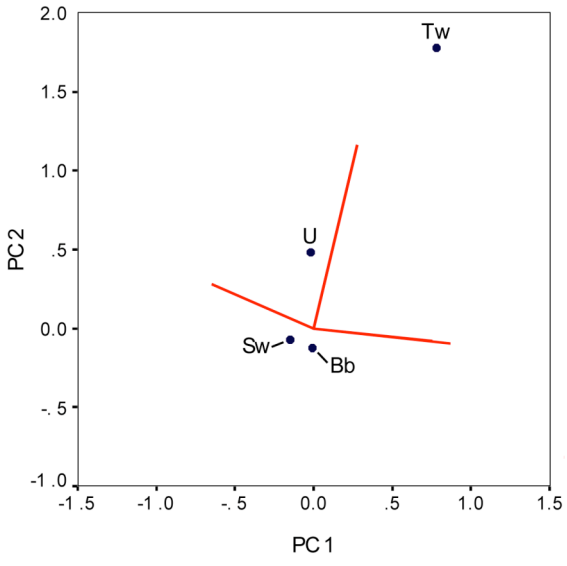

Figure 4.5: Position of group centroids for members, Tw=Tidwell Mbr., Sw= Salt Wash Mbr., Bb= Brushy Basin Mbr., and U= unknown member.

Both times have high samples sizes and each lacks only one paleoenvironment: 153 mya is missing alluvial fan, while 153 mya is missing coarse channel fill. The centroid for 148 mya is far separated from the other two times and is distinguished by occurrences with greater surface exposure and poorer preservation quality. This may be due to the overall lower sample size from this time. Furthermore, these occurrences come from terrestrial environments in the northern part of the basin.

The centroid of the Brushy Basin Mbr. is closest to the origin, possessing the greatest variety of environmental conditions, missing only alluvial fan and lacustrine deposits, and slightly smaller body sizes than the other members (Figure 4.5). The centroid of the Salt Wash Mbr. is also close to the origin and appears very similar to the Brushy Basin Mbr. except for a slight offset towards greater surface exposure and lower preservation quality. This is a remarkably robust pattern considering its much lower sample size most likely due to its missing only four environments: levee, coarse channel fill, fluvial-lacustrine, and lacustrine. The Tidwell Mbr. is represented by a single occurrence from a crevasse splay deposit, so a characterization cannot be made. The remaining occurrences with an unknown affiliation appeared most similar to the Brushy Basin Mbr. in terms of all variables except for body size, where they contain a much greater proportion of larger animals. These occurrences are from more northern localities and have many terrestrial deposits. The unknown occurrences contain nine environments, lacking alluvial fan, crevasse splay, and fluvial-lacustrine.

Paleoenvironment centroids form three loose clusters (Figure 4.6), largely along divisions of water energy and availability. Terrestrial-type environments separate to the upper left of the component plot, associated with moderate to extensive surface exposure,

fine-grained sediment, poor to medium preservation, and very large body sizes. Fluvial-type environments separate to the right, exhibiting low surface exposure, good to excellent preservation, and larger body sizes. Other aquatic–type environments differ greatly from the other two groups, diverging towards the lower left quadrant of the component space. These environments have moderate to extensive surface exposure, fine-grained sediment, poor to medium preservation quality and preserve mainly small-bodied animals. Finally, lacustrine environments appear completely different from the above named groups in carrying remains of the largest animals.

4.4 DISCUSSION

4.4.1 The Effect of Sediment Grain Size

Sediment grain size, as a proxy for hydrology, was found to be important to vertebrate preservation. Fine-grained sediments preserved far more fossils that coarse-grained sediments, supporting Hypothesis I. However, the positive correlation between grain size and preservation quality was the opposite of my predictions. Preservation quality appeared to increase with coarser grain sizes. This can be explained by the following: First, grain size alone does not take into account other factors that can alter sediment hydrology, especially in coarse-grained sediments, including water table height, porewater solute concentrations, and matrix composition, (Schaetzl and Anderson 2005). These factors can significantly decrease the movement of water through sediment porespaces by altering the size, shape, and connectivity of pores or the potential energy of water. Second, the ecology and evolutionary history of the living animals play a role.

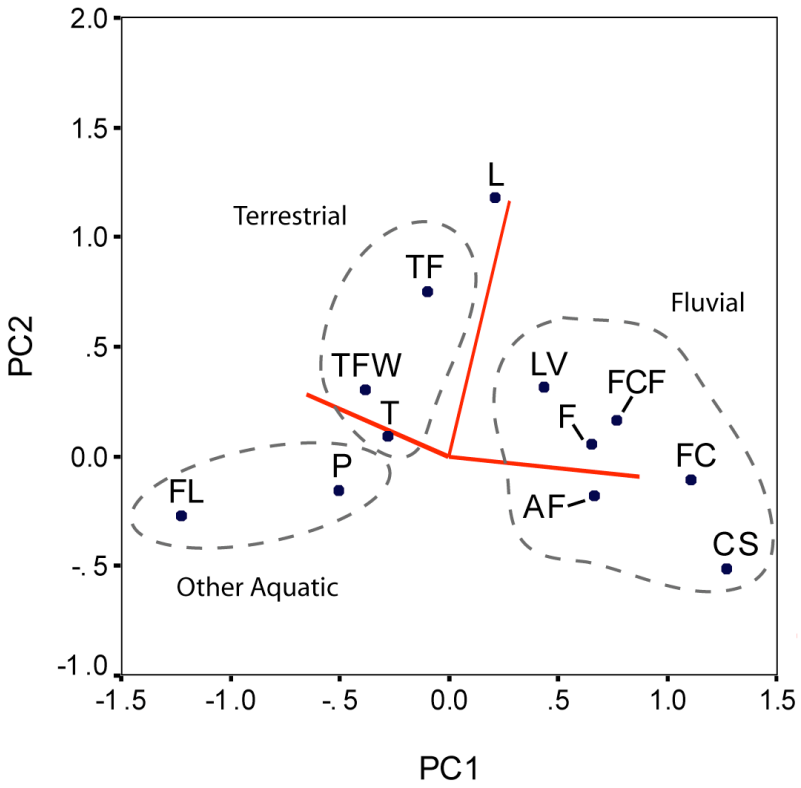

Figure 4.6: Position of group centroids for each paleoenvironment, FC=fluvial channel, FCF=coarse channel fill, F=fluvial indeterminate, FL=fluvial-lacustrine, L=lacustrine, P=pond, CS=crevasse splay, LV=levee, AF=alluvial fan, TFD=dry floodplain, TFW=wet floodplain, T-terrestrial indeterminate. Groups inside dashed lines represent environments with common taphonomic properties.

The largest and most numerous animals in the dataset are sauropods, which were exclusively terrestrial animals inhabiting the floodplains between rivers. The floodplain deposits were predominantly fine-grained with extended periods of surface exposure that likely destroyed the remains of smaller animals, having a disproportional effect on the association between body size and grain size.

Sediment redox conditions varied systematically in relation to grain size. Oxidizing conditions (red and brown) were more prevalent in coarse-grained sediments where porewater flow and oxygen infiltration would be higher. Reducing conditions

(gray and green) formed mainly in fine-grained sediment where low flow led to anoxia. The negative correlation of green with preservation quality and body size may indicate the need for reducing conditions to preserve remains of various sizes and stages of decay.

The conditions encountered in fine-grained sediments contain evidence of supporting conditions amenable to the preservation of bones of various sizes and stages of decay. Coarse-grained sediments require less degradation before burial to ensure preservation. Both of these patterns though require careful consideration of the environmental context. In light of this, Hypothesis II is considered tentatively supported, however further work is needed.

4.4.2 The Effect of Body Size

Removing animals <1 kg from the dataset does not appreciably change the relationship between sediment grain size and body size—body sizes are more or less evenly distributed across grain size categories with no major increase in the largest sizes with increasing grain size, thereby rejecting Hypothesis III. Extremely small body size played a positive role in preservation due to differing taphonomic behavior leading to an association with coarser sediments. Remains of the smallest vertebrates are often hydraulically transported, sorted, and concentrated into microsites by fluvial deposits and contain a large proportion of highly resistant skeletal elements such as teeth, scutes, and scales (Blob and Fiorillo 1996, Brinkman et al. 2004, Eberth 1990, Wilson 2008). The number of microsites in the Morrison Fm. is low, accounting for perhaps ~10% of described localities, but can be extremely diverse (Carrano and Velez-Juarbe 2006). This small number of microsites is likely having a disproportionate effect on taxonomic

diversity, adding far more small vertebrates than would be expected in the Morrison Fm. from experimental studies. Therefore, the differing taphonomic history of microsites from larger vertebrate remains precludes their direct comparison.

Results of correlation, multiple regression, and PCA suggest that body size operates separately from the other variables in determining vertebrate preservation. Instead body size appears to modify or influence the effect of the other variables studied depending on surrounding environmental conditions. As noted above, the taphonomic attributes of different bones are not directly scalable with body size. Differences in survivability due to body/bone size is thought to be a function of the surface area to volume ratio (SA:V) of the remains (Lyman 1994), which sets an upper limit on the amount of alteration a bone can undergo before it is destroyed by processes related to the variables used in this study (see Chapters 2 and 3). This alteration includes loss of the mineral and/or organic fraction of bone tissue, which leads to a loss of structural integrity over time (Fernández-Jalvo et al. 2002, Hedges 2002, Trueman et al. 2004, Chapters 2 and 3). In harsh environments with high decomposition rates, bones with a high SA:V reach this limit and are destroyed or rendered unrecognizable before low SA:V bones, which can suffer proportionally more damage. In environments where the decomposition rate is much slower, the importance of SA:V may become negligible due to the lower rate of bone tissue loss relative to diagenetic reactions that help stabilize bone tissue and are not dependent on bone size (Nicholson 1996, Nicholson 1998).

4.4.3 Taphonomic Changes over Space and Time

The peak in fossil occurrences towards the center of the Morrison depositional basin corresponds well with reconstructed paleo-drainage patterns (Demko et al. 2004, Dunagan and Turner 2004). In this central region we find conditions that were likely optimal for supporting preservation, including abundant rivers providing water and sediment that provided the means for burying remains. Numerous rivers also supported a high water table in some areas (Dunagan and Turner 2004), which is vital to the fossilization process (Hedges 2002, Hedges and Millard 1995, Pike et al. 2001).

Water availability was also reflected in the distribution of paleoenvironments throughout the basin. Floodplains, channel fills, terrestrial indeterminate (most likely paleosols), and crevasse splay deposits in the south give way to a greater proportion of fluvial, pond, and lacustrine environments as one moves north, indicating greater water availability in these areas of the basin. The greater diversity of depositional environments towards the center of the basin may have been important to supporting greater organismal diversity, as habitat heterogeneity at regional scales (~1000 km) is generally associated with increased taxonomic diversity in animals (Fraser 1998) and plants (Kreft and Jetz 2007).

Major taphonomic patterns did not vary appreciably over time, however changing conditions near the end of Morrison deposition may be reflected in the youngest occurrences. This pattern may derive from the fact that most occurrences occur predominantly towards the center of the basin where conditions remained moist and did not radically change during Morrison deposition (Turner and Peterson 2004). For this study, the use of age assignments may be more useful than member because: 1)

occurrences were not evenly spread among members over space; 2) occurrences with an unknown member affiliation are derived from mainly the northeast of the basin where conditions are less understood but appear to be predominantly terrestrial land surfaces; and 3) members are not recognized throughout the basin. Finer age and stratigraphic data are needed to properly understand this pattern.

Unfortunately the relationship between the variables, paleolatitude/longitude, member, and age appear to be contingent on sample size, with the peak in fossil occurrences also coinciding with: 1) more intensively sampled regions of the Morrison Fm. in Wyoming and Colorado, and 2) the location of two prominent microsites: the Fruita Paleontological Area in Colorado and Como Bluff Quarry 9 in Wyoming (Carrano and Velez-Juarbe 2006, Kirkland 2006). Thus there is a possibility that historical sampling bias and different taphonomic properties of microsites (see above) drives the recovered patterns over space and time. While many of the above patterns could be interpreted as supporting Hypothesis IV, these results remain equivocal until further work accounting for these biases can be performed.

4.4.4 Other Potential Sources of Bias

The PBDB includes only published fossil occurrences or those accessioned in museums. Paleontologists tend to preferentially collect and/or publish on those fossils that are most important or in best state of preservation or come from more accessible locations. In addition, differential surface exposure of fossil-bearing rock is known to exert a strong influence over paleobiological patterns studied in the fossil record (Chew and Oheim 2009, Peters 2005, 2006) and may behave similarly for taphonomic patterns.

A more thorough field-based examination that systematically surveys all remains and depositional environments across localities and corrects for surface exposure may alter the findings of the current study.

4.5 CONCLUSIONS

The distribution of vertebrate fossils and their quality of preservation in the Morrison Fm. is best explained by variation in: 1) sediment grain size, which acts as a reasonable proxy for sediment hydrology; 2) body size, where very large and very small animals have taphonomic properties enhancing their preservation; and 3) surface exposure prior to burial, which remains an important filter for remains at the surface under the semi-arid climate. Sediment color, and thus redox conditions, also played a role but samples representing oxidizing conditions few and the results may not be robust. A green sediment color though is a good indicator of reducing subsurface conditions. More indicators of biogeochemical conditions are needed. These data agree well with experimental results indicating the importance of hydraulic flow and bone size (Chapter 2).

Both physical and chemical factors involved in bone preservation are intimately related to the depositional (paleo)environment, which directs their activity on vertebrate remains. Variation in the distribution of environments, and hence vertebrate preservation, appears to be tied to shifts in water availability in the Morrison basin, which supports reducing conditions in fine-grained sediments favorable to the preservation of various

body sizes and remains in various states of decay. However the effects of sampling bias cannot be ruled out as a contributing factor at this time.

The question remains as to how faithfully the original Morrison ecosystem is represented in the fossil record. The high taxonomic diversity, relatively even proportion of preservation categories across body sizes and taxonomic groups, and similar taphonomic patterns from 153 to 150 mya suggests that the fossil record is sufficiently complete to allow an accurate representation of the ecology of the Morrison Fm. The trough-shaped body size distribution differs from patterns observed in many living and fossil communities (Behrensmeyer et al. 1979, Damuth 1982, Damuth 1992). Some workers have noted the paucity of intermediate body sizes among the vertebrate fauna of the Morrison Fm. and some Cretaceous formations attributing this to real differences in dinosaur community structure (Foster 2003, Wing and Tiffney 1987). Alternatively this pattern may still be the result of taphonomic processes due to the extreme resistance of gigantic sauropod bones to degradation and the special taphonomic properties of the smallest vertebrates, which may be easily condensed into microsites. The remains of intermediate-sized animals between 10 and 1000 kg fall outside this preservation window at each extreme by being too large to bury quickly but too small to withstand prolonged surface exposure. Therefore, future studies of Morrison vertebrate communities should pay special attention to the effect of taphonomic processes when examining large-scale paleoecological patterns. This can be accomplished through the inclusion of more detailed taphonomic information to resources like the PBDB, including data related to sediment biogeochemical conditions (color, infilling matrix, authigenic minerals), the

number and types of skeletal elements from each taxon (mandibles, ribs, teeth, etc.), and other indications of bone preservation (infilling minerals, bioerosion, completeness).

This study is among the first to examine large-scale taphonomic patterns in non-human vertebrates and will hopefully provide a hypothesis-testing quantitative framework for future studies. The nonlinear categorical regression and PCA methods described here provide an independent, statistical-based criterion for distinguishing taphonomic modes within fossil deposits and opens the opportunity for quantitatively comparing taphonomic modes between environments and across time and space in ways similar to (paleo)ecology (Behrensmeyer et al. 2003, Reed 1998, 2002, Shi 1993). Such studies have been difficult to carry out thus far, but nonlinear methods are recommended due to the unknown structure and underlying relationships between variables. These methods have the potential to detect taphonomic patterns at both small and large spatial scales. At small scales the association between taphonomic variables and interpretation of taphonomic modes can be assessed, which are functions of locality-scale processes. At larger scales, regional preservation and distribution patterns within and between stratigraphic levels can be used to understand the role of basin-wide processes and climate on environment distribution, which effects both species diversity and preservation potential. Such an approach allows for a more synthetic understanding of past biological patterns at various scales and more thorough comparison with modern examples.

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Chapter 5–Hierarchical Control of Terrestrial Vertebrate Taphonomy Over Space and Time: Discussion of Mechanisms and Implications for Vertebrate Paleobiology

ABSTRACT

There is no doubt among paleontologists that the fossil record of terrestrial vertebrates is fragmented and unevenly distributed over space and time. The underlying causes of this patchiness derive from a combination of factors occurring before and after the deposition of vertebrate remains. Large-scale vertebrate fossil distribution patterns present challenges in addressing the effects of small-scale taphonomic processes on distribution patterns, and what, if any, effect they may have on biodiversity reconstructions. This chapter presents a hierarchical model connecting small-scale taphonomic processes and large-scale fossil preservation patterns. Factors at higher scales constrain the range of taphonomic processes acting at lower scales, whereas lower scales are responsible for determining vertebrate preservation and resulting fossil record for an area. Secular changes in climate, tectonics, sea-level, etc. alter the distribution of both environments and biodiversity over time. These changes in turn may alter the congruence between standing biodiversity and the fraction of that diversity faithfully represented in the fossil record, skewing our understanding of extinct vertebrate ecosystems and their evolution over time.

5.1 INTRODUCTION

The growth of terrestrial taphonomic science requires not only developing new analytical tools and techniques, but expanding the scope of research questions into new theoretical territory. Research conditions are rapidly changing as the development of large online databases allow for the compilation of data from a variety of sources into common, searchable formats (Alroy 2003, Barnosky and Carrasco 2000, Rees and Noto 2005). This development provides an unprecedented resource for studying the taphonomy and paleobiology of terrestrial vertebrates, particularly the ability to analyze regional and global patterns of fossil distribution. The potential for discovering and analyzing large-scale patterns in fossil distribution has been discussed for decades (Behrensmeyer et al. 2000), yet it remains to be explored how taphonomic factors, acting over multiple scales, interact to influence spatio-temporal preservational patterns of vertebrates. Martin (1999) proposed that many taphonomic processes follow a hierarchical organization (Rule 19, p. 391), though uncertainty remains about the strength of interaction between different levels. This concept has yet to be comprehensively explored in terrestrial systems, least of all its effect on vertebrate preservation and interpretations of large-scale patterns in fossil distribution.

5.1.1 Top-down vs. Bottom-up Controls on Terrestrial Taphonomy

In ecology, the processes structuring ecosystems or communities can be described as being exerted from the “bottom-up” or “top-down”. Bottom-up refers to lower-level inputs (resources) exerting control over higher-level processes (community dynamics),

whereas top-down control is where the structure of lower levels (such as species diversity) depends on processes acting at higher levels (predation or environmental disturbance) (Begon et al. 2006). Taphonomic processes and their effects on the fossil record also can be approached analogously, as suggested by Martin (1999). In this case, top-down processes restrict the range of taphonomic conditions that can act on remains prior to and following fossilization. Bottom-up processes act at the level of an individual carcass or bone in response to higher-order restrictions, producing the fossil record for an area and influencing our view of fossil distribution at that time (Figure 5.1).

Climate, tectonic activity, and solar energy input exert top-down control over taphonomic processes through driving the distribution of different environments and the conditions that preserve or destroy vertebrate remains. Rogers (1993) suggested that the tectonic regime alone controls vertebrate fossil-accumulation patterns and therefore would affect paleoecological interpretations. This may be true in certain regions, especially in tectonically-active areas that experience aggradational-degradational cycles. However, climate appears to be the more important factor. Fiorillo (1999), in a review of fossil sites from the Late Cretaceous Foreland Basin of western North America, found that while regional tectonism did play a role, climatic influence was paramount in the formation of the area's vertebrate fossil record. Many studies across terrestrial vertebrate taxa have noted relationships between the distribution of fossils at local scales and regional-to-global climatic and biogeographic patterns (Barnosky et al. 2003, Benton 1985, Engelmann et al. 2004, Fastovsky 1987, Graham et al. 1996, Lehman 1997, Markwick 1998, Rees et al. 2004). Preservation patterns also vary over time in response to climate change. Millennial-scale climate changes due to plate tectonic movements and

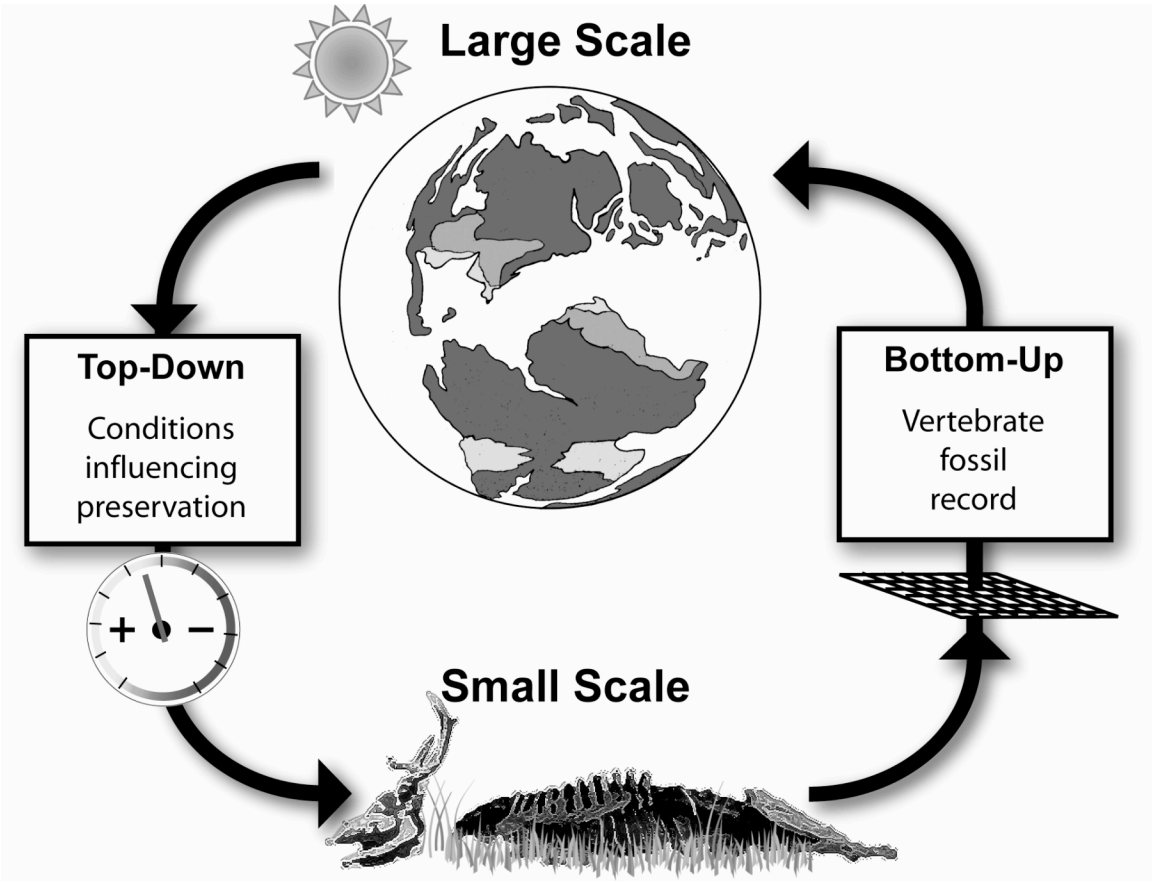

Figure 5.1: The role of top-down and bottom-up processes on the terrestrial vertebrate fossil record. Large-scale conditions (see text) influence the range of taphonomic modes available in a given local environment. Generally favorable (+) or unfavorable (-) taphonomic modes drive the probability of preservation at small scales. The combination of preservation patterns at smaller scales form the taphonomic filters responsible for creating the fossil assemblage for a given time and place. The various fossil assemblages available for study inform our view of life on Earth during the time period in question.

Milankovitch oscillations shift prevailing global climate patterns, altering not only environments and the distribution of species, but the distribution of taphonomic modes. Loope et al. (1998) and Brain (1995) found that periods of fossil assemblage formation in very different environments (eolian and cave, respectively) coincided with distinct climatic shifts towards greater precipitation, which created sedimentation events favoring vertebrate burial and eventual preservation. Outside of these intervals the vertebrate fauna went largely unrecorded. Therefore, large-scale processes determine when and where preservation may occur at smaller scales by constraining local environmental conditions and taphonomic modes.

Bottom-up control is a product of local environmental conditions and includes small-scale processes such as necrolysis, biostratinomy, and diagenesis acting on individual remains within depositional settings, creating the taphonomic modes that drive preservation (Table 1). The sum of these processes over time contributes to the formation of fossil assemblages, the composition of which may differ because each mode has its own associated set of biases (Behrensmeyer and Hook 1992). Studies of vertebrate decomposition and diagenesis following burial provide evidence that short-term, environment-dependent processes are vital in determining the long-term preservation potential of vertebrate remains (Andrews 1995, Bell et al. 1996, Berna et al. 2004, Fernández-Jalvo et al. 2002, Nielsen-Marsh et al. 2007). The distribution of environment types determines what part of the original biological signal is preserved, exerting a well-known filter over the fossil record that may persist at larger scales, contributing to large-scale spatio-temporal patterns of vertebrate fossil distribution. Behrensmeyer and Hook (1992) note that the distribution of various taphonomic modes through time likely reflects

Table 5.1: Terrestrial depositional environments that contribute to the vertebrate fossil record and some of their important taphonomic attributes. Based on information found in Behrensmeyer and Hook (1992).

Depositional Environment	Vertebrate Occurrence	Taphonomic Characteristics
Poorly-drained floodplain	present	Heavily vegetated; high water table; reducing soils; sometimes acidic; fine-grained sediments frequently deposited
Well-drained floodplain	present	Less vegetated; variable water table; well-developed, oxidizing soils; sometimes acidic; infrequent sedimentation; bioturbation
Eolian (dune, interdune, loess)	uncommon	Fine-to-coarse grained sediments; dry conditions; periods of rapid burial
Lacustrine	common	Range of productivity, sedimentation, temperature, chemistry, and oxygen content
Fluvial (channel lags, bars)	common	Low-to-high energy; rapid burial; hydraulic transport and sorting
Abandoned channel fill	common	Fine-grained sediment; abundant clays; organic-rich
Crevasse splay	variable	Coarse-grained sediment; rapid burial; hydraulic transport and sorting
Levee	uncommon	Heavily vegetated; well-drained, fining-upward sediment; soil development; bioturbation
Springs	common	Fine-grained sediment; vary in temperature and mineral content; bioturbation
Tar seeps	very common	Excellent preservation; vertical mixing; geologically unstable
Karst (caves, sinkholes, fissures)	very common	Natural sediment traps; subject to lacustrine and fluvial influence; geologically unstable
Volcanigenic (mudslides, ashfall)	uncommon	Excellent preservation; mass death; rapid burial; alter chemistry; climate independent

the sum of environmental variation at regional-to-global scales; referred to here as a taphonomic regime. Such variation in taphonomic regimes likely drives taphonomic megabiases, the existence of which is recognized, although they remain poorly understood (Behrensmeyer and Hook 1992, Behrensmeyer et al. 2000).

5.1.2 Hierarchical Integration of Terrestrial Vertebrate Taphonomy

In order to aid the development of new tools and techniques in the study of terrestrial vertebrate taphonomy, any hierarchical framework should take into account the complex relationship between Earth system processes (including climatic and tectonic processes), ecological and evolutionary responses of the biosphere, and the resulting vertebrate fossil record.

The following sections explore some of the prominent processes acting in the formation of the terrestrial vertebrate fossil record at different spatial scales. Thus providing a context and timeframe through which these processes may act and the degree to which they may be influenced by factors at other levels of the hierarchy. The purpose is not to examine every possible process that may occur, as many extraordinary examples have been documented that may not represent the typical pathway of fossil formation (Channing et al. 2005, Chin et al. 2003, Dal Sasso and Signore 1998, McNamara et al. 2006, Schweitzer et al. 2007). The focus when discussing taphonomic processes will be on the production of body fossils through bone preservation. Because widespread soft tissue preservation in terrestrial settings is relatively rare, it will not be discussed in detail here. For reviews see Martin (1999) and Schweitzer et al. (2007).

This chapter is organized into five main sections. The first section presents a brief overview of vertebrate bone and how it is affected by taphonomic processes. The second section is an overview of a proposed taphonomic control hierarchy for terrestrial vertebrates. The third section deals with the connections between these hierarchical levels and the major factors constraining processes at each level. Possible effects of the taphonomic control hierarchy on the fossil record over time and paleobiological patterns reconstructed from the fossil record are discussed in the final two sections. Finally a conceptual model is proposed for approaching changes in the fossil record brought about by environmental change.

5.2 THE STRUCTURE OF VERTEBRATE BONE

The interplay between osseous tissue properties and taphonomic processes is often underappreciated, even though such knowledge allows for better prediction of a bone's "behavior" following organismal death. Bone is a general term that describes a group of biologically-derived materials that use the mineralized collagen fibril as a fundamental element in its construction (Weiner and Wagner 1998). Bone has three main constituents: a close-packed framework of collagen fibrils, layers of carbonated apatite crystals packed in the spaces between fibrils, and a "cement" consisting of mucopolysaccharides, glycoproteins, lipids, carbonate, citrate, sodium, magnesium, fluoride, and water (Weiner and Wagner 1998).

The carbonated apatite crystals found in bone and teeth (bioapatite) have the general chemical composition of $Ca_{10}(PO_4)_3(OH)_2$, with carbonate making up 5-6 wt%

(Pasteris et al. 2004). Often F^- or Cl^- ions substitute for OH^- in the crystal lattice. Various authors refer to bone mineral as hydroxyapatite, hydroxylapatite, frankolite, or dahllite, however bioapatite differs from each of these and should be considered a unique mineral phase. Compared to the geologic standard, bioapatite demonstrates several characteristics setting it apart as a unique mineral phase, including extremely small crystal size (50×25×4 nm), poor crystallinity, and low OH^- content in the crystallites (Pasteris et al. 2004, Weiner and Price 1986, Weiner and Wagner 1998). Bioapatite is most stable under homeostatic conditions in the body. Once removed from this environment, the non-stoichiometric nature of bioapatite crystallites makes them highly unstable and prone to alteration.

In mineralogical apatite, OH^- is necessary for maintaining charge balance in channel sites of the crystal lattice; its removal would lead to a local charge imbalance (Pasteris et al. 2004, Wopenka and Pasteris 2005). In bioapatite local charge balance in the channel sites is maintained through ionic bonding between collagen, which contains many OH^- groups (mainly from hydroxyproline), and the bioapatite lattice (Pasteris et al., 2004). Sharing OH^- groups leads to a strong bond that would enable simple chemical means for rapid coupling or decoupling of the mineral-collagen bond in response to physiological needs, most likely accomplished by altering pH (Pasteris et al. 2004). Low OH^- content and poor crystallinity leads to the low buffering capacity necessary for bone remodeling; higher OH- and higher crystallinity in tooth enamel leads to better buffering capacity necessary for resisting acids such as those that regularly attack teeth (Pasteris et al. 2004, Pasteris et al. 2008). This may also explain why vertebrate teeth are more readily preserved than bone.

The structural and chemical properties of a juvenile skeleton are inherently different from those of adults. During early stages of bone development amorphous or poorly-crystalline calcium phosphate is laid down and later replaced by crystalline bioapatite (Glimcher 1984, Grynpas and Omelon 2007, Menczel et al. 1965, Termine et al. 1967). Continued bone development involves the incorporation of more carbonate and/or fluorine into the crystal lattice, especially during periods of bone growth, after which it reaches a relatively constant level (Freeman et al. 2001, Magne et al. 2001, Pasteris et al. 2004, Rey et al. 1991). During life this would serve to further stabilize the mineral in much the same way that fluoride added to drinking water prevents tooth decay. Juvenile skeletons are less mineralized; mineral density increases over time as the animal matures (Symmons 2005). Through ontogeny, ultrastructural changes within the bone also occur, representing changing metabolic strategies and physical requirements (such as rapid increases in body size) (Barreto et al. 1993, Horner et al. 2000, Montes et al. 2005). Therefore, the probability of preservation of an individual may change with ontogeny, especially between early and late life stages (Symmons 2005).

The ossified tissues of vertebrates are composed of multiple, hierarchically arranged structures, which vary in chemistry, structure, and organization (Aerssens et al. 1998, Dirrigl 2001, Enlow and Brown 1956, 1957, 1958, Weiner and Traub 1992). Differences in size, shape, and internal structure among elements exist within a skeleton and between taxa due to age, ecology, and evolutionary history. For example, small, but significant chemical and structural differences exist between cortical and trabecular bone (Aerssens et al. 1998, Bigi et al. 1997). Small changes to the chemical or crystal structure of a mineral can have large effects on its properties, altering how the mineral will react to

external conditions (Bigi et al. 1997). Structurally different regions of the same bone may follow different diagenetic trajectories. For example, the fractionation of various common elements (Mn, Fe, Cu, and Ba) (Carvalho et al. 2004) and rare earth elements (REEs) (Trueman and Tuross 2002, Williams and Potts 1988) differ between cortical and trabecular bone tissue. A similar situation exists in the fractionation of oxygen and carbon isotopes incorporated into bone tissue and dental enamel during early diagenesis (Zazzo et al. 2004). Analysis of dinosaur (Goodwin et al. 2007, Pawlicki and Bolechala 1987) and human (Lambert et al. 1983, Schoeninger et al. 1989) compact bone show that diagenesis, as measured by elemental concentrations of Ca, P, Fe, Mn, and others, proceeds differentially through the vascular canals and compact lamellae of bone due to differences in the porosity and composition of these tissues. Therefore, the diagenetic alteration of bone tissue is not uniform and can vary due to environmental differences and/or the structural and chemical properties of the tissue.

5.3 THE TERRESTRIAL TAPHONOMIC HIERARCHY

The description of any hierarchy requires a delineation of specific, inclusive levels (see Martin, 1999, p. 11). This model includes three major spatial levels: micro-, meso-, and macroscale (Figure 5.2). Each level in the hierarchy contains a set of associated biological, chemical, and/or physical processes that influence the preservation

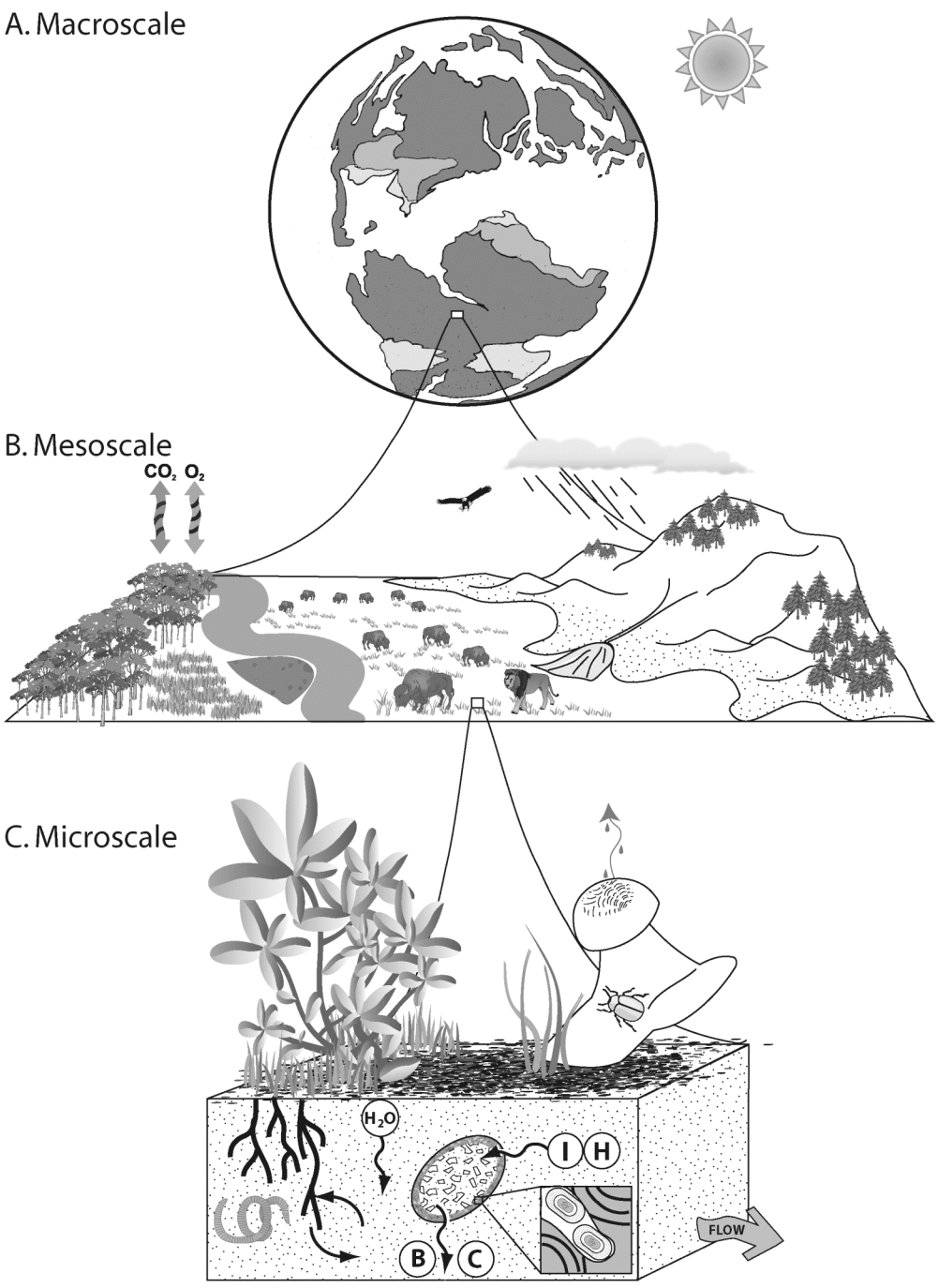

Figure 5.2: Hierarchy of terrestrial taphonomic processes and controls. A) Macroscale: distribution of continental landmasses, sea-level, ocean circulation, atmospheric composition and circulation, intensity and distribution of solar radiation on the surface, and biome distribution. B) Mesoscale: landscape characteristics, local weather patterns, species population dynamics, biogeochemical cycles, predation/death, and scavenging of remains. C) Microscale: soft tissue decay, bone exposure, desiccation and cracking from solar radiation, invertebrate utilization, bioturbation, nutrient use and organic acid release by plant roots, leaching of bone mineral (B) and collagen (C), incorporation of exogenous ions (I) and humics (H) into bone matrix, bacterial and fungal degradation, diagenesis, and hydraulic flow of groundwater.

potential of vertebrate remains. Conditions present at an overlying level restrict the range of possible taphonomic processes and biogeochemical conditions acting at lower levels. It should be noted that the temporal extent of some taphonomic processes may cross more than one level of the hierarchy. This model is intended to organize and relate the work of many different researchers and highlight important relationships among taphonomic processes that, when considered collectively and at higher scales, will lend insight into the importance of these factors in the preservation of vertebrate remains. It is also worth noting that certain processes may behave similarly regardless of scale (e.g., temperature).

Processes described at each level are split into two categories: those that act at the surface and those that act in the subsurface, following a similar approach used in marine paleontology (Behrensmeyer et al. 2000, Kidwell 1986, Plotnick et al. 1988, Walker and Goldstein 1999). Here, surface processes refer to those acting at or near the sediment surface. Subsurface processes act beneath the sediment-air or sediment-water interface and may be independent of and/or influenced by conditions at the sediment surface, especially at shallow burial depths. Together these two sets of processes describe a taphonomically active zone (TAZ) for the terrestrial realm [after Davies et al. (1989) and Lyman (1994); see also "highly dynamic mixed zone" of Behrensmeyer et al. (2000)]. Additionally, the spatio-temporal extent of processes and the elements (e.g., molecules, tissues, carcasses, assemblages) interacting at each level are discussed.

5.3.1 Microscale Processes

Microscale processes cover spatial scales in the micrometer to centimeter range and a temporal scale anywhere from ≤1 day to upwards of 100 Ky. A major difficulty in

assigning specific time estimates to the duration of microscale processes results from an inability to directly observe the processes in action. This creates uncertainty about the amount of time necessary for these reactions to go to completion. Instead, different authors have inferred the amount of time needed, using qualitative terms such as "early" or "late" diagenesis. Still, an attempt is made to estimate the time windows for these reactions when their activity is most prominent during diagenesis based on indications given in the literature. Elements interacting at this scale are molecules, cells, and tissues on both internal and external bone surfaces. This includes the components of bone tissue (collagen, bioapatite, cells, etc.), bacteria, fungi, exogenous ions, and water.

Surface Processes

Diagenetic alteration of bone can begin almost immediately following death. Within hours metabolic processes shut down and body cells undergo autolysis as their structural integrity deteriorates, releasing contents of the cytoplasm (organelles, etc.) into interstitial fluid, leading shortly to soft tissue hydrolysis (Andrews 1995, Tappen 1994). In bone, autolysis is restricted to cells only; collagen and extracellular matrix proteins ("cement") remain unaffected (Child 1995). Within days the collagen-mineral bond weakens, and the bioapatite begins to recrystallize into a more thermodynamically stable form, beginning the transition to a composition closer to the geologic standard and increasing overall crystallite size (Berna et al. 2004, Nielsen-Marsh and Hedges 1997, Trueman et al. 2004). These processes will occur regardless of surface exposure, rapid burial, or submergence under water, although the extent to which reaction rate depends on these conditions is not well understood.

Water is a strong limiting factor in determining the rate at which diagenetic change and microbial degradation occurs. Large-scale and/or rapid diagenesis and microbial attack of the remains becomes possible only when the remains are saturated with water. In submerged bodies microbial attack and diagenetic alteration to bone tissue can take place almost immediately, causing substantial damage to histological structures and altering chemical composition after only a few years (Bell et al. 1996, Davis 1997, Yoshino et al. 1991, Zazzo et al. 2004). At the sediment-air interface this does not occur usually until after burial, although archaeological and experimental evidence indicates that loss of both collagen and carbonate ions (in the form of CO_2) can occur in the absence of mineral dissolution in water (Person et al. 1996, Person et al. 1995). This difference between subaerial and buried bones has been well documented in the archeological literature (Andrews 1995, Yoshino et al. 1991), although the ability to discern between them depends on the difference between prevailing climate and surface conditions during exposure versus those below ground. When surface and subsurface conditions are divergent, different taphonomic signatures will result; when a similar set of conditions occur, such as in moist environments, the taphonomic signatures are indistinguishable (Nicholson 1996).

Bacteria responsible for initiating soft-tissue decomposition are likely of endogenous origin. As tissues hydrolyze and mucous barriers break down, bacteria from the intestinal lumen proliferate and migrate to other parts of the body through the vasculature, continuing aerobic decomposition of soft tissue; this can occur within as little as 24 hours postmortem (Dolan et al. 1971, Kellerman et al. 1976). These bacteria similarly could invade the skeleton via the vasculature and spread intracortically through

the bone vascular system (Bell et al. 1996). Predator or scavenger action that removes large amounts of viscera and vasculature may retard this type of bacterial invasion, although the removal of flesh exposes bone to potentially destructive abiotic conditions. Some researchers have noted that regions of the skeleton closest to the abdomen, such as the vertebrae and ribs, can be more degraded than distal elements due to the production of organic acids by anaerobic bacterial decomposition of soft tissue (Boddington 1987, Child 1995).

The important abiotic controls at this scale differ between aqueous and subaerial environments. At the sediment-air interface, ambient temperature, ultraviolet (UV) radiation exposure, the amount and frequency of precipitation, and the composition of the sediment or substrate where the remains lie, each play an important role. The rate of most chemical reactions depends on temperature, approximately doubling for every 10˚C increase (Henderson 1987). This relationship is especially important in determining the rate of soft tissue decay (Shean et al. 1993), collagen hydrolysis, and peptide loss in bone (Collins et al. 2002, Hedges 2002). At very high temperatures, small amounts of carbonate are released from the bioapatite crystallites in the form of CO_2 and OH^- ions are incorporated into the lattice (Nielsen-Marsh and Hedges 1997, Pasteris et al. 2004, Person et al. 1996). Temperature and UV levels are positively correlated due to their relation to sunlight: unshaded, exposed surfaces experiencing high temperature are exposed to higher levels of UV radiation. UV radiation is particularly damaging to organic components and is likely a leading cause of damage to subaerially-exposed bone (Andrews 1995, Fernández-Jalvo et al. 2002). UV facilitates the break-down of the

collagen matrix by cleaving specific peptide bonds, lowering the denaturation temperature of the collagen molecule (Sionkowska 2005).

Precipitation provides moisture that can have a variable effect on the remains: soft-tissue desiccation (a form of natural mummification) can act to preserve remains, while bone desiccation leads to cracking and loss of structural integrity (Behrensmeyer 1978, Cutler et al. 1999, Trueman et al. 2004). Large diurnal fluctuations in temperature and precipitation have an especially destructive effect on exposed bone (Martin 1999). The overall effect of temperature, UV radiation, and precipitation on exposed remains varies due to differences in latitude and seasonality; the presence of vegetation can help mitigate some of these destructive effects (Behrensmeyer 1978, Cutler et al. 1999, Tappen 1994).

The ground surface itself plays a role in mediating the effects of the above-mentioned factors (Shalaby et al. 2000). It can act as a reflector and/or radiator of incoming solar radiation, increasing the temperature experienced by remains well above that in the air a short distance above the remains. It also may extend the operable time of decomposition processes by releasing stored heat after sundown. Porous sediments with higher hydraulic flow draw moisture downwards, away from the surface, thereby accelerating desiccation. Sediment with low hydraulic flow retains moisture near the remains, retarding water loss. Under particular situations when evaporation at the surface is extreme, ground water may be drawn up through the sediment, leading to the formation of destructive evaporite minerals (e.g., gypsum) in the remains (Trueman et al. 2004).

Temperature plays the largest role in driving decomposition patterns. Under aqueous conditions, the surrounding water dulls the effect of the above factors on

submerged remains by mediating diurnal fluctuations. Higher temperatures are associated with more rapid tissue decomposition, due mainly to increased bacterial activity (Elder 1985, Elder and Smith 1988, Minshall et al. 1991). Oxygen concentration also is important, determining the availability of the remains to macroconsumers and the range of biogeochemical reactions that may occur on the remains (Elder and Smith 1988). The more anoxic an environment, the more closed it becomes to consumers. Water pH will play a role only in cases of very low pH, which is unusual in most terrestrial aquatic environments. Low pH (<5) would create acidic conditions capable of dissolving bioapatite crystallites and eroding osseous tissues (Hare 1980).

The formation of adipocere (hydrogenated fatty acids; “grave soap”) is another byproduct of decay commonly found in submerged or saturated environments, but is largely absent as a decay stage in subaerial environments (Haglund and Sorg 2002, Mellen et al. 1993, O'Brien and Kuehner 2007). Adipocere may play a role in fossilization by preserving soft tissues and/or the 3-dimensional arrangement of skeletal elements through encouraging early calcium carbonate mineralization (Berner 1968, Martill 1988). Little work has been done to understand these mechanisms, making it an area ripe for experimental work.

Subsurface Processes

The processes that occur after burial have received far less attention, despite the fact that diagenesis only begins at the surface. At least over the short-term (months to years), burial can offer protection from some of the destructive surface processes described above, such as direct UV radiation, significantly hindering their effect

(Andrews 1995, Behrensmeyer 1978, Martin 1999, Trueman et al. 2004). Once buried, many of the same processes described for surface exposure continue, however the intensity with which they occur and the factors that control them change.

Living plants affect buried remains through both physical and chemical means. Roots physically infiltrate bone, sometimes causing large cracks and opening the interior to destructive agents. Roots are also capable of chemically digesting bone as the plant seeks out nutrients and minerals, with the type of attack and its extent varying depending on the species and community composition (Berner et al. 2004, Henderson 1987). Bone boring and consumption by insects and other macroinvertebrates may also occur following burial (Paik 2000, Roberts et al. 2007), similarly exposing the bone interior and destroying its structural integrity.

Given the highly unstable nature of bioapatite crystallites in the absence of physiological maintenance, it is perhaps more relevant to ask why bioapatite crystals do not spontaneously dissolve upon death (Berna et al. 2004). Loss of the stabilizing presence of a strong mineral-collagen bond opens the crystallites to undergo further alteration by reacting with available pore water. This is accomplished through the processes of dissolution (preferential loss of less thermodynamically stable crystallites) and recrystallization (crystallites defer to a more stable state, usually incorporating exogenous ions) (Nielsen-Marsh and Hedges 1997). These two processes are by no means mutually exclusive, and may be described more accurately as end-members of a continuum in which ions are lost and gained between the crystallites and surrounding pore water. The relative difference between rates of ionic loss or gain determines the prevailing alterations to the bone. This leads to the change in mineral identity from

bioapatite to a more stable apatite phase, usually through the uptake of F and CO_3 (Hedges 2002) and Fe and Si (Johnsson 1997). The degree of alteration to bioapatite crystal structure and chemical composition is considered a relative measure of diagenesis in the bone. At this stage the stability of the bone mineral (i.e., its propensity to dissolve and recrystallize) is controlled by the pH, Eh (redox potential), and ionic concentration of the pore water.

It is unknown to what degree the intimate relationship between collagen and bioapatite influences decomposition dynamics, including whether collagen or mineral loss must occur first for diagenesis to proceed. Some authors propose that collagen protects the mineral component from significant alteration until its removal (Person et al. 1996). However, the bulk of empirical data supports the opposite scenario, in which bioapatite crystallites and inorganic matrix protect the collagen from immediate microbial attack (Collins et al. 2002, Collins et al. 1995, Nielsen-Marsh et al. 2000, Pfretzschner 2004, Yoshino et al. 1991). Collins et al. (1995) proposed that the intra-crystalline spaces of the mineral fraction are too small for microbial enzymes to penetrate, effectively forming a barrier to everything but water. Under this model, collagen loss is controlled mainly by hydrolysis and temperature, with microbial digestion playing a secondary role until significant mineral loss has occurred.

While the presence and activity of microorganisms (bacteria, fungi, and protozoans) is an accepted tenet of organic decay, the role they play (especially bacteria) in diagenesis is less clear. Several species of collagenase-producing bacteria and fungi are known from archeological bones (Child 1995). Both archaeological and experimentally manipulated bones from a variety of species and environments, covering

timescales over 1-40,000 years, show clear evidence of bacterial and fungal attack (Bell et al. 1996, Child 1995, Davis 1997, Hackett 1981, Hedges et al. 1995, Jans et al. 2004, Piepenbrink 1986, Trueman and Martill 2002, White and Hannus 1983, Yoshino et al. 1991). Zones of microbial attack, known as microscopic focal destruction (MFD; Hackett 1981), are observed readily within compact bone, usually within and surrounding osteons, and consist of individual tunnels or honeycomb-type structures 0.1-10 μm in diameter (Bell et al. 1996, Jans et al. 2004, Yoshino et al. 1991). These structures hasten collagen and mineral loss by exposing more internal surface area to dissolution and leaching (Jans et al. 2004 and references therein). Avascular bone will be less susceptible to this kind of attack, due to the lack of routes permitting access to the bone interior (Nicholson 1996).

The overall proportion of bone microstructure attacked appears relatively small and the overall number of collagenase-producing microorganisms isolated from bones and surrounding soil is low (Child 1995). Some authors conclude that biodegradation plays only a minor role in collagen loss and bone degradation, the main control instead being abiotic conditions (Child 1995, Collins et al. 1995, Pfretzschner 2004). Alternatively, the incidence of MFD in fossil bones is minimal or nonexistent compared to archeological specimens, where ~50% exhibit extensive bioerosion of histological structures (Chinsamy-Turan 2005, Hedges et al. 1995, Trueman and Martill 2002). This difference between fossil and archeological bone suggests that bioerosion is an important determinant of bone preservation and must be prevented altogether, or halted in its earliest stages, by environmental conditions for the specimen to be fossilized (Trueman and Martill 2002). However, microbial activity alone cannot account for all collagen loss

during diagenesis, especially when original histology is preserved, indicating collagen loss in bone is controlled by a separate process (Hedges et al. 1995). Therefore, bioerosion represents an early stage of diagenesis that will lead to rapid deterioration of internal structure unless quickly halted. But, over longer timescales collagen loss is controlled by abiotic factors, such as gelatinization rate (Pfretzschner 2006, Trueman and Martill 2002).

Others workers have suggested that fossilization cannot proceed without bacterial activity. It has been experimentally shown that bacteria are necessary for authigenic mineral deposition within bone (Carpenter 2005, Daniel 2003). Soil-derived bacteria recently have been shown to mediate $CaCO_3$ mineralization as a byproduct of their metabolism and it is thought this property may be common to many soil bacteria (Barabesi et al. 2007, Lian et al. 2006). Archeological bone sometimes is observed to contain additional mineral deposition lining the walls of bone tissue presumably damaged by bacterial activity (Yoshino et al. 1991). These mineral deposits are noted for having different properties from surrounding bone tissue but few have been recognized to have bacterial origins. These most likely represent the initial stages of mineral precipitation (see Daniel 2003).

Given the breadth of environments covered in taphonomic studies, it is more likely that conditions present in the burial environment are regulating which fraction of the osseous tissue—organic or mineral—is degraded and/or removed first. Therefore, as a general precondition, degradation in at least one fraction must occur in order for diagenesis to proceed. As diagenesis proceeds, especially in the early stages, bone porosity initially increases as collagen is lost, with the intervening spaces filled by the

mineral as it recrystallizes and increases in size (Hedges 2002, Hedges and Millard 1995). Where pore-size distribution shifts to larger diameters, a greater surface area is opened to reaction, facilitating mineral loss through diffusion to the pore water. This process appears to take place over a timescale of hundreds to a few thousand years. Environmental settings that inhibit this initial precondition will delay the onset of diagenesis and potentially act to stabilize the remains against future destructive change from geochemical and/or biological agents. Binding of collagen with humic substances released from decaying plant matter can stabilize collagen against hydrolytic loss and biodegradation (Collins et al. 2002). Clay minerals may have anti-enzymatic properties that could prohibit many types of biodegradation (Butterfield and Nicholas 1996, See Gaines 2008 for an alternative view of this mechanism).

Sediment hydrology is the single most important factor determining the decay and diagenesis of buried remains, influencing numerous biogeochemical properties of the sediment. Two factors determine the moisture regime: i) how water moves through a sediment, called the hydraulic conductivity; and ii) the potential for that water to migrate within the pores of the sediment via osmosis or capillary action, called the hydraulic (matric) potential (Brady 1974, Hedges and Millard 1995, Retallack 1990). These two factors determine the overall solute concentration surrounding a bone and the maximum pore size within a bone that will be occupied by groundwater (Pike et al. 2001). It is expected that diagenesis will proceed only when internal bone pores are in contact with water (Hedges and Millard 1995). The hydraulic properties of the sediment control oxygen availability, thereby exerting a strong influence on the nature and depth of the terrestrial TAZ. Water movement influences organismal abundance and activity, as

highly conductive sediments provide oxygen to the large proportion of aerobic organisms residing in the sediment, while anoxia resulting from low flow depresses biological activity. Oxygen availability also determines the redox potential, which will determine the range of possible chemical reactions affecting the remains and surrounding sediment (Retallack 1990). Redox conditions, especially in submerged sediments, may be important to the formation of certain authigenic minerals such as pyrite (FeS), which are often associated with fossilized bone (Leng and Yang 2003, Pfretzschner 2000, 2001a, b).

The effect of temperature on decay and diagenesis varies because of differences in latitude, season, and depth of burial. Areas with little seasonal variation in temperature should experience higher rates of degradation, as opposed to those places where the ground remains frozen for part of the year (Henderson 1987). This variation affects not only chemical reactions, but the influence of soil biota as well. Freezing of the ground causes most biotic activity and water movement to cease.

5.3.2 Mesoscale Processes

While it may be easier to differentiate between micro- and macroscale processes, the "middle ground" between them, mesoscale processes, are more difficult to distinguish. Mesoscale processes form the bridge connecting localized biogeochemical conditions with regional-level distribution patterns of preserved bone. The spatial scale used here encompasses areas on the order of 10^0-10^4 meters: a scale that is expected to include areas subject to the same local environmental conditions and regional climatic regime. Temporally, mesoscale processes may be more constrained than at other levels, covering ~1 day up to 10^2-10^3 years. Individual bones up to whole carcasses will be

affected at this level, with alterations brought about through interactions with local biota, geomorphological features of the landscape (including river and lake beds), and biogeochemical characteristics of the surrounding sediment.

Surface Processes

Disarticulation, skeletonization, desiccation, and bone utilization by vertebrate, invertebrate, and fungal consumers are among the main forces acting on vertebrate remains at the surface. In aquatic environments, fresh carcasses may go through a well-known process of bloating, tissue decay, bone exposure, and finally disarticulation (Anderson and Hobischak 2004, Haglund and Sorg 2002). The soft tissues of a carcass often are consumed by predators and scavengers and this is a well known part of the taphonomic process, with examples reaching back into the fossil record (Rogers et al. 2003, Spencer et al. 2003). The rate and extent of soft tissue removal determines when and how much of the skeleton is exposed to the surface environment, with important implications for bone survival prior to and following burial (Andrews 1995, Andrews and Cook 1985, Behrensmeyer 1978, Henderson 1987, Weigelt 1989).

Subsequent movement by fluid transport will physically abrade and damage exposed bone after deposition. The degree of movement is regulated by flow rate, bed morphology, and skeletal element size, shape, density, and degree of articulation (Boaz and Behrensmeyer 1976, Coard 1999, Coard and Dennell 1995, Elder and Smith 1988, Voorhies 1969). Both physical transport and consumer behavior can then lead to the selective removal and/or concentration of certain elements (e.g., limbs), age classes, and/or species (Lyman 1994, Martin 1999, Norman 1987, Wood et al. 1988).

Following skeletonization various organisms may utilize exposed bone. Many mammals are known to break open bones to consume the energy-rich marrow within or gnaw them to obtain essential nutrients, however there is no direct evidence of this strategy outside of Mammalia (Fiorillo 1991, Reisz and Tsuji 2006, Van Valkenburgh and Molnar 2002). If the environment contains sufficient moisture, fungi will colonize any exposed bone, using the surface as a growth substrate while digesting the composite matrix beneath (Nicholson 1996, Piepenbrink 1986). Various species of insects also utilize bone, either by excavating the surface or boring into the interior, consuming the bone tissue and weakening the ultrastructure (Kaiser 2000, Paik 2000, Roberts et al. 2007). In aquatic environments, bone may be colonized and consumed by vertebrates, macroinvertebrates, and algae (Davis 1997, Goffredi et al. 2005, Haefner et al. 2004, Haglund and Sorg 2002, Hobischak and Anderson 2002). Still, little is known about freshwater decay processes and their consequences for preservation (Hobischak and Anderson 1999).

Species identity, size, age, sex, and health at the time of death affect how the remains respond to surface processes (Behrensmeyer et al. 2003, Martin 1999). Species vary in the chemistry, structure, and organization of their ossified tissues, which affects the size, shape, and density of elements. Body size determines the surface-area-to-volume ratio of the entire carcass, and individual elements available to interact with the environment, with smaller taxa and elements more prone to loss and destruction than larger counterparts (Martin 1999, Munoz-Duran and Van Valkenburgh 2006, Nicholson 1996, Von Endt and Ortner 1984). Under certain conditions large carcasses may decompose faster because they attract more consumers (Hewadikaram and Goff 1991).

The age (ontogenetic stage), sex, and health of the individual at death may be more important than size in determining decay susceptibility because of the close relationship between these factors and bone structure. Juveniles not only tend to be smaller than adults but their skeletons are less mineralized and differ chemically (Symmons 2005). Reproductive status may play an important role, as the females of many vertebrate groups utilize calcium reserves from the skeleton during gestation (e.g., egg production) and parental care (e.g., lactation, brooding, protection) (Arias and Fernandez 2001, Randall et al. 1997, Schweitzer et al. 2005). Many of the factors described above are also affected by individual health, but diseases that affect the mineral density and structure of bone may contribute to loss of bone integrity following death and can occur regardless of age (Henderson 1987).

On the ground surface temperature, precipitation, solar energy input, and sediment/soil type continue to affect vertebrate remains at the mesoscale. In submerged environments, temperature, pH, light availability, nutrient availability, flow regime, and sediment/substrate type play a similar role (Barnes and Mann 1991). Their interactions, together with local geomorphology, determine the suite of flora and fauna that forms the local community of which the remains are a part. Both the diversity and numbers of predators, scavengers, and decomposers influence the extent of soft tissue removal and bone tissue modification. On land surfaces foliage can modify local conditions and provide a certain degree of protection for exposed remains by decreasing diurnal fluctuations in temperature and moisture and/or obscure the remains from detection. This can lead to the long-term survival of bones on the surface in vegetated areas compared to

those exposed only a short distance away (Behrensmeyer 1978, Cutler et al. 1999, Kerbis Peterhans et al. 1993, Sept 1994, Shean et al. 1993, Tappen 1994).

The greater habitat heterogeneity a local environment supports, the larger the number of potentially favorable microenvironments that exist to protect the carcass from the most destructive conditions (of course, depending on where the animal comes to rest after death). The frequency and intensity of changes in the local environment determines how long surface conditions last, including seasonal changes (de Carvalho and Linhares 2001, Dubiel et al. 1991, Rogers 2005) and episodic events such as fires, floods, or mudslides, that may occur over cycles from decades to centuries (Greenwald and Brubaker 2001, Loope et al. 1998, Watson and Alvin 1996). The distribution of landscape features (rivers, hills, plains, caves, etc.) interacts with local flora to control rates of sediment aggradation and erosion over sediment surfaces, which in turn help drive burial of exposed remains (Lyman 1994).

Subsurface Processes

Mesoscale subsurface processes involve mainly diagenetic alteration of the sedimentary body and the effects this has on the diagenesis and preservation of buried remains (Lyman 1994, Tucker 1991). Both aquatic and ground surface sediments are altered though a suite of physical, chemical, and biological processes that are controlled by land surface morphology (topography), sediment characteristics (composition, grain size, chemistry) and moisture availability (precipitation, water table). Subaerially-exposed sediments may also undergo weathering, considered a set of specific alterations related to but separate from diagenetic processes, although significant overlap exists

(Middleton 2003). Weathering reactions play a large role in both erosion and soil formation (Retallack, 1990).

Physical processes acting on sediment bodies include loosening/cracking caused by heating-freezing expansion cycles and the movement of water and gasses. Chemical alterations result from four principal reactions: hydrolysis, oxidation, hydration, and dissolution (Brady 1974, Retallack 1990). Hydrolysis leads to the displacement of cations by hydronium ions, creating a new, insoluble mineral product. Oxidation involves reactions in which electron loss forms new compounds. Hydration includes the addition of water into the mineral structure. Dissolution is the disaggregation of a compound into ions, a classic example being a salt cube (NaCl) dissolving in water into Na^+ and Cl^-. Biotic influences on sediment alteration are profound. Living organisms influence the availability of nutrients through their life processes and alter the physical structure of the sediment profile through bioturbation and the release of various byproducts (Retallack 1990). Many groups of bacteria create biofilms that can significantly slow the movement of water through sediment, which can alter biogeochemical conditions from those predicted by sediment characteristics alone (Battin and Sengschmitt 1999, Baveye et al. 1998, Vandevivere and Baveye 1992a).

Soils and paleosols are common environments of vertebrate preservation and the degree of soil development plays an important role in vertebrate preservation. Soil formation is a complex process involving the interaction of climate, living organisms, the nature of the parent materials, topography of the area, and time that parent materials are subject to alteration (Retallack 1990, Schaetzl and Anderson 2005). Over time a dynamic balance is reached between sedimentary and organic inputs with their biogeochemical

modification that may last thousands of years. These prevailing conditions determine bulk soil properties, making them environment-specific. Therefore, different environments can be characterized by their soils, even long after the conditions that created them cease to exist (Retallack 1990). Over the long-term, soil formation is affected by: i) shifts in regional tectonics, which alter basin drainage and sediment aggradation patterns; ii) volcanic activity, depositing ash and altering atmospheric chemistry; iii) changes in atmospheric or ocean circulation patterns, altering precipitation patterns; and iv) alterations in the level of solar radiation reaching the surface (Martin et al. 1999, Retallack 1990). Over time the evolution of the sediment profile changes preservation conditions through alteration of the biogeochemical properties of the sediment, for example the production of clays or iron oxides (Martin 1999, see Retallack 1990 for detailed description of processes).

Changing sediment-moisture content causes many clay minerals, such as montmorillonite, present in the sediment to shrink or swell, which can physically distort or damage bones lying within clay-rich sediment. The shrink-swell cycles of clayey sediments may cause more distortion than sediment compaction can over time because they occur more frequently and result in movement in multiple directions, while sediment compaction is a long-term and unidirectional event (Henderson 1987, Retallack 1990).

Sediment properties along with topography influence local hydrological conditions, including the height and relative flow of the water table. Changing hydrologic conditions over both space and time have been implicated in patterns of bone decay and diagenesis by determining the amount of hydrologic recharge and solute concentration surrounding the remains (Hedges and Millard 1995). Under these conditions, it may not

be possible for bones to undergo preservative diagenesis (that is, stabilization of the organic and/or mineral components) and fossilization until they are beneath the water table, where they are buffered against rapidly shifting biogeochemical conditions. The faster remains come to lie beneath the water table, the greater their chances of preservation. A similar taphonomic model is proposed for plants, in which regional changes in sediment aggradation and accommodation that lead to base level change and subsequent rise in water table are best for plant preservation (see Gastaldo et al., this volume). Even if the biogeochemical requirements for vertebrate and plant preservation differ, the lower the residence time in the terrestrial TAZ above the water table, the more likely the remains will be preserved. This may help explain the relative wealth of vertebrate remains from lacustrine, palustrine, and fluvial environments, and from those settings with relatively high water tables such as wet floodplains in close proximity to water sources that frequently deposit sediment (Noto, unpublished data).

5.3.3 Macroscale Processes

The macroscale consists of many large-scale phenomena not often considered in studies of the vertebrate fossil record. These processes occur over spatial scales of 10^1-10^4 kilometers and temporal scales ranging from 10^2-10^6 years. Note that the spatial and temporal boundaries for this level fall within the resolution considered typical for most terrestrial fossil assemblages (Behrensmeyer and Hook 1992). The leading control at this level is the global climate regime, driven ultimately by the interplay of plate tectonics and Milankovitch cycles altering the distribution of land area and arrangement of continents, eustatic sea-level, atmospheric concentrations of carbon dioxide and oxygen, volcanism,

mean global temperature, and global atmosphere and ocean circulation patterns (Behrensmeyer and Hook 1992, Martin 1999). This complex interaction determines the distribution of biomes. Biomes represent large regions united by similar climatic and ecological conditions, which produce distinct assemblages of organisms (Begon et al. 2006). Because the range of taphonomic processes acting within a particular area is determined by the environment and local biota, many areas within the biome are united under a similar taphonomic regime. The distribution of biomes and their constituent environments will influence community composition and patterns of biodiversity. When coupled with variation between taphonomic regimes, these will have a direct impact on how different communities and species are preserved in the fossil record. The relative stability of these factors will determine the type of fossil accumulation formed (if any at all) and its fidelity to the original biota.

Surface Processes

Large-scale factors control several key processes at this level. First, weathering processes, while highly variable at small spatial scales, are coordinated regionally, altering the land surface for thousands of square kilometers in a similar way (Simon-Coinçon et al. 1997). Changes in weathering regime can be traced through time and correspond to shifts in sea-level, topography, and climate. Similarly, the distribution and morphology of water bodies and associated features are influenced by geomorphology, tectonics, sea-level, biota, and climate (Blum and Tornqvist 2000, Leier et al. 2005, Prothero and Schwab 1996). Second, the dynamics of plant and animal populations vary with changing abiotic conditions, which can alter the size and location of species'

geographic ranges (Dynesius and Jansson 2000). The expansion and contraction of species ranges over time affect the distribution of biodiversity. For example, large-scale climate patterns have been shown to drive population dynamics in groups of caribou and musk oxen, each separated by more than 1000 km of ice on the coasts of Greenland (Post and Forchhammer 2002). Because individual species can respond differently to climate change, community assemblages change over time as new communities are created through species reorganization (Stone et al. 1996). Third, and perhaps of greatest interest to paleontologists, is the close relationship between development of Earth's abiotic systems and the evolution of its biotic inhabitants. The positions of continents, sea-level, tectonic activity, and climate regime have all played important roles in the history of life, influencing the evolution and extinction of taxa. Orbitally-driven oscillations in climate patterns have been implicated with species-range dynamics at different latitudes, related to the amount of seasonality and environmental heterogeneity (Dynesius and Jansson 2000). These dynamics vary spatio-temporally, affecting speciation rates, speciation mechanisms, and degree of adaptive specialization. This variation leads to differing evolutionary rates over both space, in the form of latitudinal gradients in species richness (Wright et al. 2006), and time, in secular patterns of global species diversity (e.g., Sepkoski 1998).

Subsurface Processes

Changing climate and tectonic conditions over time can effectively alter the subsurface environment and establish biogeochemical conditions that promote the physical and/or chemical decomposition of organic remains. Long-term development of

the soil profile in conjunction with a lowering of the regional water table can lead to expansion of the terrestrial TAZ, spreading oxidative conditions, bioturbation, and consumer access to buried remains. This is most common in areas that support high productivity and biodiversity due to relatively stable climatic and tectonic conditions over 10^4 –10^5 year timescales. Not all soil development is necessarily destructive. Certain soil orders, such as the aridisols and mollisols, contain calcium carbonate-bearing horizons at relatively shallow depths (~30-60 cm) (Brady 1974), that can provide a ready source for calcite formation within the bone and/or sediment during diagenesis. Several productive fossil formations, mainly from the Mesozoic and Cenozoic, consist primarily of paleosols at low to moderate stages of development that were formed within seasonal or semi-arid environments (Badgley and Gingerich 1988, Bown and Kraus 1981, Clyde et al. 2005, Downing and Park 1998, Maas 1985, Paik 2000, Winkler 1983). As a general rule, environments that support a greater degree of soil development lead to biogeochemical conditions promoting organic decomposition and, in extreme cases, leaving only the most recalcitrant remains behind (see Retallack 1990 for more extensive description).

Water and sediment availability, geomorphology, topography, and tectonic stability influence riverbed geometry and flow dynamics. These factors affect the sinuosity and lateral migration rate of the riverbed, as well as the size and distribution of overbank deposits (Einsele 2000, Prothero and Schwab 1996). Highly sinuous and mobile rivers cut into the surrounding landscape, reworking the sediment and exhuming previously buried remains. Over time this reworking process creates time-averaged assemblages of varying duration and composition (Behrensmeyer 1988, Behrensmeyer

and Hook 1992). This process favors the preservation of more resistant skeletal elements, including teeth and large bones or fragments within the most active of fluvial systems.

As sediment accumulates on the surface, underlying layers experience compaction, cementation, and authigenesis as lithification proceeds (Prothero and Schwab 1996). Since many fossil bones demonstrate some amount of structural deformation, prolonged sediment compaction likely plays a role in this phenomenon. This distortion has the potential to artificially inflate skeletal element variability and confuse the taxonomic assignment of the remains (Wilborn 2007). Grain size, pore space, and bone size and shape determine the extent of compaction and its effect on the interred bone (Prothero and Schwab 1996, Smoke and Stahl 2004). Cementation depends on the hydrology and chemistry of the ground water, but silica or calcite typically forms the cement. Early cementation has been suggested as a pathway for fossil preservation, especially in soft tissues (Briggs and Kear 1993b, Sagemann et al. 1999). The presence of calcite within fossil bone has been implicated as a condition favoring preservation (Berna et al. 2004, Fernández-Jalvo et al. 2002, Holz and Schultz 1998, Wings 2004). Diagenetic concretions may even form, preserving small-bodied and delicate taxa that would otherwise be destroyed (Downing and Park 1998). Authigenesis leads to the deposition of new or altered mineral species within and around remains and, due to the environmental-specificity of mineral formation, can provide a detailed diagenetic history (Bao et al. 1998, Clarke 2004).

The extent of diagenetic alteration depends on sedimentary composition, depth of burial, temperature at depth, and the length of time the unit is exposed to these conditions. Depth of burial is particularly important, because certain diagenetic

changes—including dewatering, cementation, recrystallization, dissolution, and replacement— can occur at shallow depths of 1-3 km (Prothero and Schwab 1996). The survival of fossils within the unit is contingent upon the extent of these alterations, potentially destroying or rendering unidentifiable fossils that were stable at shallower depths. It appears that plant fossils, which are far more delicate than bone, can withstand moderate to high diagenetic processes at depths of 3.8-5.2 km and temperatures between 150-170˚C (Howe and Francis 2005).

While the stability of bone apatite at different pressures and temperatures has yet to be comprehensively studied, the diagenetic behavior of another bioapatite—from conodonts—has been well described and may provide a useful model. Color changes in conodont elements have been linked with an increase in the temperature experienced by the enclosing rock, providing a relatively precise scale from low (pale yellow, <80˚C) to high (black, >300˚C) temperatures (Epstein et al. 1977, Prothero and Schwab 1996). Conodont elements contain structures homologous to vertebrate bone (Sansom et al. 1992) and undergo a similar change in crystallite size during diagenesis (Noth 1998). The bone of more advanced vertebrates may react similarly and help to explain the wide diversity of colors observed in bone from terrestrial fossil assemblages, providing valuable insight into the diagenetic conditions experienced by the sedimentary unit.

McKean et al. (2007) hypothesized that bone color change results from geothermal alteration of the bone's remaining organic content. They found that bone color (yellowish-white to black) and organic content correlate with depth of burial if one assumes a geothermal gradient of 27.5˚/1000 m. This represents a promising first step, but more work on this is certainly necessary. This relationship is relevant to those

studying rare earth element (REE) signatures in fossil bone for use in paleoenvironmental reconstruction, because the REE signature of conodont elements is altered at high temperatures due to recrystallization (Armstrong et al. 2001). These results could have a significant impact on environmental reconstructions that use REE signatures of fossil bones and merits further investigation.

5.4 LARGE-SCALE SPATIO-TEMPORAL CONTROLS OVER TAPHONOMIC PROCESSES

Changes in the global climate regime, the ultimate causes of which are still not fully understood, have a far-reaching impact on not only the history of life by driving extinction and evolution, but also the fossil record, by controlling the distribution of environments and taphonomic modes. Hence, not only do the players change, but the stage changes as well. Within the relatively narrow temporal window provided by many fossil occurrences, these long-term secular changes in taxa and environments play a relatively minor role in fossil assemblage formation, occurring near the minimum resolution recordable by the fossil record (Behrensmeyer et al. 2000). The effect of secular changes on preservation cannot be fully appreciated by studying individual fossil assemblages.

Large-scale environmental changes due to changing tectonic activity, atmospheric CO_2 concentration, and/or insolation patterns may shift the taphonomic window of preservation, altering the biota we are likely to recover in the fossil record. This dynamic may explain why the fossil record can dramatically improve or deteriorate (widen or

narrow the taphonomic window) during suspected periods of major environmental change (also see Frasier et al., this volume). Alteration to taphonomic modes can be subtle, such as is often found with changing sedimentation rates brought about by changes in erosion patterns (Behrensmeyer et al. 1997, Martin 1999). Changing environmental conditions may create or remove critical depositional environments and taphonomic modes over time (Retallack 2005b, Smith and Botha 2005, Smith and Swart 2002). On the extreme end, environmental changes behind mass extinction events may severely perturb preservation conditions, leading to unusual, short-term taphonomic modes. For example, during the biotic crisis surrounding the Permian-Triassic transition elevated volcanic activity altered atmospheric chemistry, leading to massive plant die-offs and extensive terrestrial erosion that was rapid and short-lived (Arche and Lopez-Gomez 2006, Huey and Ward 2005, Retallack 2005a, Sephton et al. 2005). In all of these examples, higher-level changes are required before large-scale patterns in environmental distribution and taphonomic modes can proceed.

5.4.1 Geophysical Dynamics

Above all, vertebrate remains must be buried before they can fossilize. Tectonic activity, primarily uplift and subsidence, is the ultimate control of sediment erosion and deposition. Subsidence increases basin accommodation and allows for rapid burial, even in the absence of high sedimentation rates. Continental accretion and mountain building affects topography and can generate regionally higher rates of sediment accumulation in fluvial, lacustrine, and deltaic environments distal to the uplifted area (Behrensmeyer and Hook 1992, Behrensmeyer et al. 2000). Tectonically active periods also tend to see an

increase in volcanism. Volcanoes deposit various silica-rich particulates which, when weathered, alter sediment chemistry and provide an important source of diagenetic materials (Behrensmeyer and Hook 1992, Downing and Park 1998, Martin 1999). Increased volcanism may form rift valleys in zones of continental extension, providing a basin for sediment deposition and altering the local water table, which can create river and lake systems in valley interiors, leading to important fossil accumulation sites (Rogers et al. 2001, Smith and Swart 2002).

Significant alterations of geomorphology that affect burial can occur even in the absence of tectonic activity. For example, the development of continental glacial conditions during "icehouse" periods promotes widespread eolian silt (loess) deposition, alluvial outwash, and lake formation from meltwater over land surfaces in areas proximal to the glacial front (Behrensmeyer and Hook 1992, Prothero and Schwab 1996). In other, more distant areas the onset of glaciations leads to a marked shift in temperature and precipitation patterns. These environments promote burial of remains, especially those influenced by periodic flooding from glacial meltwater. Glacial retreat exposes new depositional basins and topographic sources for weathering, and enhances erosion by altering base level following isostatic rebound. These features create new opportunities for both terrestrial and freshwater preservation following glaciation. Glacial mass compacts any underlying non-consolidated sediments. Over larger spatial scales, glacial formation reduces sea-level, expanding continental area. Larger land areas support an overall greater abundance of species, although the exact mechanisms underlying the pattern are still under scrutiny (Chown and Gaston 2000, Rohde 1992, Storch et al. 2005). The species-area effect has been observed to operate in the late Cenozoic for various taxa

and at multiple scales, signifying its importance in understanding paleobiodiversity patterns (Barnosky et al. 2005, Flessa 1975, Marui et al. 2004).

Continental drift transports a land surface, submitting it to changing climatic conditions even when global climate remains stable. The effect of drift vs. large-scale climate change can be difficult to discern from the fossil record of a particular region if widespread fossil localities are available to place the inferred changes into a larger context. New technology, in the form of GIS software, coupled with geophysical models of crustal plate movement[1], allows paleontologists to reconstruct the probable pathways and extents of regional movement over time, providing an additional comparison between climate change and drift-induced changes (of course these need not be mutually exclusive). If continental drift has a similar effect on environmental distribution as climate change does, then we can expect the prevailing taphonomic regime to change as a result.

5.4.2 Atmospheric Carbon Dioxide

The concentration of atmospheric CO_2 is one of, if not the most, important drivers of global taphonomic patterns because of its role in determining both global temperature and biogeochemical cycles at multiple spatio-temporal scales. Two sets of carbon cycles control CO_2 concentration: i) the short-term exchange between the biosphere, soil, ocean, and atmosphere, operating on a 10^0-10^4 year timescale; and ii) a long-term exchange between the atmosphere, rocks, and ocean on a 10^5-10^9 year timescale (Rothman 2001 and references therein).

[1] Paleogeographic Atlas Project at the University of Chicago (pgap.uchicago.edu) and the Paleomap Project at the University of Texas, Arlington (www.scotese.com)

Periods of elevated atmospheric CO_2 accelerate chemical weathering of silicate rocks, providing calcium, bicarbonate, and silicon ions for the formation of $CaCO_3$ and SiO_2 in marine and terrestrial environments (Martin 1999). Changing atmospheric CO_2 concentrations, due to volcanism or climate change, alter the cycling of critical elements like C, N, Ca, and P. However, the relationship is complex, involving several coupled feedback mechanisms between terrestrial, marine, and atmospheric sources (Igamberdiev and Lea 2006).

Carney et al. (2007) found that experimental doubling of CO_2 in a forest community actually enhanced terrestrial carbon cycling instead of leading to greater plant assimilation by altering the relative abundance and activity of soil microbes. This discrepancy is due to differences between photosynthesis and respiration, with photosynthesis being more temperature sensitive, placing a lower maximum response limit to CO_2 enrichment than respiration (Allen et al. 2005, Igamberdiev and Lea 2006). In other words, an increase in atmospheric CO_2 leads to relatively minor gains in plant productivity (which will scale with size) while supporting a much greater increase in decomposition, labile C cycling, and microbial biomass within soils (Allen et al. 2005).

When metabolically or structurally critical elements are abundant in the burial environment, extraordinary preservation can result, but their absence leads to extensive biogeochemical recycling and subsequent destruction of remains (Behrensmeyer and Hook 1992). Many of the extraordinary fossil Lagerstätten, such as the Early Cretaceous Liaoning deposits (Zhou 2006), were formed during periods of high atmospheric CO_2, when perturbations to major biogeochemical cycles led to periods of exceptional preservation (Retallack 2005b), perhaps driving tissue carbonization as a major mode of

preservation. As paleogeographic and paleoclimate models improve, it should become possible to explicitly test changes in biogeochemical cycles due to climate and tectonic change at varying spatio-temporal scales.

5.4.3 Orbital Cycles in Solar Energy

The geometry of Earth's orbit varies over time, causing changes in the amount of solar energy received on the surface. These Milankovitch oscillations are long-term cyclical changes in eccentricity (100 Ky period), obliquity (40 Ky period), and precession (26 Ky period) (Prothero and Schwab 1996). Individually, the adjustments in orbital geometry are small, but the combination of these cycles over millennia affects how and where solar energy is distributed, and they have been implicated in causing periods of rapid regional-to-global climate change (Rial 2004, Wright and Vanstone 2001).

Due to the semi-chaotic nature of Earth's orbital geometry it is nearly impossible to accurately project these oscillations into the distant past (>40-50 Ma) (Laskar et al. 2004). However, the large-scale effect of changes in these values on climate is observable in the fossil record. Some examples reach as far back as the Devonian (Yang et al. 1996) and cover climatic responses in both the marine (Balog et al. 1997, Fenner 2001, Gibbs et al. 2004, Wendler et al. 2002, Yang et al. 1996) and terrestrial (Miller and Eriksson 1999, Olsen et al. 1991, Retallack et al. 2004) records. Such responses induced major changes to atmospheric and ocean circulation patterns, sea-level, seasonality, precipitation, and surface temperature. Changes in these patterns have widespread effects on continental weathering and sediment transport (Van der Zwan 2002; and see below), and therefore the number and distribution of depositional systems and fossil-bearing units.

Cycles in solar activity have been found to drive short-term increases (100 Ky cycles) in global temperature and CO_2 release into the atmosphere (Rial 2004), although the overall effect on global climate dynamics appears small compared to that of orbital oscillations (Cubasch et al. 2006).

5.5 IMPLICATIONS FOR THE TERRESTRIAL VERTEBRATE FOSSIL RECORD

5.5.1 The Existence of Terrestrial Megabiases

Megabiases result from the combined effect of multiple, often secular, changes in taphonomic processes controlling the destruction of remains (Behrensmeyer et al. 2000). Megabiases were first recognized and studied in the marine invertebrate fossil record, foremost among them cycles of preservation and biomineralization (Martin 1999). Together changes in these factors over time profoundly affect reconstructions of biodiversity and macroevolutionary patterns in the marine fossil record (Bush and Bambach 2004, Martin 2003, Smith et al. 2001). Although Behrensmeyer and Hook (1992) noted the possibility of a megabias in the terrestrial fossil record and recommended further research, actual research into the existence of terrestrial megabiases similar to those found in the marine realm have yet to infiltrate large-scale studies of the terrestrial fossil record.

When major trends in terrestrial fossil preservation are considered, they are interpreted in light of marine trends, i.e., sea-level change as a driver of terrestrial fossil preservation (e.g., Sereno 1997, Wolfe and Kirkland 1998). Fara (2002), in a study on gaps in the Late Jurassic–Eocene terrestrial fossil record, found no evidence that sea-level

change influenced continental fossil preservation. Instead he suggests that the marine and continental records behave independently of each other. However, Van der Zwan (2002) found that sea-level effects on continental sediment supply depend on global climate. Milankovitch cycles are more important during "greenhouse" intervals, whereas sea-level change dominates during "icehouse" intervals. Regardless, examining marine megabiases should lend some insight into potential parallel patterns in the terrestrial record. The marine record demonstrates many processes, acting at similar spatio-temporal scales and falling under the same influences as the continental fossil record.

Long-term changes in sea-level and atmospheric CO_2 lead to multiple, cascading alterations in the habitat and sediment character of marine environments, affecting: i) the spatial distribution of environments, ii) species diversity and abundance levels, and iii) preservation of the biotic assemblage; all these factors changing predictably with depth (Martin 2003, Smith et al. 2001). A similar pattern exists in terrestrial systems, where changes in the sedimentary record often are observed to coincide with noticeable changes in vertebrate fossil accumulations (Bown and Beard 1990, Maas 1985, Martin 1999, Smith and Botha 2005). In terrestrial environments elevation and atmospheric CO_2 (a factor in long-term climate change) control the same set of habitat and sediment character changes. These factors change predictably with elevation: both environmental distribution and taxonomic diversity vary with altitude (Gaston 2000) and the opportunity for burial and fossilization decreases as one moves from low-lying areas of net deposition to elevated areas of net erosion. The poor representation of highland environments is a well-known feature of the terrestrial record. It has yet to be identified as a true megabias, possibly due to the difficulty in distinguishing the effect of elevational changes from

other factors (although methods are improving). Regions experiencing increased tectonic activity or isostatic rebound most likely are affected by this megabias.

Marine $CaCO_3$ saturation decreases at higher latitudes as shallow waters become cooler—the "latitudinal lysocline"— causing dissolution in $CaCO_3$ skeletons at higher latitudes (Martin 1999). Atmospheric CO_2, tectonic, and climate changes mediate the strength and steepness of the lysocline over time by shifting water depth and continental shelf area (Martin 1999, Pearson and Palmer 2000). Bone preservation may be similarly controlled by the position of the Intertropical Convergence Zone (ITCZ), a wide belt of precipitation following seasonal north-south movement cycles, which changes in response to continental arrangement and land area (Ziegler et al. 2003). Together these factors influence the geographic range and position of moist, seasonally wet/arid, and arid environments in tropical and temperate regions.

The greatest extent of moist conditions in tropical and temperate regions are supported during times of high sea-level and continental divergence, forming a continuous latitudinal band at the equator and two others at mid to high latitudes (Ziegler et al. 2003). Low sea-level and continental accretion lead to greater seasonality and aridity, reducing the size of the equatorial moist tropical zone while leaving the high latitude moist temperate zone intact, forming a precipitation gradient extending down to the low latitude arid zones. Predominantly moist or arid zones contain a lower diversity of depositional environments and taphonomic modes favorable to bone preservation (sedimentation rates, sediment biogeochemistry, biotic activity, etc.). Intermediate regions that receive enough seasonal precipitation to support a variety of favorable environments for preservation are more likely to form a substantial fossil record because

more opportunities for burial exist. Bone preservation in very moist or arid regions does occur but may be more infrequent and subject to seasonal patterns or other intermittent changes in climate that shift conditions towards favoring burial and preservation (Fastovsky et al. 1997, Loope et al. 1998, Rogers 2005). It appears this pattern has remained relatively stable through most of the Phanerozoic because of Hadley cell circulation (Ziegler et al., 2003), with the steepness of moist-arid gradients mediated by sea-level and continental configuration. This taphocline has important consequences for vertebrate paleobiology, because most of what we know about extinct life in the terrestrial fossil record comes from seasonal intermediate regions at mid-latitudes. Such a pattern has been observed in Mesozoic terrestrial ecosystems (Anderson et al. 1998, Rees et al. 2004; Noto, unpublished data) but remains to be studied in other vertebrate groups and other times.

Another potentially widespread cause of megabias is the evolution of vascular land plants, whose morphological and metabolic adaptations have altered biogeochemical cycles over time (Berner et al. 2004). This is especially true in the replacement of gymnosperms by angiosperms as the dominant flora is most terrestrial environments, starting in the Cretaceous. Many studies have found distinct differences between the two groups in their effect on sediment biogeochemical processes, which influences the type of weathering regime found in the host soil (Berner et al. 2004, Kelly et al. 1998). Significant disagreement exists as to which group promotes greater weathering. The evidence is slightly in favor of gymnosperms, although a great deal of variability exists between taxa (average ratio of angiosperm over gymnosperm weathering rate is 0.5–1.5) within each group, requiring much more work (see Berner et al. 2004).

Geologic measures of weathering may not be as important in bone decomposition as other soil properties under gymnosperm vs. angiosperm cover. Grown in the same conditions, soil under gymnosperms tends to be more acidic, contains less exchangeable Ca (due to lower Ca content of leaf litter), and a lower abundance of heterotrophic consumers (Reich et al. 2005). The low sediment pH will be more destructive to buried bone over time than microbial or fungal activity. Each group alters soil texture and composition differently. Gymnosperm-altered soils are more organic-rich and sandy, while angiosperm-altered soils are more clayey and dense (Andrews et al. 2006), affecting soil hydrologic properties and chemistry. Higher sand content permits greater fluid flow through the sediment and creation of biogeochemical conditions detrimental to the stability of osseous tissue. High clay content reduces fluid flow, slowing bioapatite and collagen loss, while encouraging early diagensis (see section 3.2.3).

These differences may have led to greater bone destruction in the gymnosperm-dominated communities of the Paleozoic and Mesozoic than in later angiosperm-dominated communities of the Cenozoic, though this may have been offset somewhat by the higher consumer abundance and decomposition supported in angiosperm-derived soils. Furthermore, differences between the soils in gymnosperm vs. angiosperm communities are dependent on external environmental factors and therefore will not act uniformly across environments. Particular combinations of parent sediment, plant taxa (or functional group), and climate are likely more important than plant type alone.

The dramatic rise in terrestrial vertebrate diversity starting in the Cretaceous (Benton 1985) may not only be the result of "pull of the recent" effects or rock volume/exposure area bias, but a long-term change in the biogeochemical conditions of

environments where angiosperms proliferated, creating conditions more favorable for bone preservation. Further work on paleosols from the late Mesozoic and early Cenozoic are necessary to track the chemical and physical changes to the soil profiles before, during, and after angiosperms diversified.

5.5.2 Examples of Changing Taphonomic Regimes Over Time

Paleozoic

The fossil record of terrestrial vertebrates begins in the late Devonian with the evolution of tetrapods and their first forays onto land. Early tetrapods inhabited marginal-marine, deltaic, and fluvial environments in seasonally wet, semi-arid climates during a time of high global mean temperature and elevated CO_2 and low O_2 concentrations in the atmosphere (Berner 2006, Cressler 2006, Scotese 2009). Two major gaps exist in this record: one during the Famennian (374-360 mya) and the other between the late Devonian and early Carboniferous, known as "Romer's Gap". Both gaps have been interpreted as a true decrease is tetrapod diversity resulting from the sharp drop in atmospheric oxygen concentration during this period (Ward et al. 2006). However, a comprehensive examination of the fossil record from this time reveals changes in tetrapod morphology, diversity, and fossil distribution that are more compatible with a taphonomic interpretation (Clack 2007, Coates et al. 2008).

In early tetrapodomorphs ("stem tetrapods") such as *Eusthenopteron*, *Tiktaalik*, and *Panderichthys*, large body size, obligatory aquatic lifestyle, presence of scales, and well-ossified skeletal elements may have aided in their preservation. Decay dynamics of these taxa may have been more like those of large, bony fish such as the alligator gar

(*Atractosteus spatula*). Gars may provide a viable model for early tetrapod taphonomy, not only because of their large size, but their ecology and habitat preferences closely match those of the earliest tetrapods. Well-preserved taxa like *Tiktaalik* (Daeschler et al. 2006) and *Eusthenopteron* (Schultze and Cloutier 1996) demonstrate taphonomic features, such as the broad head resting parallel to the bedding plane and dorsoventral flattening of the axial skeleton, similar to those described in carcasses of alligator gar deposited following tropical storms on the gulf coast of Texas (Weigelt 1989).

Later more derived, limbed taxa like *Acanthostega* and *Ichthyostega* inhabited freshwater fluvial and shallow-water environments under semi-arid climate conditions (Long and Gordon 2004). Under these environmental conditions early tetrapod remains were at risk of prolonged subaerial exposure. These taxa also show loss or reduction of scales on the body (Coates et al. 2008). Scale loss may have made the bodies of these animals more prone to disarticulation due to gas bloating and/or scavenger consumption. These factors likely affected their preservation, as seen in the prevalence of isolated postcranial elements and/or large, robust skulls, contributing to the lack of fossil material during much of the Fammenian.

Starting in the late Devonian, terrestrial plants underwent a rapid evolutionary radiation, expanding into a variety of new niches and culminating in the first recognizable forests (Bateman et al. 1998). An overall rise in secondary plant productivity, as evidenced by larger, woody stems with deeper roots, resulted in deeper weathering of the soil profile. This was especially true in warm temperate and tropical everwet environments (Algeo et al. 1998, Retallack 1997, Scheckler and Maynard 2001). During the early Carboniferous the onset of Pangean assembly drove the development of

extensive ice sheets in the southern hemisphere (Rygel et al. 2008). The ice sheets would have prevented the spread of vertebrates to the south, but created ecological opportunities in the north. Glaciation altered global climate and supported a differentiation and expansion of tropical and temperate biomes, with retraction of arid regions (Scotese 2009). All of this added up to increased ecological opportunity for tetrapods, who likely began radiating into these new environments. However, low atmospheric oxygen favored smaller body sizes (Clack 2007). Smaller average body sizes and increased weathering of temperate and tropical soils was a likely driver of Romer's Gap during the early radiation of terrestrial tetrapods.

This trend continued until the late Carboniferous when widespread glaciation at high latitudes led to increasing seasonality and contraction of the tropical biome. Increasing atmospheric oxygen and development of the amniotic egg allowed tetrapods to increase in size and expand into more seasonal environments with higher preservation potential (DiMichele and Hook 1992). Cyclical glacioeustatic sea-level changes occurred frequently from late Carboniferous to early Permian (Rygel et al. 2008), driven by Milankovitch oscillations (Wright and Vanstone 2001). Sea-level changes created repeated cycles of continental sediment erosion and deposition (Van der Zwan 2002) that increased preservation opportunities during specific intervals.

During the Permian, continued assembly of the large Pangean landmass continued the drying trend begun in the late Carboniferous. The southern hemisphere ice sheet disappeared. Atmospheric circulation and precipitation distribution (i.e., ITCZ position) was highly monsoonal (Ziegler et al. 2003). With the drying of the continental interior and strongly seasonal precipitation pattern, tropical everwet and warm temperate

conditions were rare on the main continental mass. More environments favorable for bone preservation became available, as evidenced by the reasonably good vertebrate record (DiMichele and Hook 1992, Sander 1987, Sander 1989, Sidor et al. 2005, Smith 1993). Extreme aridity in some places led to highly destructive environmental conditions. Evidence for extensive (≥200K km^2) red bed formation in North America during the mid-Permian shows extremely acidic (~pH 1) groundwater and soils, which would have destroyed any buried bone (Benison et al. 1998). Given these hostile environments, it is likely that vertebrate diversity in these regions was also low.

Mesozoic

A rapid increase in atmospheric CO_2 concentration at the beginning of the Triassic (Berner 2006) relaxed the latitudinal temperature gradient as mean surface temperatures increased, establishing even more widespread aridity—perhaps one of the most arid periods in Earth history. The absence of polar ice caps meant warm temperate conditions extended all the way to the poles for most of the Mesozoic. The symmetrical arrangement of Pangea about the equator created a "megamonsoonal" precipitation regime, with a wide latitudinal excursion for the ITCZ that made climate patterns highly seasonal (Ziegler et al., 2003). Vertebrate preservation was best at low- to mid-latitudes, where the monsoonal precipitation lead to seasonal flooding, rapidly burying exposed remains under poorly developed soils with high water tables that promoted early diagenesis (Dubiel et al. 1991, Smith and Swart 2002). Like the Permian, the most hostile desert regions (e.g., much of the continental U.S.A) sport few fossils due to poor preservation and low diversity.

As CO_2 levels declined from the mid-Triassic to mid-Jurassic, tropical and warm temperate biomes once again expanded their ranges and a seasonally wet tropical biome was reestablished at the equator. There is no good evidence of tropical everwet (i.e., rainforest) conditions throughout the Jurassic due to a weakened but still operational monsoonal circulation (Ziegler et al., 2003). As such, biome distribution remains more or less stable during the Jurassic, with an increase in global temperature and humidity as Pangea began to rift apart and CO_2 levels once again peak in the Late Jurassic, before beginning a steady decline in the Cretaceous (Berner 2006, Price and Sellwood 1997, Sellwood and Valdes 2006).

The Late Jurassic contains spectacular assemblages of dinosaurs and other vertebrates, preserved mostly in the seasonally-dry biomes at mid-latitudes. The number of vertebrate fossils drops sharply at higher latitudes, coinciding with the transition to the warm temperate biome, where the peak in plant fossil diversity occurs (Rees et al. 2004). This drop in vertebrate preservation is likely due to the relatively poor preservation conditions that existed in high latitude forests. The record for Early and Middle Jurassic vertebrates is not as good but demonstrates the same pattern: the vertebrate fossil peak follows the north-south migration of the biome (unpublished data). It is interesting that the Middle Jurassic vertebrate record is so poor, considering it contains the same basic arrangement of continental area and biomes. Further work on this time period will be necessary to tease out the cause of this idiosyncrasy.

The Cretaceous was perhaps one of the most equable times in Earth history. Global temperature cooled as CO_2 levels fell, most likely due to the increased weathering and runoff from the diverging continents (Donnadieu et al., 2006). As the continents

drifted further apart, the smaller continental interiors became moister and the large desert biomes characteristic of the Triassic and Jurassic were greatly reduced. Instead, widespread seasonally wet savannah-like environments persisted in the tropics at the low to mid latitudes (Upchurch et al. 1999). Small patches of tropical rainforest were restricted to the equator, while warm- and cool-temperate forests reached all the way to the poles. Widespread seasonally wet conditions persisted across much of North America, Europe, and China. Global temperature and humidity were still higher relative to today.

Cretaceous vertebrate fossils are relatively widespread, found at some abundance in most biomes and latitudes. This is in stark contrast to previous patterns, where the greatest number of vertebrate fossils is restricted to a narrow range of environments. High sea-level, in concert with the seasonal precipitation pattern, promoted broad plains proximal to sea shores (Horner 1989, Horner et al. 1992), creating ideal environments for bone accumulation and burial. In tropical environments, these conditions contributed to the formation of lagoons and other brackish water bodies, which provide an outstanding record of soft-tissue preservation (Dal Sasso and Signore 1998, Zhou et al. 2003).

By the Late Cretaceous, angiosperms are important members of the flora, found in every major environment. Their modifications to the burial environment potentially contributed to the apparent rise in diversity by promoting conditions more amenable to bone preservation. Indeed, a survey of vertebrate fossil distribution does appear to show more fossil localities near shorelines. The lack of a fossil record across the K/T boundary may as much be a function of loss of these habitats due to lowering sea-level and

increasing aridity, which destroyed the most faithful recorders of the terrestrial biota, as it was widespread extinction (Fastovsky 1990).

5.6 IMPLICATIONS FOR VERTEBRATE PALEOBIOLOGY

5.6.1 Changing Patterns of Species Diversity

Cycles of evolutionary and ecological change observed in the fossil record are not surprising, considering the control that the global climate and tectonic regimes exert on both biogeochemical processes and species' population dynamics. These cycles are explicitly linked because they are controlled by the same set of factors, yet the changes they elicit often are treated separately. Given the hierarchical nature of both biotic and abiotic response to climate and tectonic changes, how each level of the hierarchy interacts during these transitions to form the fossil record takes on special importance.

As Behrensmeyer and Hook (1992, p. 88) observe, "[m]any paleoecologic studies have emphasized the role of global climate as the major factor controlling biotic change, but climate pattern alone neither explains nor predicts the composition of subsequent biotas." Climate and tectonic changes that bring about environmental change lead to shifts not only in floral and faunal assemblages but in biogeochemical cycling as well, thus altering the suite of taphonomic processes operating in the area, in effect creating the very real problem of distinguishing between local shifts in species distributions and large-scale biotic events. The use of other time-equivalent deposits for reference is required to understand the scope and nature of the perceived change (Behrensmeyer and Hook 1992). This idea needs further enhancement by extending the phenomenon to a larger scale.

At the global scale, shifting environmental parameters and species ranges are symptomatic of long-term alterations to the properties and distribution of the major biomes, themselves dependent on the state of tectonic activity and insolation. As the biomes change, this will also significantly change the overall nature and distribution of taphonomic regimes, effectively moving the taphonomic window of preservation and our view of life during the periods of time in question. It is not the completeness of the terrestrial fossil record *per se* that is at issue here but how this sliding taphonomic window affects our ability to reconstruct the ecology and evolution of extinct species, specifically the distribution of regional biodiversity. Much of the research concerning biodiversity patterns has focused on quantifying global patterns, charting the rise and fall of life's diversity through time, while neglecting potentially important dynamics occurring at the regional level (Miller 2003). It is precisely the nature and effect of these dynamics in determining species distributions that continues to be a major source of study for ecologists, the most important pattern being latitudinal gradients in species richness.

The current latitudinal gradient consists of highest diversity in the tropics, which decreases with increasing latitude toward the poles. This pattern has been demonstrated in plants, mammals, reptiles, amphibians, insects, and fish (Rosenzweig 1995). Although well documented, the mechanisms driving this pattern of species distribution still are debated actively, being most strongly related to productivity and/or evolutionary rate (Gaston 2000).

Several examples of latitudinal diversity gradients are also known from the fossil record, found in plants (Crane and Lidgard 1989, Haskell 2001, Silvertown 1985),

dinosaurs (Rees et al. 2004), radiolarians (Kiessling 2002), bivalves (Crame 2002), and brachiopods and foraminifera (Stehli et al. 1969). Given the growing interest in the effect of ecological interactions on speciation and evolutionary rates among paleontologists and neontologists alike, the presence of latitudinal gradients in the fossil record suggests that the mechanisms driving these patterns are an ancient phenomenon.

Studying regional patterns of alpha, beta, and gamma diversity in the fossil record enables a better understanding of the effects of environment and ecology on micro- and macroevolutionary processes in ways that may only be addressed with the fossil record (Jackson and Erwin 2006, Miller 2003). Allison and Briggs (1993) found that, since biodiversity varies with latitude, the latitudinal range sampled by the fossil record at a particular time will influence estimates of extinction and origination rates, especially when comparing patterns from times that experienced different global climate regimes.

A global point of view is necessary to place local- and regional-scale fossil distributions within the context of global taxonomic diversity patterns, but few studies have addressed this directly. Applying these principles to the terrestrial fossil record will first require a better understanding of how taphonomic bias due to environmental differences influences large-scale patterns. Once addressed, it will be possible to implement correction factors to the diversity data. Such an approach was applied to Middle Paleozoic and Late Cenozoic marine benthic communities (Bush and Bambach 2004).

5.6.2 Model of diversity gradients and climate change

Modern continental surfaces can be grouped into broad regions of common climate and ecology to form biomes (see section 3.4.1). The latitudinal and longitudinal extent of each biome depends on the distribution of constituent environments and biota, which is driven largely by precipitation and insolation patterns (Begon et al. 2006). These same factors also lead biomes to support different levels of biodiversity; moist, high-energy areas support more species than dry, low-energy areas (Evans et al. 2005, Hawkins et al. 2003, Kreft and Jetz 2007). Specific chemical, physical, and biological processes present within an environment define a taphonomic mode, with particular modes preserving vertebrates more frequently in certain environments over others (Behrensmeyer and Hook 1992).

In the proposed model, vertebrate taxa differ in the taphonomic modes necessary for fossil preservation and vary in abundance due to ecological requirements. The number of different taphonomic modes together describes the taphonomic regime for a given biome. The greater the heterogeneity of taphonomic modes, in particular the proportion of these modes with conditions necessary for preservation of Taxon X, the greater the possibility of it entering the fossil record. Therefore the fossil record of Taxon X varies between biomes due to both abundance and preservation requirements, creating latitudinal and longitudinal gradients between taphonomic regimes. The collection of all taphonomic regimes, in conjunction with the level of biodiversity supported in each biome, produces the overall fossil record for a given time period. This model then allows one to explore changes to the fossil record over time brought about by changes in climate, biodiversity, and taphonomic processes.

Consider the following scenario shown in Figure 5.3. At Time A the prevailing climate regime supports three major biomes: a moist, high-latitude Biome 1; a seasonally-wet Biome 2; and a moist, equatorial Biome 3. Biodiversity is highest in Biome 3, decreasing with increasing latitude towards the poles (3 > 2 > 1). When living biodiversity is surveyed at Time A, the resulting diversity pattern is a unimodal curve, similar to that observed today. However, when forming the fossil record under the conditions during Time A, the probability of vertebrate preservation in Biome 2 is greater than either Biomes 1 or 3 (2 > 3 > 1) due to supporting a greater variety of taphonomic modes. The resulting paleolatitudinal diversity curve represented by the fossil record of Time A would appear bimodal instead of the actual unimodal pattern.

When we move forward to Time B, climate patterns have shifted, altering environmental and taxonomic distributions. Thus there is a reorganization of diversity and taphonomic regime within the biomes. The major biomes at Time B include: a high-latitude Biome 1; a moist, temperate Biome 2; a seasonally-wet, tropical Biome 3; and a seasonally-arid, equatorial Biome 4. The diversity pattern is now 3 > 2 > 4 > 1, creating a bimodal diversity curve. Although possessing fewer taxa in this hypothetical world, Biome 4 contains a wide range of taphonomic modes due to a seasonal climate. Increasing moisture and decreasing diversity as one moves away from the equator leads to depressed vertebrate preservation at higher latitudes. The resulting preservation pattern 4 > 3 > 2 > 1 yields a unimodal paleolatitudinal diversity curve from the fossil record of Time B.

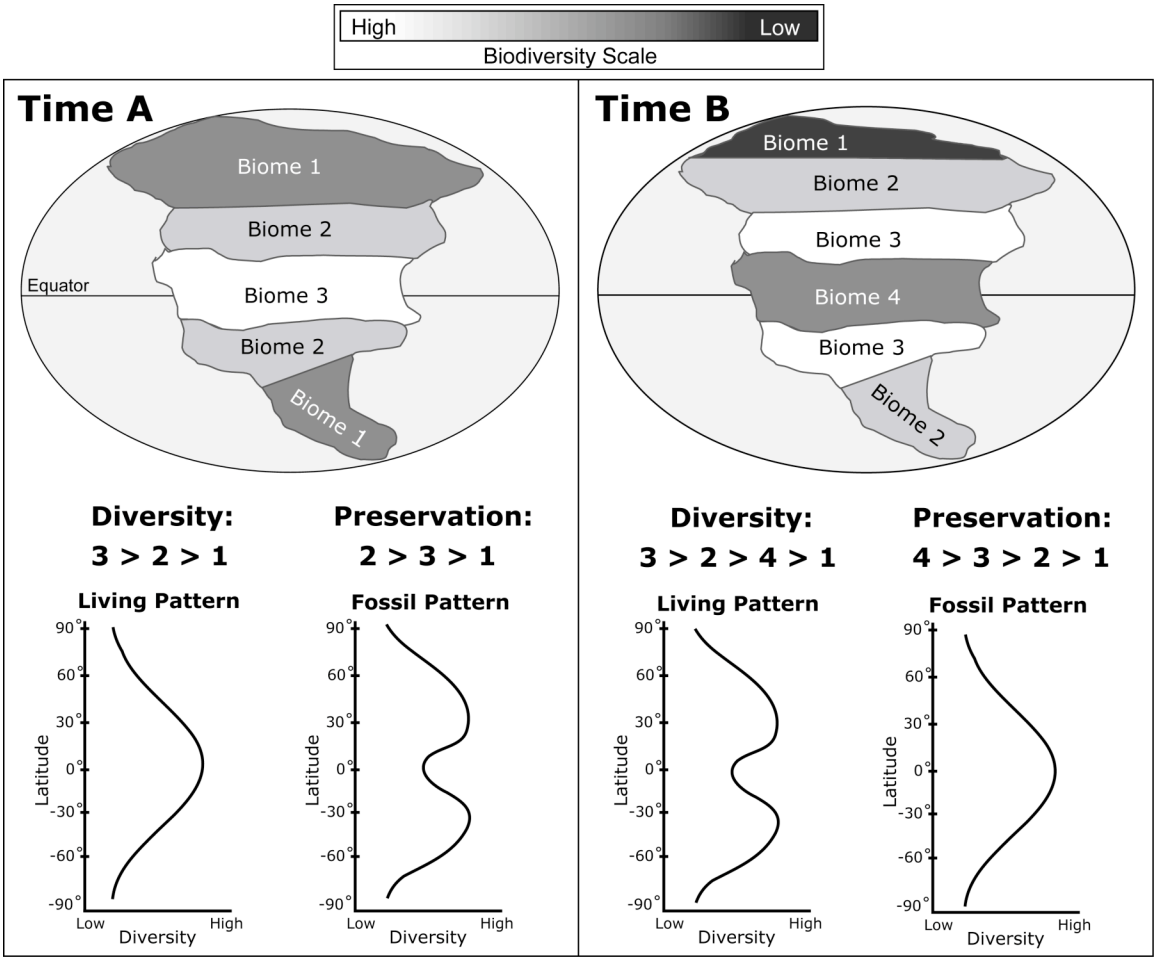

Figure 5.3: Conceptual model of diversity patterns and fossil preservation for a hypothetical landmass at two different times: Time A and Time B. Global climate patterns have changed in the transition from Time A to Time B, changing the distribution and types of biomes on the continental surface (see text), which has altered both biodiversity and vertebrate preservation patterns. The preserved fossil pattern differs significantly from the living biodiversity curve for each time period. Light shades represent higher and dark shades lower biodiversity levels in each biome.

Comparing diversity curves between Times A and B, from both the original living distribution and reconstructed fossil distribution, reveals two very different and conflicting patterns. Contrasting interpretations can be drawn regarding ecological properties of the biosphere at each time and evolutionary responses to climate change during the transition from Time A to B. For example, based on the fossil record from both times, Biomes 2 and 4 appear to support the greatest biodiversity, which could lead to erroneous conclusions about productivity patterns and their effect on the biota. Biased fossil diversity patterns could further lead to an underestimate of morphological and/or adaptive space occupied by a taxon or community, because areas of high biodiversity usually contain the greatest ecological diversity due to intense competition for resources (Pfennig et al. 2007 and references therein). From an evolutionary perspective, comparing terrestrial diversity patterns over time, in the manner of Sepkoski and others, may lead to gross over- and underestimations of diversity depending on how the living diversity patterns were filtered by prevailing taphonomic conditions at the time in question. Fossil diversity estimates could, in part, be a function of alignment between living diversity patterns and favorable taphonomic conditions.

While not quantitative, this model offers a predictive framework for hypothesis testing. The reconstruction of extinct communities usually is accomplished by examining the fossil assemblage for patterns, then comparing these patterns with present knowledge derived from community and landscape ecology to create a meaningful picture of the biota and its environment. Awareness of the many filters this information passes through is part of the process. Nevertheless, an incomplete understanding of the factors controlling these filters may be playing a direct role in how one interprets biologically

relevant information from the fossil record and consequently how the same patterns are viewed today. If we were to create a fossil record for the present world based on what we know about preservation, what would it look like? Does the distribution of fossil diversity from different times in the past match with what we would predict based on environmental and climatic reconstructions? Such exercises may prove useful when considering the spatio-temporal patterns of biodiversity for different times in the past.

5.7 SUMMARY AND CONCLUSIONS

Beyond simply cataloging new specimens, paleontologists desire to understand sparse fossil remains, not only as once living individuals, but within their community and ecosystem structure. Understanding the dynamics of past ecosystems has important consequences for how we view biogeographic and evolutionary patterns. To detect ecological and evolutionary patterns from the fossil record, we need a comprehensive taphonomic framework that acknowledges the multiple, hierarchical factors controlling the surface and subsurface destruction of remains in different environments, herein termed the micro-, meso-, and macroscales. Each level represents the spatio-temporal extent over which a set of taphonomic processes act.

Every environment contains a specific set of taphonomic conditions that act on remains above and below the sediment-atmosphere interface, and together represent the combined influence of local conditions (e.g., landscape, precipitation, temperature). Local conditions are controlled by global patterns of climate, tectonics, and insolation.

Therefore, the taphonomic processes acting on a set of remains at the microscale reflect the prevailing conditions at the macroscale during exposure and diagenesis.

While particular taphonomic processes (modes) are associated with certain environments, environments, in turn, can be grouped together as biomes. Each biome contains a subset of taphonomic modes and can be referred to collectively as a taphonomic regime. As biomes shift in response to macroscale change, the nature and distribution of taphonomic regimes also changes, creating cascading effects through the lower levels. These lead not only to ecological and evolutionary change but also to changes in taphonomic processes, which directly impact the subsequent fossil record. Distinguishing between fossil patterns formed by these very different processes may be difficult unless hierarchical taphonomic change and initial conditions are explicitly considered.

With a hierarchy of taphonomic control, paleontologists must recognize that preservation bias is passed on to larger spatio-temporal scales, directly impacting ecologic, evolutionary, and biogeographic reconstructions. This perspective provides a powerful tool for analyzing fossil datasets by constraining the range of potential alteration to the original biotic community, allowing for a more comprehensive assessment of information loss (and gain) for different regions of the Earth at different times.

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Chapter 6

6.1 CONCLUSIONS

Taphonomic processes operate at a variety of spatiotemporal scales, however the basic unit of preservation rests at the level of individual remains and their interaction with the immediate biogeochemical environment. Individual taphonomic processes (or factors) are constrained by these conditions, altering the target remains within a range dictated by the environment. Alteration can take many forms, but usually includes a loss, gain, or chemical modification of organic molecules and their products. When present, inorganic structures also undergo loss, replacement, or *in situ* modification. Therefore, most taphonomic processes are inherently destructive, since the original structure and composition of the remains is modified and rarely, if ever, preserved in their original form. While destructive at the molecular level, certain alteration processes can improve the stability of remaining components and prevent further alteration. On the other hand, modification or loss of particular molecular components, such as proteins, is disproportionately destructive because the importance of certain elements to the structural integrity of bone tissue is not evenly shared among components. No set of remains goes unaltered through this transition, only the type, rate and degree of alteration differ between factors and not all components are equally affected.

The specific combination of factors present in the surrounding environment is responsible for determining the rate, degree, and method of alteration. Individual

environments contain a multitude of taphonomic factors, which combine to form a taphonomic mode that is responsible for determining the overall fate of remains, which have long been acknowledged in the literature (Behrensmeyer 1988, Behrensmeyer and Chapman 1993, Behrensmeyer and Hook 1992, Behrensmeyer et al. 2000, Eberth and Currie 2005, Hedges 2002, Olszewski 2004). It is still not well understood the degree to which surface versus subsurface processes differ within taphonomic modes and how this ultimately affects vertebrate preservation. I would like to propose that taphonomic modes are composed of one or more taphonomic trajectories, which describe the set of processes responsible for altering the remains over time (sensu Smith et al. 2007). Differences between surface and subsurface trajectories ultimately define the resulting preservation pattern, which is interpreted as a taphonomic mode. Fossil preservation then depends on the combination of trajectories present in an environment. Extremely poor preservation or destruction of remains may occur when trajectories are mutually destructive. Concordance between Morrison Formation data and experimental results suggest that surface and subsurface trajectories were mutually favorable towards preservation, which may explain why it is such a diverse assemblage. These results confirm the importance of sediment hydrology, body size, and surface exposure among the principal components of terrestrial taphonomic trajectories. At least in the Morrison Fm. both surface and subsurface processes are vital to vertebrate preservation.

Over space and time environmental conditions determine not only taphonomic modes but also influence species diversity patterns (Chown and Gaston 2000, Fischer 1960, Fraser 1998, Hawkins et al. 2003, Pagel et al. 1991, Rosenzweig 1995). When studying the fossil record the degree to which the taphonomic modes and diversity

pattern covary over environmental gradients becomes problematic (Bush et al. 2004, Smith 2001). Analysis of the Morrison Fm. data suggests that taxonomic and body size sampling over a broad range of environments is relatively good, even among small taxa. Thus, spatial changes in taxonomic composition may represent real community-level change across a gradient. When the number of sampled environments goes down, an increase in taphonomy-driven patterns can be expected. However, it is worth noting that including data from highly disparate taphonomic modes, such as microsites, may skew the perceived paleobiologic patterns. Large-scale biodiversity and paleoecological studies of extinct terrestrial communities are therefore possible if sample-level taphonomic factors (i.e., environmental variation) can be accounted for. We may then be able to examine spatial diversity patterns of vertebrates in ancient terrestrial ecosystems and compare them with patterns in living communities (Reed 1998, Reed 2002). This is particularly important for studying communities lacking modern analogs and tracking changes in vertebrate community composition and ecomorphological diversity over time.

6.2 FUTURE DIRECTIONS

One can take the results of this research in a number of potential directions. I divide these into experimental- and field-based work, the focus being on practical applications of this research to further our understanding of subsurface taphonomic processes and their relationship to different environments, both past and present.

6.2.1 Experimental Work

Of primary interest in following up the current research will be further taphonomic experiments that work to refine the general patterns observed and extend the methodology to address additional questions. Since the experiment described here focused on variation in external conditions relative to a constant bone condition (fresh and defleshed), further data are needed on the relation between surface exposure and preservation potential. This would provide an important connection between surface and subsurface taphonomic processes by examining the relationship between the condition of remains prior to burial with different subsurface conditions. Additional avenues include measuring the effect of multiple bones placed together versus singly, as synergistic effects between the decay products of groups of bones may further retard decomposition through buffering the surrounding conditions. Many of the best-preserved fossil bones tend to be buried in groups, not singly, and one contributor to this pattern could be this synergistic buffering effect.

Experimental manipulation of authigenic mineral formation and diagenetic alteration to bone apatite represents another direction. Future work should focus on how differences in the type and concentration of dissolved chemical species influences bone and plant diagenesis. This includes the role of clay minerals, which are important constituents of many terrestrial deposits and contribute important products during diagenesis (Butterfield 1990, McSween et al. 2003). Rapid mineralization of bone and soft tissues has been observed in the laboratory but only under a very narrow range of conditions (Briggs 1995, Brock et al. 2006, Carpenter 2005, Daniel and Chin 2004). Manipulation of chemical species and biogeochemical conditions may help produce

conditions of fossilization not often observed near the surface. To date, no laboratory studies have demonstrated rapid mineralization of soft tissue in vertebrates.

Further experiments related to the role of both living plants and plant organs in bone diagenesis are likewise necessary. Future work should focus on identifying diagenetic properties of remains under different plant functional groups as a way to better understand common features of diagenesis versus those related to particular taxonomic and functional groups. Use of live plants versus detached plant organs should be used to determine which may be more important to bone decomposition. The roots of living plants are known to attack bones with organic acids in order to scavenge vital nutrients (Nicholson 1998). Any of the positive benefits of plant association noted in the experimental results may be overshadowed by the metabolic activities of living plants. These data would have important implications for how spatiotemporal changes in plant species distributions affect fossil preservation, providing further connection between surface conditions and fossil preservation dynamics.

6.2.2 Field Work

Despite the successful recovery of important taphonomic information from the Morrison Fm. dataset, such large-scale work is best suited for examining patterns of distribution but reveals little information on the processes responsible for fossil preservation. Experimental and observational data both have provided information on physical, sedimentary, and geochemical indicators of particular preservative mechanisms. This information now must be taken into the field and used as the basis of field survey work, looking at fossil bones and plants from a variety of depositional environments to

collect sedimentary and taphonomic information in context. Much of this information is permanently lost once a fossil is removed from a sedimentary rock body. Once collected, these fossils can be brought back to the laboratory for a series of quantitative and qualitative analyses to look for fossil features that are indicative of particular preservation mechanisms or paleoenvironments. These criteria can then be applied to fossils in existing collections lacking such contextual information. Drawing the connection between observed mechanisms and fossil occurrences is the next crucial step to better understanding fossil preservation in general and explain the preservation of extraordinary features such as soft tissues, cells, and biomolecules. The contextual information (such as authigenic minerals like vivianite) may also be useful in reconstructing paleoenvironmental conditions or determining levels of time averaging based on the presence of different preservation modes in a fossil locality.

By combining further experimental and field-based methods, it will be possible to build the necessary theoretical and observational background to begin understanding the processes responsible for vertebrate fossilization. Finally, data from the field and lab-based studies can be combined with fossil distribution data into a hierarchical model of vertebrate taphonomy. Such a framework is necessary for understanding the impact of small-scale biogeochemical conditions acting on remains with the larger-scale fossil distribution patterns observed in the rock record. It can be used to help organize this vast array of information and use it to generate new taphonomic hypotheses. Use of the hierarchy and innovative research methods will help drive the field forward.

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