

ABSTRACT

Taphonomic and Mass-Extinction Research from an Ichnological Perspective

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The assemblage of Pleistocene megafauna at Waco Mammoth National Monument (WMNM) and the terrestrial Cretaceous-Paleogene (K-Pg) boundary at Big Bend National Park are just two examples that demonstrate the peril effects of an extreme environmental perturbation on ancient ecosystems. Ichnology is the study of traces that are generated by organismal behavior; therefore, analyzing major die-offs through an ichnological lens can provide a unique perspective to understand the ethology of the survivors. At WMNM trace-fossil analysis was combined with taphonomy, which revealed that the Columbian mammoth herd was subjected to extensive vertebrate and invertebrate scavenging. These findings necessitated a re-evaluation of the causal mechanisms responsible for the death of the herd, as well as demonstrated that scavenging organisms out-survived, at least for some time, the large herbivores in this case. The application of ichnology to the terrestrial K-Pg boundary revealed new findings about the surviving organisms in response to the end-Cretaceous extinction. Herbivorous, soil-dwelling insects, as evidenced from analogous traces, were significantly reduced in body size (Lilliput effect) following the aftermath of the event. These findings, in

conjunction with research on marine-organism responses, provide empirical evidence that the Lilliput effect was a phenomenon that affected surviving organisms across highly disparate trophic levels and ecosystems. Lastly, a hybrid approach of ichnology and zooarchaeology was used to develop morphological criteria for taphonomic analysts to differentiate between carnivore traces and unintentional, preparator air-scribe marks, which can be more similar than one might imagine. Utilization of an ichnological perspective to study survival behaviors from the ancient past may one day help address some of the decisions regarding our current mass extinction.

Taphonomic and Mass-extinction Research from an Ichnological Perspective

by

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CHAPTER ONE

Introduction

This dissertation is composed of four scientific articles, organized as the subsequent four chapters. These articles were generated through a collaborative effort with scientists from diverse areas of research, spanning a total of four different departments. It is through this interdisciplinary collaboration that the following scholarship was generated.

Chapter Two, “Terrestrial evidence for the Lilliput effect across the Cretaceous-Paleogene (K-Pg) boundary” was co-authored by Logan A. Wiest, William E. Lukens, Daniel J. Peppe, Steven G. Driese, and Jack Tubbs. This study provides the first empirical evidence that the Lilliput effect was not restricted to marine environments during the aftermath of the K-Pg mass extinction. The project was conceived and led by LAW. LAW, WEL, and Yohan Letourmy conducted the fieldwork and data acquisition. LAW, WEL, and JT analyzed the data. WEL wrote portions of the manuscript regarding the paleopedology. DJP wrote portions of the manuscript regarding the paleobotanical aspects. All co-authors provided discussion and editorial comments.

Chapter Three, “The Waco Mammoth National Monument may represent a diminished watering-hole scenario based on preliminary evidence of post-mortem scavenging” was co-authored by Logan A. Wiest, Donald A. Esker, and Steven G. Driese. This study demonstrates that the Columbian mammoth herd at Waco Mammoth National Monument was subject to subaerial exposure, scavenging, and skeletonization

prior to burial, rather than being killed and buried in a single event. This study shifts the plausible mechanism of demise for the Waco mammoths to drought instead of the long-held assumption of catastrophic landslide or flood. LAW and DAE conceived the project and conducted the analysis. LAW led the ichnological assessment and beetle experiments. DAE led the investigation of bone weathering and fracture aspects. All co-authors provided discussion and editorial comments on the manuscript.

Chapter Four, “Reply: the Waco Mammoth National Monument may represent a diminished watering-hole scenario based on preliminary evidence of post-mortem scavenging” was co-authored by Logan A. Wiest, Donald A. Esker, and Steven G. Driese. This Reply Article is in response to a published Comment by Smith (2017). In this chapter we clarify and highlight the empirical basis for the interpretation presented in Chapter Three. LAW and DAE re-analyzed the original bonebed maps, the 1996 replica of Bull Q, and the excavation photographs archived at the Baylor University Mayborn Museum Complex. All co-authors discussed and edited this Reply Article.

Chapter Five, “Morphological characteristics of preparator air-scribe marks: implications for taphonomic research” was co-authored by Logan A. Wiest, Joseph V. Ferraro, Katie M. Binetti, Steven L. Forman, Donald A. Esker, and Bernd Zechmann. This is the first study that details morphological criteria to recognize or falsify air scribe preparator damage on taphonomic assemblages. JVF and KMB conceived this project. LAW, JVF, and KMB led the analysis and write-up. SLF provided guidance and discussion throughout the study. DAE assisted with the analysis. LAW and BZ conducted the microscopy. All authors discussed and edited this manuscript.

Chapter Six provides a summary and suggested directions for future research.

CHAPTER TWO

Terrestrial Evidence for the Lilliput Effect Across the Cretaceous-Paleogene (K-Pg) Boundary

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Abstract

Recent research has demonstrated that the Lilliput effect (reduction of body size in response to a mass extinction) affected all trophic levels in the marine realm following the Cretaceous-Paleogene (K-Pg) event. However, it is unclear if this size change was strictly a marine signal, or a global phenomenon that also affected continental ecosystems. Herein we present the results of an ichnological proxy for body size of soil-dwelling insects across the K-Pg boundary in Big Bend National Park, Texas, U.S.A. Quantitative efforts focused on *Naktodemasis* isp., which are characterized as unbranching burrows composed of ellipsoidal packets of backfill menisci. These traces were likely produced by beetle larvae or cicada nymphs based on previous comparison with structures generated in modern soils and laboratory experiments. As an approximation for the body size of the subterranean insects, this dataset indicates that a smaller *Naktodemasis* diameter (D_N) is statistically correlated ($\alpha < 0.05$) with several edaphic factors including poor drainage and weak development (Entisols). Additionally, the D_N in strata immediately superjacent to the highest Cretaceous-specific taxa is smaller by 23% (5.6 ± 1.8 mm) in comparison to D_N within the subjacent Cretaceous interval (7.3

± 2.7 mm). This abrupt shift occurs in a well-drained Inceptisol, and cannot be attributed to facies changes, drainage, or paleosol maturity. Furthermore, a reduced D_N (6.6 ± 2.3 mm) persists above this anomalous shift for at least 20 stratigraphic meters within chron 29r. The cause for this negative response in body size within soil-dwelling biota may be attributed to a shift in plant ecology. This study provides empirical evidence that the Lilliput effect was not restricted to marine environments during the aftermath of the K-Pg event.

Introduction

Recent studies have demonstrated that planktic foraminifera (Keller and Abramovich 2009), coccolithophores (Gardin and Monechi 1998), marine mollusks and vermiform organisms (Gallagher 1990, Aberhan et al. 2007; Łaska et al. 2017), decapod crustaceans (Wiest et al. 2015, 2016; Martínez-Díaz et al. 2016; 2017; Łaska et al. 2017), and lamniform sharks (Belben et al. 2017) experienced a reduction in body size during the aftermath of the Cretaceous-Paleogene (K-Pg) extinction event. Importantly, this reveals that the Lilliput effect (c.f. Twitchett 2007; Harries and Knorr 2009) occurred at all trophic levels in the marine realm. In this study, the term “Lilliput effect” refers to extinction selectivity for small sizes (phyletic dwarfism), and also small-sized organisms preferentially surviving the extinction event and replacing the larger-sized clades. Changes in body size provide insight into the response of organisms to large-scale environmental perturbations operating in ancient ecosystems, and understanding the magnitude and extent of this phenomenon from past events may help constrain predictions for current biodiversity loss (Bottjer and Droser 1994; Morrow and Hasiotis 2007; Sheridan and Bickford 2011; Cheung et al. 2013).

It remains uncertain if the Lilliput effect following the K-Pg event was strictly a marine signal, or a global phenomenon that also affected continental ecosystems. This study focuses on terrestrial ichnotaxa preserved in paleosols. These traces formed *in situ*, are well-preserved, and are sensitive metrics of subterranean-organism biology and behavior, and environmental conditions (Bown and Kraus 1983; Hasiotis and Bown 1992; Hasiotis 2002; Rodríguez-Tovar 2007; Smith et al. 2009; Wiest and Buynovich 2015). Furthermore, soils have been hypothesized refugia for terrestrial organisms during the widespread environmental disturbance associated with the K-Pg event (Harries et al. 1996; Robertson et al. 2004; Bardeen et al. 2017). The response of soil-dwelling invertebrates to environmental disturbance may serve as a proxy for overall ecosystem health across the K-Pg interval because these organisms inhabit low trophic levels.

Herein we report the results of a quantitative ichnological study that reveals an abrupt and persistent reduction in body size within the soil-dwelling community across the K-Pg boundary from Big Bend National Park, Texas, U.S.A. This dataset provides empirical evidence that the Lilliput effect also occurred in terrestrial settings during the aftermath of the K-Pg mass extinction, and implies that burrowing insects were also substantially affected by the event.

Geologic Setting

The Upper Cretaceous (Maastrichtian) and lower Paleocene (Danian) strata within the Dawson Creek section of Big Bend National Park, Brewster County, Texas, U.S.A., consist of southwestward dipping channel sand bodies, fluvial overbank deposits, and associated paleosols (Fig. 2.1; Lehman 1985, 1990, 1991; Atchley et al. 2004). The Dawson Creek exposure within the Tornillo Basin is an extensively studied continental

K-Pg section in the southern United States. The framework of this particular outcrop includes biostratigraphy (Wilson 1970; Schiebout 1974; Standhardt 1986; Schiebout et al. 1987; Lehman 1991), magnetostratigraphy (Rapp et al. 1983; Leslie et al. 2015, in press), terrestrial sequence stratigraphy (Atchley et al. 2004), paleopedology (Nordt et al. 2003, 2011), and paleoenvironmental reconstruction (Lehman 1990). Previous studies of the paleosols occurring throughout the stratigraphic succession suggested that paleoclimate conditions were subhumid to semiarid, vegetation was predominantly dry woodland, and the paleosols resemble modern Entisols, Inceptisols, and Vertisols (Atchley et al. 2004; Nordt et al. 2011). Of particular note was the documentation of two greenhouse events preceding the K-Pg impact and extinctions by Nordt et al. (2003), based on analyses of stable isotopes of pedogenic carbonates.

The analysis focused on the stratigraphic interval that includes the Upper Cretaceous Javelina Formation, as well as the lowermost Paleocene Black Peaks Formation (Fig. 2.2). The formational contact between the Javelina and Black Peaks is conformable (Lehman, 1990), occurs within chron 29r (Leslie et al. in press), and has been interpreted to represent the K-Pg boundary (e.g., Lehman 1990; Nordt et al. 2003, 2011), although there remains an apparent absence of diagnostic impact indicators such as shocked minerals, impact-derived spherules, or geochemical anomalies (e.g., iridium), nor have there been recovered identifiable palynomorphs. The highest Cretaceous-specific remains recovered from this section are disarticulated *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from a fluvial sandstone body between paleosol 21 (P21) and P22 within the Javelina Formation (Fig. 2.2; Lawson 1972, 1975; Lehman 1990). Paleocene mammals occur within the Black Peaks Formation 20 m above the last

occurrence of Cretaceous fossils in a channel complex (superjacent to P28) that is interpreted to be unconformable at its base (Atchley et al. 2004; Lehman and Busby 2007, Leslie et al. 2015; Cobb 2016). Reanalysis of the Black Peaks mammalian faunas, coupled with revised magnetostratigraphy for the section indicate that the mammals occur within the Torrejonian North American Land Mammal Age and were deposited in chron 27r (Leslie et al. in press).



Figure 2.1. Location of Dawson Creek K-Pg section; A) position of Texas (red box) on North American continent; B) position of Big Bend National Park (blue box) relative to Texas; C) yellow star indicates location of Dawson Creek site ($29^{\circ}17'36''$ N; $103^{\circ}31'45''$ W)

Methods

A series of field excursions were conducted within Big Bend National Park during the spring and fall of 2015. All field activities complied with U.S. National Park Service regulations. Individual stratigraphic units and paleosols documented in Nordt et al. (2003, 2011) and in Atchley et al. (2004) were located via GPS coordinates in conjunction with photomosaics labeled with stratal surfaces and paleosols tops, which were generated in the field with a laptop during 2002 (S. Atchley, pers. comm. 2015). Assignment of stratigraphic position in meters, paleosol nomenclature, facies associations, and drainage parameters were adapted from Atchley et al. (2004; cf. their Fig. 2.3). Paleosol drainage was characterized by Atchley et al. (2004) based on matrix color, where poorly drained paleosols were gray to blue-gray, moderately drained paleosols were yellow or brown, and well drained paleosols were red to purple. Accordingly, these drainage indices were easily confirmed in the field. Interpretations of paleosol taxonomic order assigned by Atchley et al. (2004) followed USDA-NRCS soil taxonomy and were cross-checked in the field based on paleosol morphology and horizonation. Entisols were typically stacked A-C horizons without subsurface B horizon development, Inceptisols had weakly developed B horizons (typically Bw), and Vertisols contained pedogenic slickensides in Bss horizons.

Multiple, laterally distributed, fresh excavation surfaces within each sedimentary unit were examined in the field for biogenic structures (plant and animal). Trace fossils were described based on surficial and architectural morphology, dimensions, and burrow fill. The depth of maximum bioturbation was determined with a measuring tape for each paleosol. The minimum inner diameters of shafts and tunnels of each trace observed were

measured with a digital caliper to the nearest 0.1 mm, except for root traces, which were distinguished by their characteristic tapering and bifurcation (Retallack 1988; Driese et al. 1997; Elick et al. 1998). The semiquantitative ichnofabric index of Droser and Bottjer (1986) was used to characterize the degree of bioturbation where 1 = no bioturbation; 2 = discrete, isolated burrows; 3 = 10-40% of bedding is disturbed; 4 = nearly complete bioturbation; and 5 = complete bioturbation. Burrow diameters were evaluated using the nonparametric Wilcoxon/Kruskal-Wallis Test for mean ranks, with post-hoc analyses using Tukey's honest significant difference (HSD) to test for directionality in mean sizes using JMP (v.13) statistical software.

Results

Celliforma isp. (capsule-shaped, smooth cells) and *Skolithos* isp. (vertical cylindrical tubes) occur in Cretaceous portions of the study interval, but quantitative analysis focused on *Naktodemasis* isp., also referred to as adhesive meniscate burrows (Smith and Hasiotis 2008; Smith et al. 2008; Counts and Hasiotis 2009), due to the pervasiveness of this structure throughout the section and occurrence in both Cretaceous and Paleocene strata (Fig. 2.3).

Naktodemasis morphology

The *Naktodemasis* observed from the Dawson Creek section are characterized as unlined, unbranching burrows composed of densely packed meniscate backfill. The traces do not differentially weather from the outcrop or exhibit any relief, but are otherwise apparent on freshly broken ped surfaces because of differences in menisci color in comparison to host matrix (Fig. 2.3). Traces are readily visible in areas of the paleosols that do not have a homogenous color. Burrows are generally straight, and are highly

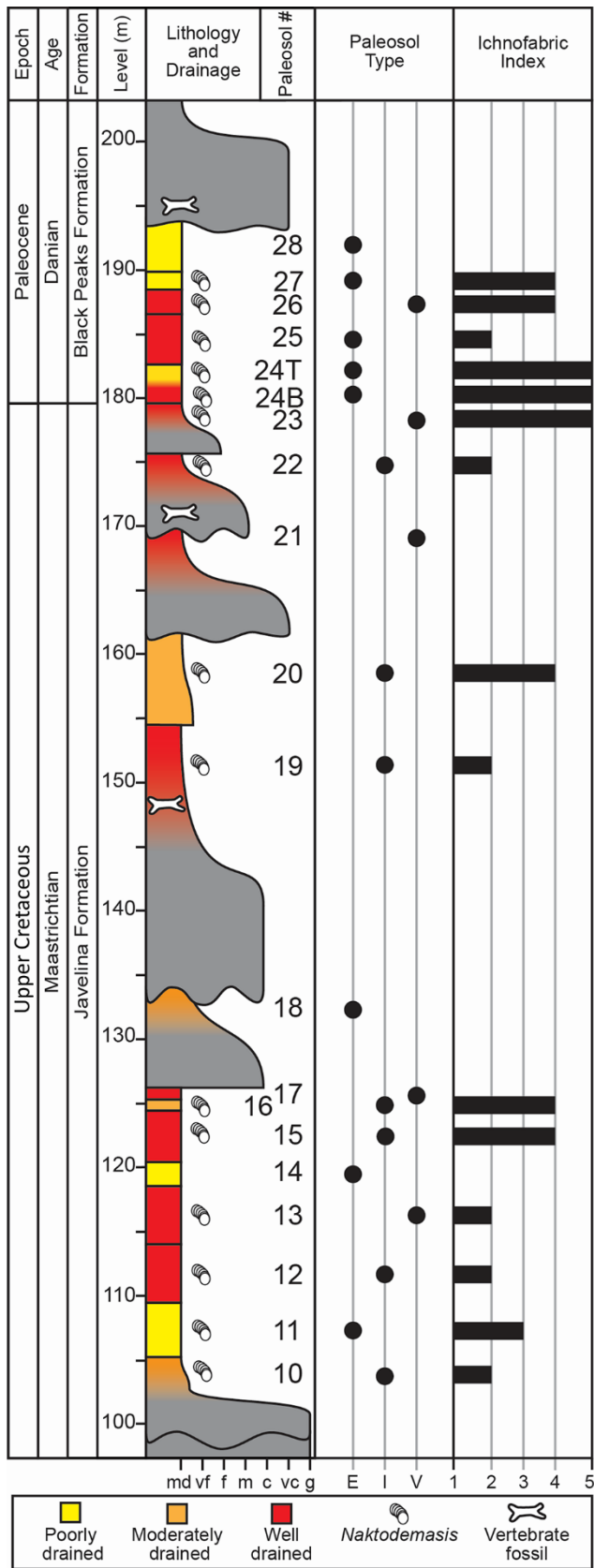


Figure 2.2. Dawson Creek stratigraphic section modified from Nordt et al. (2003) and Atchley et al. (2004). Paleosol type E = Entisol; I = Inceptisol; V = Vertisol. See Methods for explanation of ichnofabric index values.

variable in orientation, ranging from vertical to horizontal. True branching was not observed, however, burrows commonly overlap each other in intensely bioturbated intervals and seldom generate what appears to be false branching. *Naktodemasis* were only observed in fine-grained mudrocks, and were not found in lithologies composed of only clay or well-sorted sand (Fig. 2.2).

Naktodemasis size and edaphic controls

In total, 808 inner diameters of *Naktodemasis* (D_N) were measured from 15 paleosols distributed over approximately 85 m of stratigraphic section (Fig. 2.4). Summary statistics for D_N are presented in Table 2.1; all measured D_N and associated paleosol characteristics are reported in Wiest et al. (2018) A1. Where possible, a minimum of 35 measurements of D_N was acquired for each paleosol.

The abundance of D_N in each paleosol was characterized using ichnofabric index (Droser and Bottjer 1986). Whereas differences were observed between ichnofabric index (ii) categories, D_N decreases in a non-sequential order of ii = 4, 2, 5, and 3. Ichnofabric index values are not homogeneous across categories of stratigraphic age (K vs. Pg), drainage, soil order, or paleosol number (chi-square, $p < 0.001$ for each). Drainage conditions are a significant predictor of ichnofabric index, with more well-drained paleosols tending to have a larger ichnofabric index value (Fig. 2.2). The distribution of ichnofabric index values varies across the measured section - the base of the section generally has lower ichnofabric index values on average, and a series of high ii values (5) were observed only in P23 and P24 (Fig. 2.2). Regardless of this, the number of

measured D_N per paleosol is not correlated with mean (F-test, $p = 0.56$) or median ($p = 0.63$) D_N .

Poorly-drained paleosols contain D_N significantly different than both moderately drained and well-drained paleosols ($p < 0.01$ for both), whereas there is no significant difference in D_N between moderately and well-drained paleosols ($p = 0.8$). Tukey's HSD run post-hoc demonstrates that D_N within poorly drained paleosols is smaller than those occurring in moderately and well-drained paleosols ($p < 0.05$ for both).

Finally, D_N is significantly different in Entisols compared to both Inceptisols ($p < 0.001$) and Vertisols ($p < 0.01$). Tukey's HSD indicates that D_N is smaller in Entisols than in Inceptisols ($p < 0.001$) and Vertisols ($p < 0.05$).

Table 2.1. Summary statistics for *Naktodemasis* diameter

	Min	Mean	Max	SD	n
<i>Age interval</i>					
K	2.8	7.3	15.0	2.7	425
Pg	2.4	6.6	13.8	2.3	383
<i>Drainage category</i>					
Poor	2.8	6.4	13.8	2.4	177
Moderate	2.9	7.1	15.0	2.5	218
Well	2.4	7.1	14.6	2.6	413
<i>Paleosol type</i>					
Entisol	2.4	6.5	13.8	2.4	277
Inceptisol	2.9	7.2	15.0	2.7	361
Vertisol	2.8	7.1	14.0	2.4	170

Note: Dimension values are in mm.

The population of *Naktodemasis* from the interval below P22, which is known to be of Cretaceous age, contains D_N significantly different than those above the highest known Cretaceous vertebrate fossil (P22 and above; $p < 0.001$), regardless of paleosol

type or drainage. Tukey's HSD run post-hoc indicates that the population above the Cretaceous taxa have smaller D_N than those within the Cretaceous interval ($p < 0.001$).

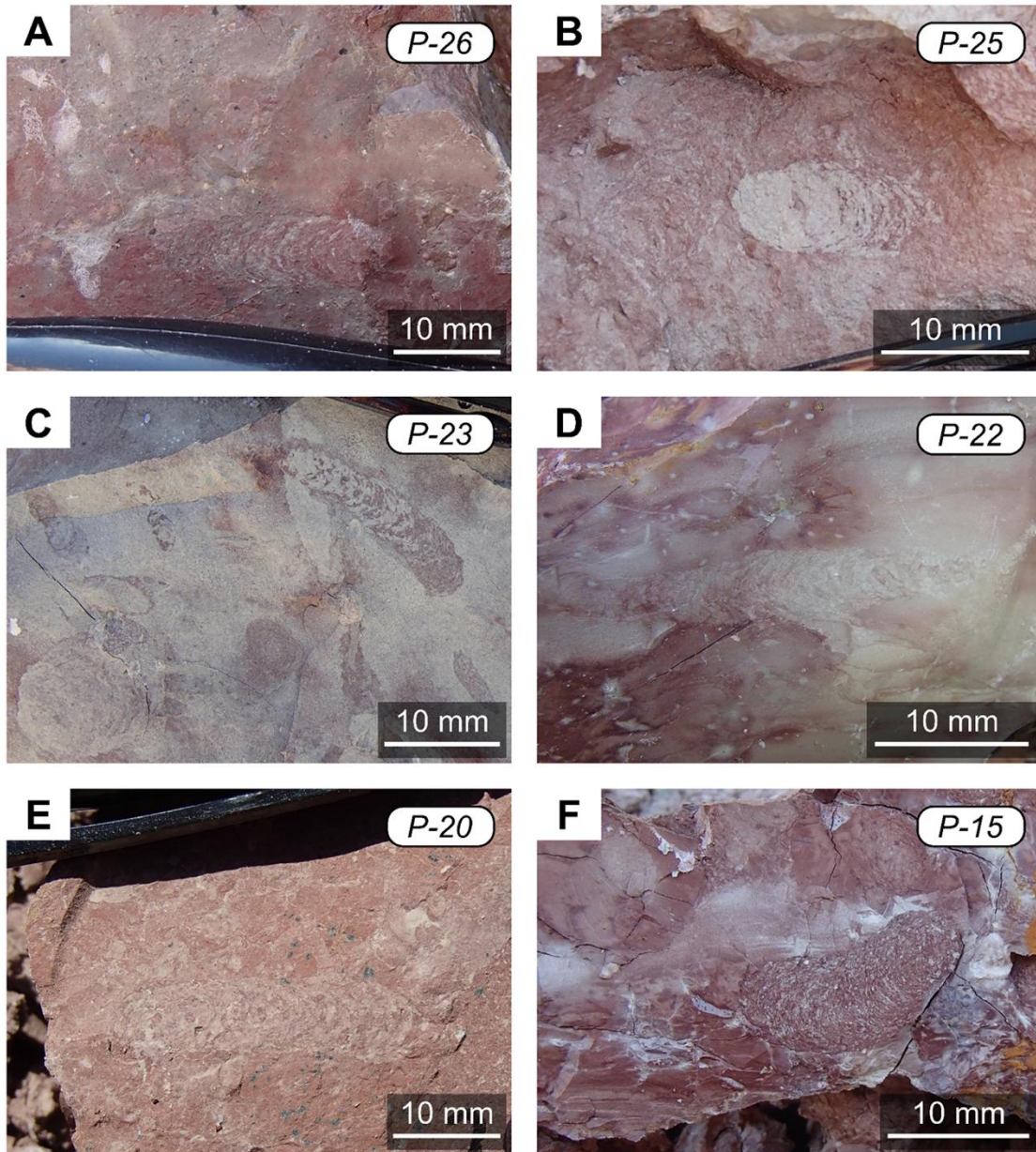


Figure 2.3. *Naktodemasis* in pedogenically modified overbank deposits from the Dawson Creek K-Pg section; A) horizontal burrow in P26; B) two burrows with differing contrast to P25 host matrix; C) multiple backfilled traces in P23; D) single tunnel from P22; E) several traces ranging in diameter in an unoriented ped from P20; F) multiple traces displaying various contrast to P15.

Discussion

Ethology of the tracemakers

The *Naktodemasis* structures were likely produced by cicada nymphs or beetle larvae, based on comparison with structures generated in modern soils and laboratory experiments (Smith and Hasiotis 2008; Smith et al. 2008; Counts and Hasiotis 2009). Body fossils of cicadas (Cicadoidea) and beetles (Coleoptera) have been recovered from as early as the Triassic (Lefebvre et al. 1998; Rasnitsyn and Quicke 2002; Grimaldi and Engel 2005). The subterranean nymphs and larvae of certain species of cicadas and beetles, respectively, burrow through the soil to feed on the xylem sap of plant roots, living plant roots, and disseminated soil organic matter (White and Strehl 1978; Tashiro 1987). Smith and Hasiotis (2008) and Counts and Hasiotis (2009) demonstrated through laboratory experiments that *Naktodemasis* were generated as an open, elongate or ovoid cell that was continuously moved forward as the tracemaker repeatedly removed material from the front of the cell, rotated to transport the sediment, and packed the material in the back of the cell.

Mechanisms for reduced body size of soil-dwelling fauna

Trends in D_N , similar to the results reported herein, have been previously documented across the Paleocene-Eocene Thermal Maximum (PETM) in paleosols similar to those within the Dawson Creek section from Big Bend National Park - the reduction in trace-fossil size generated by soil-dwelling insects was attributed to 1) drier floodplain conditions (lower soil moisture), 2) higher surface temperatures, or 3)

vegetation (food source) with diminished nutritional value (see Smith et al. 2009 and references therein).

Whereas drier soil conditions have been correlated with smaller D_N across the PETM interval and in some species of extant dung beetles (Vessby 2001), a reduction in soil moisture is an improbable forcing mechanism for the K-Pg trend observed in Big Bend for multiple reasons. First, as mentioned previously, larger D_N were observed in well-drained paleosols compared to poorly drained conditions (Table 2.1). Second, soil drainage appears not to systematically change from the Upper Cretaceous through the lower Paleocene (Atchley et al. 2004). Finally, paleosols in the Dawson Creek section generally have deeper carbonate horizons and less weatherable base oxides up-section, suggesting that the climate gradually became wetter in the early Paleocene, but not coincident with the proposed extinction interval between P21 and P22 (Lehman 1990, Nordt et al. 2011). These observations indicate that edaphic and climatic variables are not dominant factors in the dramatic and persistent decrease in D_N that begins in P22.

The Late Maastrichtian Event (LME), which is a transient episode of increased atmospheric CO_2 and surface temperature just below the K-Pg boundary, has been previously identified at this same outcrop succession based on paleosol proxies (Nordt et al. 2003). The CO_2 and warming spike was observed in P19 (Fig. 2.2; Nordt et al., 2003). P19 also contains abundant *Naktodemasis* therefore presents an opportunity to assess the correlation between $p\text{CO}_2$, increased surface temperatures, and D_N (Fajer et al. 1989; Atkinson 1994; Sibly and Atkinson 1994; Parmesan 2006). Surprisingly, we found no evidence of a change in D_N over the interval of elevated $p\text{CO}_2$ and temperature reported in Nordt et al. (2003). Moving forward on the assumption that active pedogenesis of P19

occurred during a time of intensified greenhouse conditions, and that P23-P28 were developed during a relatively cooler period (Nordt et al., 2003, their Fig. 3), it is improbable that increased temperature is a driving mechanism for the negative response in D_N for this dataset.

The biogeochemistry of paleosols throughout the Dawson Creek section was reconstructed by Nordt et al. (2011), which provided results pertinent to our study. First, there is no observed change in overall soil quality or biogeochemical function in the paleosols across our study interval. The paleosols were generally nutrient-rich, had relatively high-water holding capacity, and ranged from circumneutral to alkaline pH. Accordingly, no evidence exists for aluminum or sodium toxicity, which can occur at extreme low and high pH, respectively, and limit nutrient availability in soils (Delhaize and Ryan 1995; Beyrouthy et al. 2000; Qadir and Schubert 2002). Taken together, there were no systematic changes in possible edaphic controls for the habitability of the paleosols in the section, therefore, forcing mechanisms external to the substrate must account for the observed overall up-section reduction in D_N .

Plant tissue forms the base of the soil food web, and alterations in diet quality and/or plant type affects physiological determinants of herbivorous-insect body size (Frajer et al. 1989; Young et al. 1998; Davidowitz et al. 2004; Smith et al. 2009). Thus, a shift in plant ecology and/or reduction of detrital-plant nutritional value between the Cretaceous and Paleocene could have been a primary driving mechanism for the Lilliput effect in soil-dwelling organisms. There was a major, abrupt extinction of Cretaceous plant taxa across the K-Pg boundary, which caused significant changes in plant communities globally (e.g. Vadja and Bercovici 2012; Nichols and Johnson 2008). While

there is no fossil plant record from the Big Bend area, records from across North America, including from the geographically proximate Raton Basin, document a 30 to >50% extinction of plant taxa at the K-Pg boundary followed by a short-lived interval dominated by fern taxa (the “fern spike”) and then a prolonged recovery dominated by angiosperms (Vadja and Bercovici 2014, and references therein). When compared to their Cretaceous counterparts, Paleocene floras were lower in diversity and were dominated by a few species that were geographically widespread (e.g. Wing et al. 1995; Wilf and Johnson 2004; Peppe 2010). Given that this pattern has been observed across North America, it is very likely that the Big Bend region experienced a similar extinction of plants and plant community response across the K-Pg boundary. Therefore, we interpret the observed reduction in D_N at Dawson Creek to have occurred contemporaneously with the plant extinction at the K-Pg boundary. In addition to a significant extinction of Cretaceous taxa, there is evidence for a shift in plant ecology across the boundary. A study of fossil leaves from the Williston Basin in North Dakota documents the selective extinction of slow-growing evergreen plant species across the K-Pg boundary, which suggests a fundamental shift in plant ecological strategies towards taxa that favored fast growth strategies with minimized high carbon assimilation rates and low carbon investment (Blonder et al. 2014). Generally, leaves of plants with fast growth strategies are associated with high amounts of insect damage because they are thinner and have higher nutrient content making them more palatable to insect herbivores (e.g. Coley and Barone, 1996; Wilf 1998; Royer et al. 2007; Currano et al. 2008). The combination of a major plant extinction and a shift in plant ecological strategies across the K-Pg boundary would have caused fundamental alterations in the diet of the *Naktodemasis* tracemakers.

Thus, we hypothesize that the dramatic plant-community shifts that occurred at the K-Pg boundary were an important forcing mechanism for the observed Lilliput effect in subterranean insects.

The Lilliput effect in D_N documented across the K-Pg boundary could reflect either a reduction in organism body size (phyletic dwarfism) or the replacement of larger-bodied clades with smaller-bodied forms or species that generate morphologically identical structures. Though the insect fossil record is relatively limited, insect damage on fossil leaves is a proxy for insect herbivory, and in turn insect diversity; and therefore, can be used to assess changes in insect diversity and compositional heterogeneity (Carvalho et al., 2014). Analyses of insect damage on Cretaceous and Paleocene floras from the Western Interior of the United States have documented a significant change in insect herbivory, and by extension in insect communities across the K-Pg boundary (e.g., Labandeira et al., 2016 and references therein). In particular, detailed studies of insect damage across the K-Pg boundary in the Williston Basin in North Dakota document a substantial decrease in insect herbivory, a significant decline in intermediate and specialized leaf mines, and a major extinction of leaf-mining insect species at the K-Pg boundary, as well as a significantly unbalanced plant-insect food web in the early Paleocene (Labandeira et al. 2002a, b; Wilf et al. 2006; Donovan et al. 2014). This major insect extinction and community change has been hypothesized as a cascading response to the extinctions of Cretaceous host plant species (Labandeira et al. 2002a). Based on these records from North America, it seems reasonable that there was also a significant extinction of insects across the K-Pg boundary in the Big Bend region. Therefore, it is possible that the reduction in body size we document in our trace fossil analyses could be

a reflection of an extinction of larger-bodied tracemakers and/or a change in the insect community structure and composition.

Stratigraphic position of the K-Pg boundary within the Dawson Creek section

There is currently no definitive age control on P22-P28, except that this conformable succession of stacked paleosols occurs between Maastrichtian fauna (~172 m; Fig. 2.2) and early Paleocene fauna (~195 m; Lawson 1972, 1975; Lehman 1985; 1990; Standhardt 1986; Schiebout et al. 1987). It is possible that the K-Pg boundary occurs at the unconformity surface immediately superjacent to P28. If this is the case, this entire dataset and interpreted environmental disturbance would have occurred prior to the K-Pg event sometime within chron 29r. However, this interpretation is very unlikely based on the reversed polarity of the sequence, the occurrence of the Late Maastrichtian Event (LME) in P19, and sedimentation-rate calculations based on magnetostratigraphy and pedogenesis (Nordt et al. 2003; Leslie et al. in press). Therefore, we proceed with the existing rationales that suggest the chronostratigraphic K-Pg boundary is at or near P23 (Fig. 2.2; e.g., Lehman 1990; Nordt et al. 2003; Atchley et al. 2004; Lehman and Busby 2007; Cobb 2016; Leslie et al. in press).

Trace-fossil analysis has been previously demonstrated as an effective tool for refining the sedimentological history and stratigraphic relationships at other K-Pg exposures (Ekdale and Bromley 1984; Savrda 1993; Ekdale and Stinnesbeck 1998; Twitchett and Barras 2004; Rodríguez-Tovar et al. 2004; 2010; Rodríguez-Tovar 2005; Chin et al. 2013; Sosa-Montes De Oca et al. 2013; 2016; Horner et al. 2016). Thus, in the absence of diagnostic K-Pg boundary indicators, we propose that the trace fossil dataset

herein can be used to refine the stratigraphic position of the K-Pg event in the Dawson Creek section. Our ichnological proxy indicates a significant reduction in tracemaker body size in P22, which is similar to patterns seen across other K-Pg boundary sections in North America and Europe (e.g., Wiest et al. 2015; 2016; Łaska et al. 2017). Based on these results, we interpret the trace fossils within P22 to represent a post-event recovery community, stratigraphically above the K-Pg transition. This implies that the chronostratigraphic boundary is associated with the channel-sand body containing reworked pterosaur remains just below P22 (~172 m; Fig. 2.2; Lehman 1990). Thus, we posit that the apparent absence of extraterrestrial-impact indicators at this site (e.g., Lehman, 1990) is potentially attributed to widespread erosion that occurred contemporaneous with or shortly after the K-Pg event. Current and ongoing advancements in absolute dating of sandstones may permit further testing of this hypothesized placement of the stratigraphic K-Pg boundary in the future.

Is there a common forcing mechanism?

Each of the studies that have documented the Lilliput effect across the K-Pg boundary thus far have provided rationale for marine-environmental mechanisms that could have potentially driven the phenomenon for that particular type of taxon. It has been demonstrated that planktic foraminifera can experience the Lilliput effect from a diverse range of stressors including greenhouse warming, anoxia/dysoxia, restricted basins, and volcanism (Keller 2003; Keller and Abramovich 2009). The dwarfism of some coccolithophore species during the earliest Paleocene is attributed to unfavorable environmental conditions such as anomalous fluctuations in primary productivity and

poor stratification of surface waters (Gardin and Monechi 1998). Aberhan et al. (2007) found that the most likely explanation for a reduction in body size within mollusk-dominated benthic shelf ecosystems is a reduction in nutrient availability associated with the decline in primary production. Likewise, dwarfism of marine vermiform organisms has also been attributed to limited food supply associated with a collapse of the food web in the latter stages of the extinction event (Hsü and McKenzie 1985; Hansen et al. 1993; Łaska et al. 2017). The reduction of body size of infaunal crustaceans from diverse, widespread shallow-marine environments is most likely attributed to either a decrease in oxygen availability following the extinction event (Savrda et al. 1984; Ekdale 1985; Savrda and Bottjer 1987a, 1987b; Wiest et al. 2015), a restricted nutrient supply, or a combination of these factors (Łaska et al. 2017; Wiest et al. 2016). In addition to bony fish, lamniform sharks, which were apex marine predators across the K-Pg transition, also experienced the Lilliput effect (Belben et al. 2017). This phenomenon, as evidenced by quantitative shark-tooth morphometrics, is attributed to taxonomic turnover, as well as major shifts in ecological function, such as changes in the available prey and/or dietary preference of the sharks (Belben et al. 2017).

Conclusions

In the aftermath of the Cretaceous-Paleogene mass extinction event, the Lilliput effect occurred across many trophic levels and ecosystems, including both marine and terrestrial environments. There does not appear to be an unambiguous, all-encompassing explanation to account for this widespread phenomenon, but it does seem to be a universal response to different components of a complex, interrelated disruption of the food web. The driving mechanism for the reported decrease in the body size of

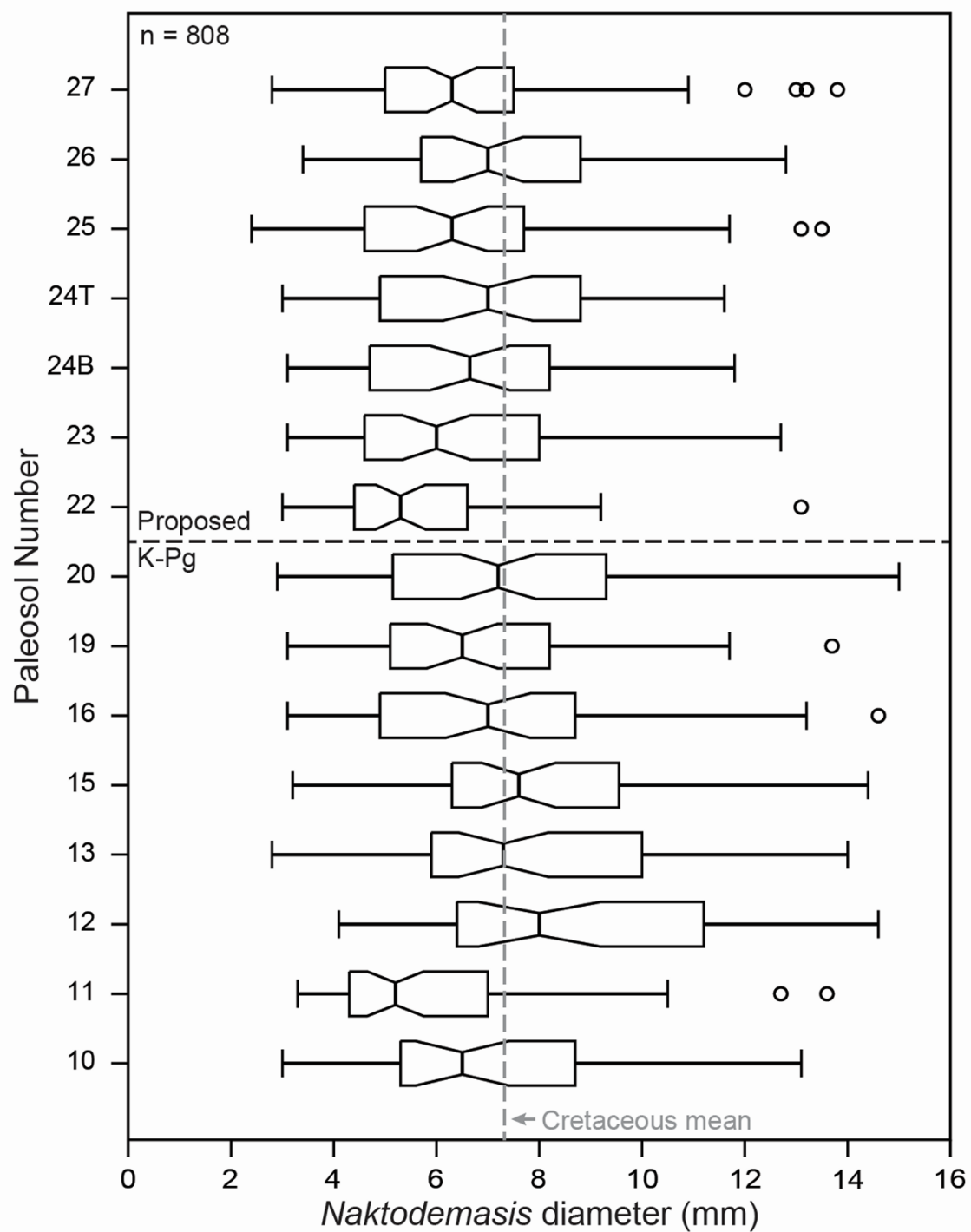


Figure 2.4. Notched-box plots of *Naktodemasis* diameter (D_N) from the Dawson Creek K-Pg section. Notches on the boxes represent the 95% confidence interval for the mean. See section 5.1 for discussion on K-Pg boundary position.

herbivorous, subterranean insects is probably the abrupt shifts that occurred in plant ecology. Future studies should focus on extending such datasets from diverse ecosystems and depositional environments, particularly within the continental realm, in order to better understand the spatial, temporal, and ecological extent of this phenomenon as it relates to the K-Pg mass extinction.

Acknowledgments

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CHAPTER THREE

The Waco Mammoth National Monument May Represent a Diminished Watering-Hole Scenario Based on Preliminary Evidence of Post-Mortem Scavenging

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Abstract

The Waco Mammoth National Monument (WMNM) potentially represents the only recovered Columbian mammoth (*Mammuthus columbi*) herd to date, but the “herd” interpretation is dependent on the demographics of the accumulation as well as a catastrophic kill mechanism. The demographics are consistent with an extant elephant herd that is lacking only infants, and the generally accepted cause of death is a catastrophic flood and rapid burial based primarily on fossil articulation and associations with an ancient river channel and aquatic fauna. Herein we present new ichnological evidence of post-mortem biogenic bone modification contrary to a flood scenario with rapid burial. Traces on bone include branching furrows (*Corrosichnia* type), paired grooves (*Machichnus regularis* and *M. bohemicus*), arcuate grooves that penetrate the cortical material (*Brutalichnus brutalis*), roughly triangular punctures with jagged margins (*Nihilichnus nihilicus*), and hemispherical borings (*Cubiculum isp.*). The branching furrows are interpreted as root-dissolution features, whereas the remaining suite of traces demonstrate scavenging of the mammoths by rodents, carnivores, and hide beetles during a period of dry-decay and prolonged subaerial exposure. We propose that a drought scenario is a more plausible kill mechanism for this particular assemblage

because: (1) a diminishing watering hole concentrating the local fauna explains the high taxonomic diversity; (2) migration to a distant water source explains the absence of *M. columbi* calves; and (3) a drought provides a parsimonious explanation for the site history in light of new observations regarding vertebrate and invertebrate scavenging. Under this scenario, the mammoths of WMNM represent at least one social group that perished during an anomalously dry season.

Introduction

The Waco Mammoth National Monument (WMNM) is a fossil assemblage in central Texas (Fig. 3.1) that has thus far produced 25 Columbian mammoths, as well as a western camel, a saber-toothed cat, a dwarf pronghorn, a bison, a horse, a peccary, an American alligator, an unidentified species of tortoise, several genera of freshwater turtles, freshwater drum, and gar. If the collection of mammoths represents a herd, and not an attritional accumulation, the WMNM would constitute the only recovered Columbian mammoth (*Mammuthus columbi*) social group to date, and further inferences could be made regarding the social hierarchy, behavior, and size of a *M. columbi* matriarchal herd.

Previous work has indicated that the demographics of the recovered-mammoth population are consistent with an extant elephant herd that is lacking only infants (Haynes 1992). Furthermore, a detailed analysis of the alluvial stratigraphy and geochronology has established that at least 16 (perhaps up to 22) of the mammoths perished in a single catastrophic event on a sandy point-bar environment at the confluence of two rivers (dated to 66.8 ± 5.0 ka; Nordt et al. 2015). There are two, prominent fossiliferous bedding surfaces identified at WMNM (stratigraphically

separated by approximately 1.0 m; Fig. 3.1D) with the majority of mammoths (at least 16) occurring on the lower level (L1). Relatively fewer mammoths, including the only recovered bull mammoth, are on the upper level (L2). The generally accepted cause of death for the L1 assemblage is a catastrophic flood and rapid burial, which is primarily based on the association with the ancient river channel, aquatic fauna within the assemblage, and a high degree of articulation of the specimens (Naryshkin 1981; Bongino 2007; Nordt et al. 2015). The L2 assemblage is thought to be the result of a similar event(s) at a later time (Nordt et al. 2015).

The aim of this study is to utilize an ichnological perspective to investigate the post-mortem biogenic bone modification in order to shed light on pre- and post-burial taphonomic processes and constraints (Bromley 1996; Buatois and Mángano 2011). Herein we present new findings of bioerosive trace fossils on the mammoth bones that are indicative of several types of scavenging, which demonstrate dry-decay and prolonged subaerial exposure prior to burial and have direct implications for reinterpreting the history of the site.

Background

Geologic Setting and Alluvial Stratigraphy

WMNM is located in Waco, Texas (31°36'N, 97°11'W), within the interfluvium of the Brazos and Bosque Rivers ~2.5 km NW of the present confluence (Fig. 3.1C; Fox et al. 1992). The bedrock in this region is largely late Mesozoic sedimentary strata that dip gently toward the southeast (Barnes 1979). The bedrock subjacent to the site is Cretaceous Austin Chalk (Nordt et al. 2015). Pleistocene deposits in this region are composed of alluvium from rivers and streams draining southeast into the Gulf of Mexico

(Fig. 3.1C). Sediments from the Brazos River drainage tend to be relatively siliceous, whereas the alluvium at the WMNM is compositionally similar to the silicate-poor Bosque River deposits (Bongino 2007).

Quaternary alluvial deposits around the locality are in the form of a modern floodplain and three alluvial terraces - Terrace 1 (T1) is the lowest and youngest, whereas T3 is the highest and oldest (Bongino 2007). Fossils at WMNM are confined to T2. The absolute ages of T1 and T3 have not been determined, but optically stimulated luminescence (OSL) dating of the fossil-bearing T2 sediments demonstrates that deposition occurred during the Marine Oxygen Isotope Stage 4 (MIS4) glacial stage (Nordt et al. 2015). Isotopic analysis of organic carbon and paleosols at the site suggest a generally cool and wet past environment (Bongino 2007; Meyer et al. 2013; Nordt et al. 2015). Whereas the regional record demonstrates wet conditions, global proxies suggest MIS4 was a period of increased aridity (Jouzel et al. 1993).

The fossils discovered thus far are in a NNE-SSW oriented paleochannel. The channel likely represents a low-order tributary flowing southward into the ancient Bosque River (Bongino 2007). The L1 mammoths recovered from the southern portion of the site rest directly on a coarse river gravel, whereas those from the northern end of the site rest on a buried Bk horizon, which represents an eroded soil (Smithson paleosol; Fig. 3.1D; Nordt et al. 2015). The Smithson paleosol has Fe/Mn concentrations that indicate alternating wet/dry cycles, illuviated clays indicative of good drainage, and abundant pedogenic calcite resulting from periods of aridity (Bongino, 2007). The L2 assemblage is approximately 1 m above L1 with no discernable unconformities in between (Fig. 3.1D). L2 was eventually covered by 2-3 m of clay loam that has served as the parent

material for the modern Sunev soil, a fine-loamy, carbonatic, thermic Udic Calciustoll (Bongino 2007; Nordt et al. 2015). The carbonatic system of the Sunev soil and Smithsonian paleosol aided in the preservation of the fossils by providing an alkali environment.

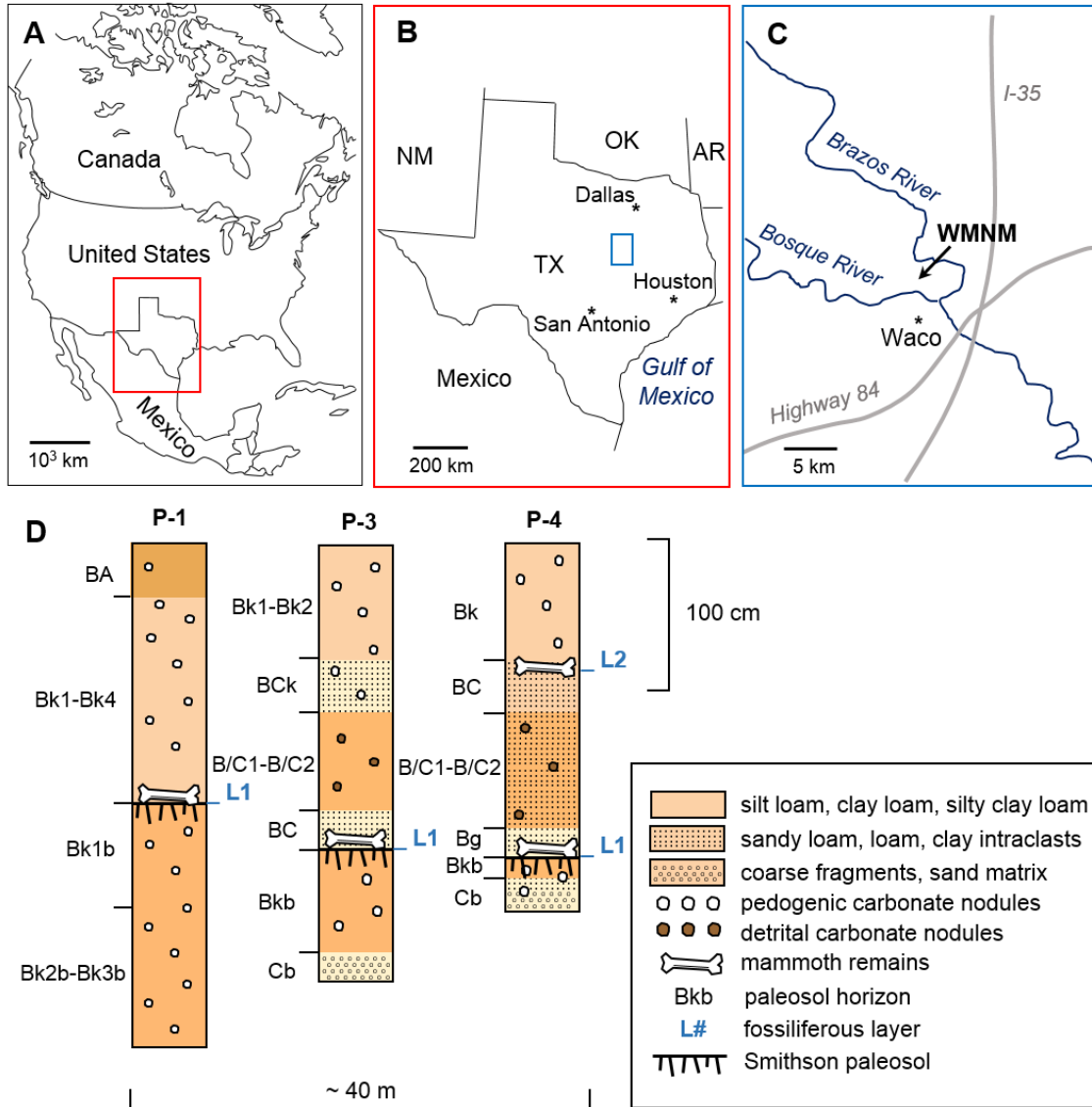


Figure 3.1. Site location map. **A**) Position of Texas on the North American continent. Red box indicates area depicted in Fig. 3.1B. **B**) Position of Fig. 3.1C (blue box) relative to major cities in Texas (TX). NM = New Mexico; OK = Oklahoma; AR = Arkansas. **C**) WMNM location. **D**) Paleosol profiles at WMNM modified from Nordt et al. (2015).

Fossil Distribution

Nearly all of the WMNM mammoths are articulated to semi-articulated skeletons, although most are missing tails and foot elements (e.g., phalanges, carpals, tarsals). Early descriptions of the site describe the L1 assemblage as being in a ‘defensive circle’ with the younger mammoths at the center - this observation was treated as evidence that the animals were killed and immediately buried where they stood (Fox et al. 1992). The 15 mammoths uncovered prior to 1992 give the impression of a defensive circle, but additional excavations have not supported this interpretation, nor does the orientation of the fossils appear to have been influenced by preferential flow (see bonebed maps in Naryshkin 1981).

The majority of the non-mammoth taxa recovered at WMNM are known only from disarticulated elements, with the exception of the complete camel in L1. The aquatic fauna (i.e., alligator, turtle, and fish) are attributed to L1, whereas the tortoise is assigned to L2. The horse and bison were recovered from float before the L2 excavation began. The saber-toothed cat canine was seemingly recovered from L2, but the stratigraphic position of the incisor is not documented clearly.

The bone deposits excavated and mapped so far cover a roughly rectangular area extending NNE-SSW ~26 m, and WNW-ESE ~10 m (Bongino 2007; Nordt et al. 2015). During the construction of the present dig shelter, mammoth material was found around the perimeter of the 24 m by 37 m building, and probable bone fragments were extracted from a drill core ~20 meters N of the excavation boundary (Nordt et al. 2015), therefore it seems likely that the area excavated to date represents only a portion of the entire bonebed.

Materials and Methods

Bioerosion trace fossils, which are biogenic structures that cut or destroy hard osseous tissue structures (Pirrone et al. 2014a), on archived and *in situ* bones were examined and imaged under low-angle, polarized-LED illumination at the Baylor University-Mayborn Museum Complex (BU-MMC) in Waco, Texas and at the WMNM, respectively. High-magnification images were obtained with the extended depth of field (EDOF) setting on a Dino-Lite Edge digital microscope (AM7915 Series).

Comparative invertebrate traces were generated by providing recently deceased wild-hog heads (*Sus scrofa*) to a captive hide-beetle colony (*Dermestes maculatus*) in an enclosure that isolated the colony from other necrophagous insects. The specimens were left in the enclosure until all the non-osseous tissue was consumed, and the resulting biogenic structures on the skulls were likewise examined and photographed under low-angle, polarized light.

From the collections at the Mayborn Museum, specimens labeled 1-BU-MMC through 272-BU-MMC have a previously established provenance, whereas label designations ≥ 273 -BU-MMC cannot be definitively attributed to L1 or L2. Specimens at WMNM (see mammoth letter designations) are exposed *in situ*, therefore can be confidently attributed to L1 or L2. The methodology used in describing and naming the bioerosion structures follows the proposed ichnotaxobases of Pirrone et al. (2014a) and nomenclature of Mikuláš (1999) and Mikuláš et al. (2006).

Results

Ichnology

Recurrent morphotypes of bioerosion trace fossils from WMNM mammoths include: (1) sinuous furrows with simultaneous-type branching; (2) paired grooves; (3) arcuate grooves that penetrate the cortical material; (4) roughly triangular holes (punctures) with jagged margins; and (5) hemispherical borings.

Branching Furrows.-

Branching furrows with an arcuate cross-section are the most common bioerosive element on the WMNM assemblage (*Corrosichnia* type; Mikuláš 1999). The furrows are smooth-walled and range from sub-mm to several mm wide and up to several cm in length (Fig. 3.2). The morphology of the furrows is generally sinuous and irregular with simultaneous-type branching, meaning the traces consist of a network of passages that are/were simultaneously opened (see Bromley and Frey, 1974; D'Alessandro and Bromley, 1987). This bioerosive structure is present on cortical and cancellous material, as well as ivory, in both L1 and L2. The L2 assemblage has a much higher density of this type of trace relative to the fossils in L1. In the few instances that the stratigraphic upper and lower sides of the fossils can be determined and simultaneously examined, branching furrows are more abundant on the top surface relative to the underside, although such structures are not absent on the stratigraphic bottom. In rare instances modern roots are present in the furrows, but typically they are sediment filled. Fractures are generally not associated with the furrows.

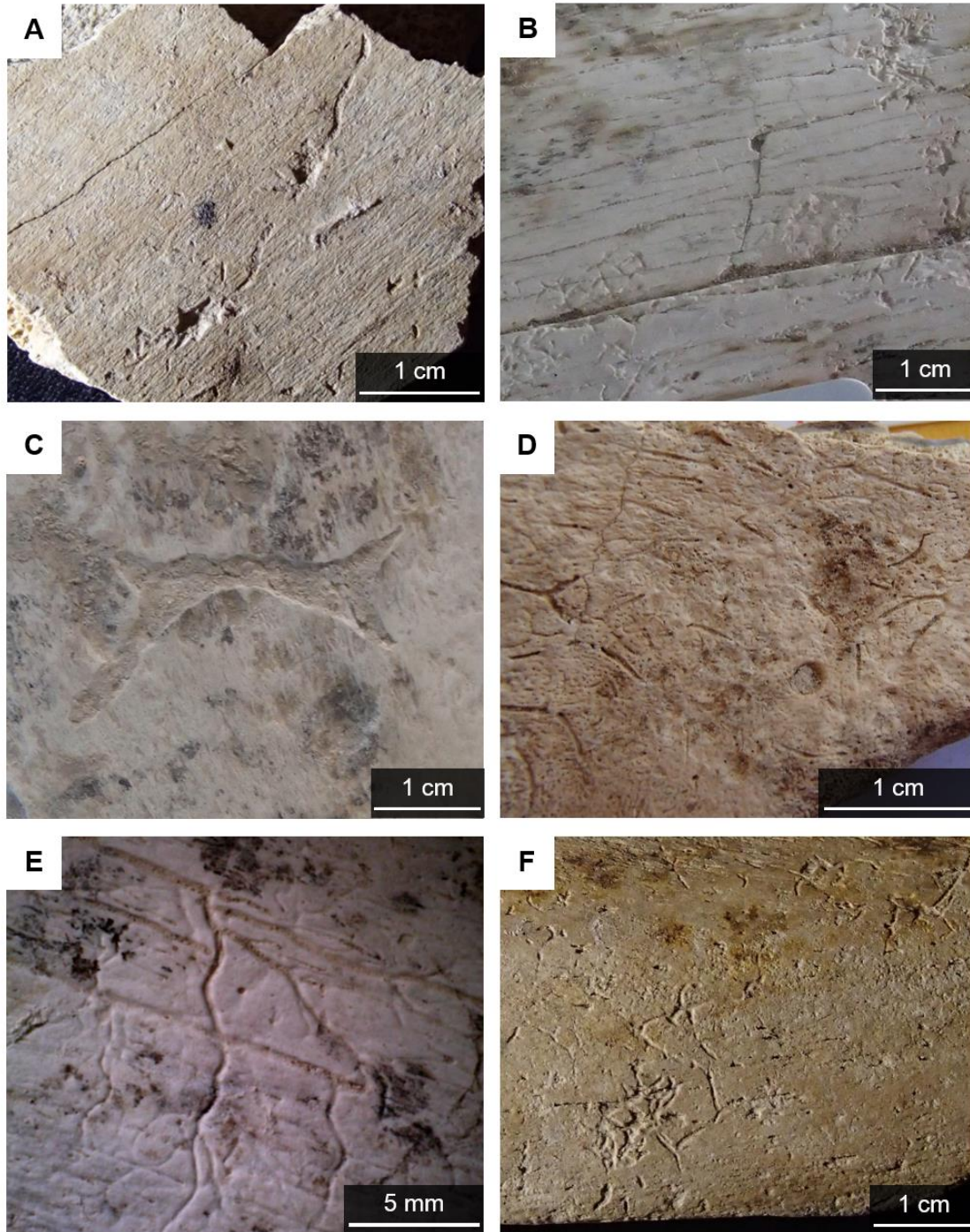


Figure 3.2. *Corrosichnia*-type root traces on various fossil material. **A)** Sinuous root traces on *M. columbi* rib 764b-BU-MMC. **B)** Fine root-dissolution features on ivory tusk of bull mammoth Q. **C)** relatively wide, branching root trace on bull-mammoth Q scapula. **D)** Fine, branching root-dissolution features on disarticulated turtle shell from WMNM. Notice the foramen with smooth margins, which is distinct from the punctures in Fig. 3.6 and bores in Fig. 3.7. **E)** Furrows with dendritic morphology on *M. columbi* fragment 785a-BU-MMC. **F)** Multiple, fine root traces on *M. columbi* rib 27-1/2a-BU-MMC.

Paired Grooves.-

Two distinct size classes of paired grooves occur on individual specimens from both L1 and L2. The larger-size class is composed of parallel to subparallel sets of shallow, thin, grooves (*Machichnus bohemicus*; Mikuláš et al. 2006) that have a center spacing ranging from approximately 3-5 mm. Each individual groove is ~ 1 mm in width (Fig. 3.3). The roughness of the grooves is the result of differential penetration of several layers of cortical lamellae (e.g., Figs. 3.3A, E). The length of the parallel grooves varies from several mm to several cm. Pairs generally occur as an individual set on a single bone, but multiple sets with cross-cutting relationships have been observed (Fig. 3.3B). These traces are most common on the outer portion of ribs with an orientation that is perpendicular to sub-perpendicular to the long axis of the bone. The paired grooves are shallow and do not completely penetrate the cortical bone. These traces can also be observed on the *in situ* camel in L1 (Fig. 3.3F).

The smaller-size class of reoccurring paired grooves are shallow, approximately 1 mm in width with sub-mm center spacing, and range in length from a few mm up to 1.0 cm (*Machichnus regularis*; Mikuláš et al. 2006). The pairs occur as a series of many overlapping sets and are found exclusively on the edges of several different skeletal elements (Fig. 3.4). Paired grooves are oriented perpendicular to sub-perpendicular to the edge of the bone, whereas the lateral series of pairs tend to closely parallel the margin (Fig. 3.4C-E). The grooves are arcuate in cross-section and occur on bone material from L1 and L2, most often on the base of the skeletons near the paleosurface. Bone weathering generally crosscuts these paired grooves (Figs. 3.4C, 3.4D), but rare examples of *Machichnus regularis* are found to have post-dated the bone weathering (Fig. 3.4B).

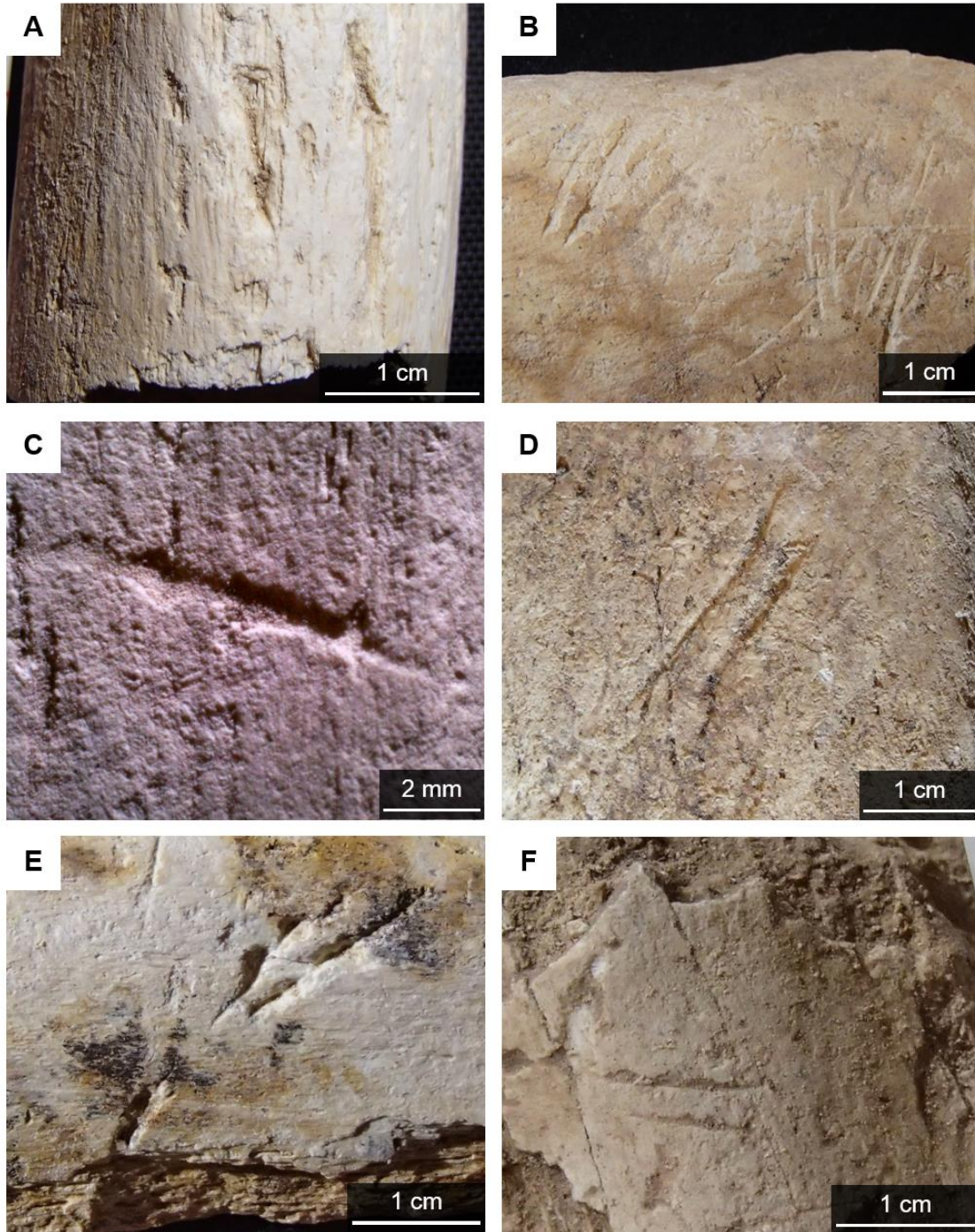


Figure 3.3. *Machichnus bohemicus* on various *M. columbi* skeletal elements (unless otherwise noted). **A)** Several sets of paired grooves on 728a-BU-MMC. **B)** Many, crosscutting paired grooves on rib 755a-BU-MMC. **C)** Close-up image of one groove in a parallel pair on a rib fragment from mammoth M. **D)** Paired grooves on rib 789a-BU-MMC. **E)** Unusually deep, subparallel grooves caused by differential penetration through bone lamellae on rib 764a-BU-MMC. Notice the diagenetic discoloration that crosscuts the trace. **F)** Paired grooves on *in situ* transverse process of camel in L1.

Arcuate Grooves.-

Relatively wide (up to >1 cm), widely spaced, subparallel arcuate grooves are noted on a variety of mammoth skeletal elements. The individual grooves are narrow at the origin and widen as they penetrate deeper through the cortical bone and into the cancellous bone (Fig. 3.5). In one instance, a quasi-symmetrical set of arcuate grooves occurs on the opposite side of the femoral head (Fig. 3.5A). These arcuate grooves are tentatively classified as *Brutalichnus brutalis* based on the morphology and breakage of the cortical bone into the internal part (Mikuláš et al. 2006). These structures occur on fossils from L1 and L2, and > 90% of the *Brutalichnus brutalis* are constrained to the ends of the bones or edges of the bone fragments.

Punctures with Jagged Margins.-

Holes with a roughly triangular/variable geometry and irregular, jagged margins occur on a diversity of bones from L1, L2, and the non-provenance material (Fig. 3.6). These traces are flat bottomed and display broken cortical material that is pushed into the cancellous portion of the bone (*Nihilichnus nihilicus*; Mikuláš et al. 2006). Individual (non-patterned) punctures are most typical, but sets of up to four equidistant indents are observed (Fig. 3.6A). Diameters range from several mm to approximately 8 mm, and depths are typically < 5 mm. Less conspicuous traces, such as isolated grooves/lines, are usually apparent on the same specimens (Fig. 3.6F).

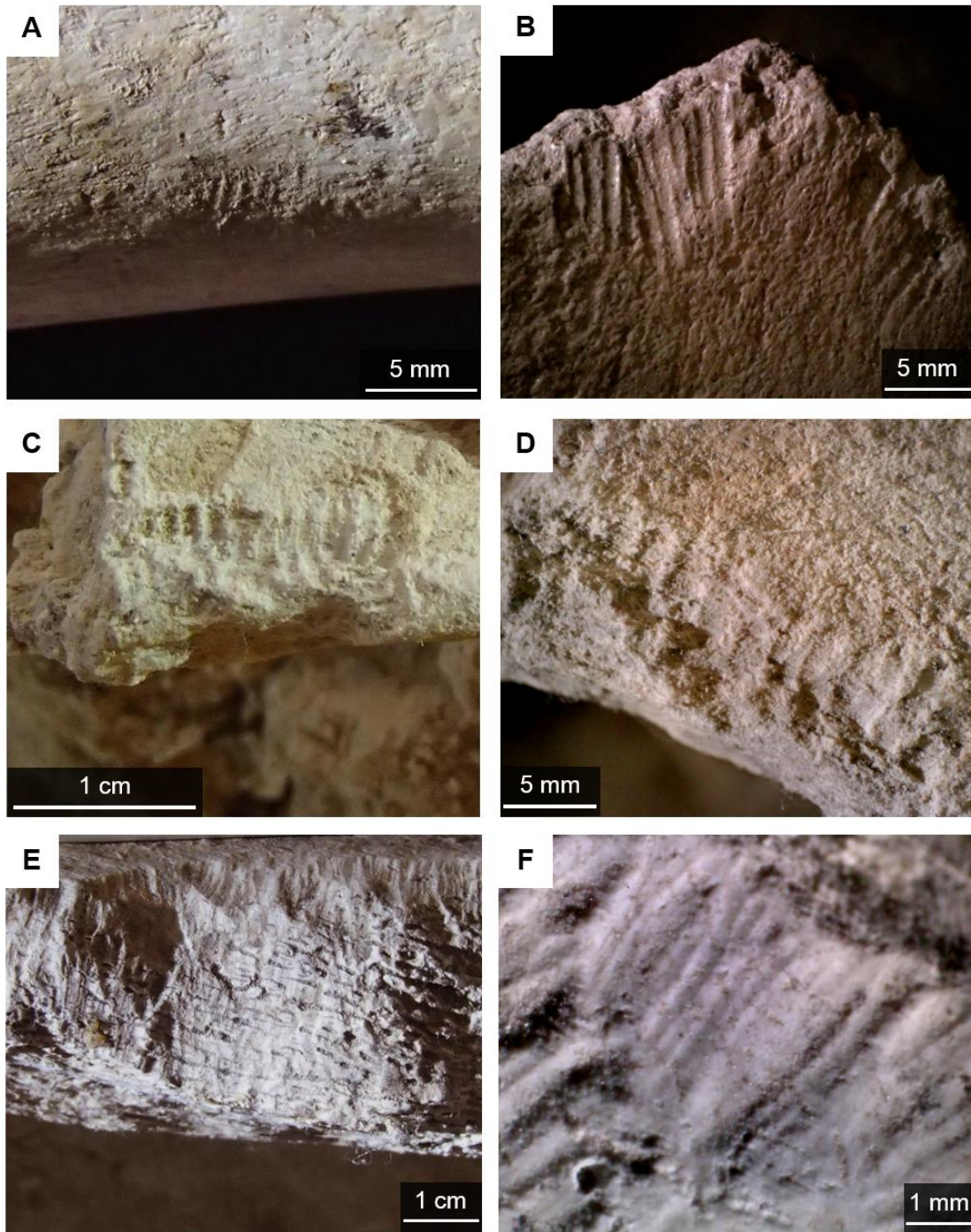


Figure 3.4. *Machichnus regularis* on various skeletal remains of *M. columbi* (unless otherwise noted). **A)** Rodent gnaw marks on rib 764b-BU-MMC. **B)** Rodent traces on mammoth E limb fragment 203a-BU-MMC. **C)** Rasps on vertebra of *in situ* camel. **D)** Rodent gnaw marks on *in situ* neural spine of juvenile mammoth T in L1. **E)** Rodent traces on *in situ* left scapula of bull mammoth (Q) in L2. **F)** Close-up image of the same trace depicted in E.

Hemispherical Borings.-

Shallow bores occur on a variety of skeletal elements from L1 and L2. The diameter of the borings typically range from 2.3 - 5.2 mm (mean = 3.7 mm) with rare (<1%) exceptions nearing 1.0 cm. The depth of the borings is generally less than the diameter, and a hemispherical morphology is most recurring (Fig. 3.7A-E; *Cubiculum isp.*; Roberts et al. 2007; Pirrone et al. 2014b). The majority of bore openings are spherical, but elliptical openings are not exceptional (Fig. 3.7A). Borings generally originate from the surface (cortical) bone and terminate slightly below the cortical material in the cancellous bone, although few bores can be found exclusively in the spongy bone along fracture surfaces (Fig. 3.7E). Bioglyphs are not on the inner walls of the *Cubiculum*. In some instances, intense bone weathering crosscuts the borings (Fig. 3.7D). Through-going or deeply penetrating bores are not observed.

A comparative structure was generated by captive hide beetles (*Dermestes maculatus* DeGeer) on a wild-hog skull (*Sus scrofa*) during consumption of the dried carrion in a controlled setting. The comparative boring has a diameter of 3.5 mm and a hemispherical morphology that terminates in the cancellous bone (Fig. 3.7F).

Taphonomy

Weathering.-

A narrow majority of fossils recovered from both L1 and L2 exhibit cracking parallel to the fiber of the bones, with a mosaic of fractures on articular surfaces (Stage 1 of Behrensmeyer 1978). Many mammoth fossils from L1 and L2 also exhibit flaking of the concentric outer layers of the cortical bone (Stage 2 of Behrensmeyer 1978). Figure

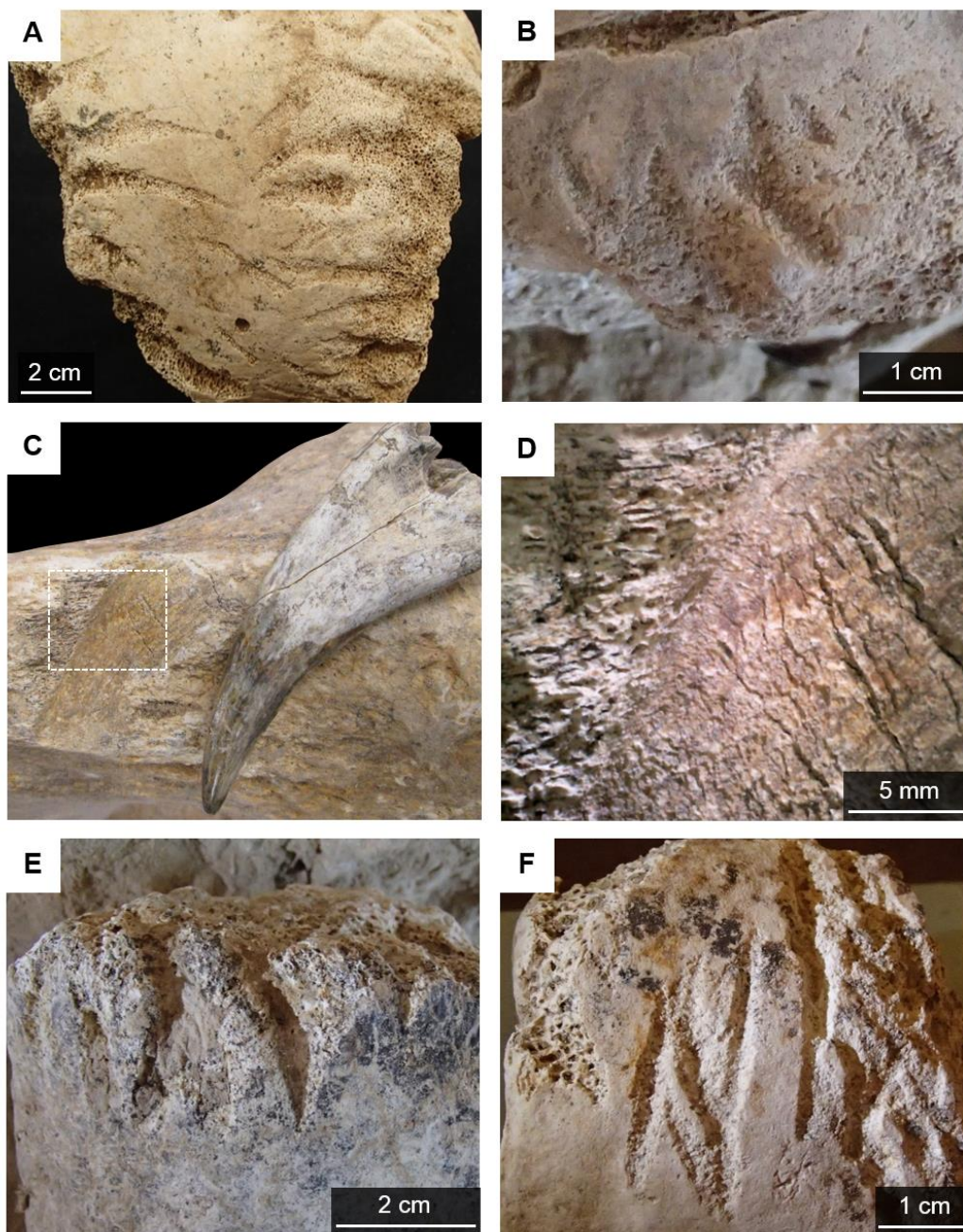


Figure 3.5. *Brutilichnus brutalis* on *M. columbi* skeletal elements. **A)** Arcuate grooves on femoral head 761a-BU-MMC. **B)** Relatively deep, arcuate grooves on mammoth Q *in situ* patella. **C)** Isolated arcuate groove on proximal radius (40-BU-MMC) of mammoth B. Note the similarity in curvature between the arcuate groove and the saber-toothed cat incisor recovered from WMNM. The incisor is 6.4 cm for scale. Also note the faintly colored lines that are parallel to the arc of the groove. Dashed white box highlights the area depicted in Fig. 3.5D. **D)** Close-up image of groove depicting the microfractures within the trace on 40-BU-MMC. Notice how the fractures are all open towards the upper-right corner of the image, indicating the trace was generated from a force moving from the upper right towards the lower left. **E)** *In situ* femur of bull mammoth at WMNM. **F)** Arcuate grooves on mammoth Q phalanx 522-BU-MMC.

3.8A shows concentric flaking cross-cut by diagenetic mineral staining. Stage 3 of the Behrensmeyer (1978) model is achieved when all of the concentrically-layered cortical bone has flaked away resulting in a rough, fibrous texture - intense weathering to this degree is observed on approximately 5% of bones (see Fig. 3.8B for Stage 3 weathering cross-cut by diagenetic mineral staining).

Bone Fractures and Trampling.-

The fossil bones at WMNM are heavily fractured, with only a few small sturdy elements like carpal and tarsal bones left intact. Many of the bones from L1 and L2 have longitudinal fractures (parallel to the grain of the bone) and transverse fractures, which form approximately perpendicular to the grain of the bone. In addition, spiral fractures and stepped spiral fractures are also observed from L1 and L2 material (Fig. 3.8C-E). Many of the spiral fractures have rounded edges and diagenetic mineral staining the crosscuts the eroded edges (Fig. 3.8D). The bull mammoth has a fractured depression on its right scapula that is approximately the size of an adult-mammoth foot (Fig. 3.8F).

Discussion

Ethologic Interpretation of Animal Traces

Machichnus bohemicus. - The relatively widely spaced, paired grooves are interpreted as incidental scrapes inflicted by the sharp, upper canine teeth of a small carnivore (cf. Longrich and Ryan 2010, their Fig. 3.1A). A slight variation of the morphology is depicted in Fig. 3.3E, which may have a different origin although the crosscutting relationship with diagenetic discoloration is evidence against a post-burial tool-mark interpretation. The wide spacing between the individual grooves is not

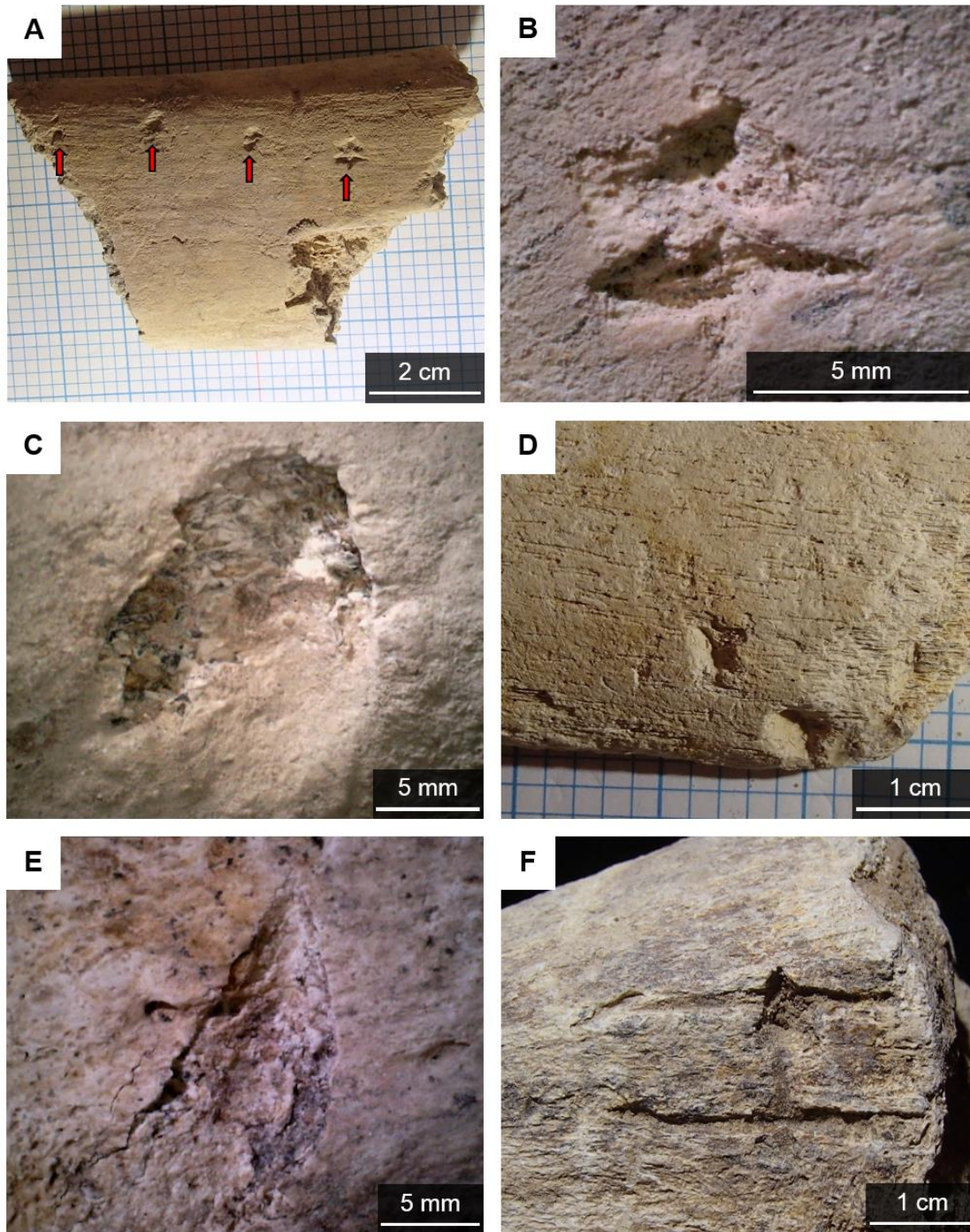


Figure 3.6. *Nihilichnus nihilicus* on various *M. columbi* bones. **A)** Equidistant bite marks on rib 841a-BU-MMC under low-angle illumination. **B)** Close-up image of bite mark depicted in Fig. 3.6A. **C)** Relatively large puncture on radius shaft (40-BU-MMC) of mammoth B. Note the cortical material pressed into the cancellous portion of the bone. **D)** Pair of bite marks on rib 836a-BU-MMC. **E)** Triangular puncture on mammoth C vertebra (95-BU-MMC). **F)** Isolated bite mark crosscutting a pair of parallel grooves on the distal end of long bone 19a-BU-MMC. Notice the right side of the bone, which has been gnawed off.

consistent with rodent anatomy (Haglund 1992; Patel 1994; Pokines 2015), and the generally-isolated occurrence of scrapes on individual bones suggests that the contact was not intentional. These grooves were likely generated as a by-product during consumption of the soft or dried tissue surrounding the bone (Pobiner 2008). In the case of *M. columbi* ribs and long bones, nearly all of the flesh would have been removed prior to the emplacement of these relatively small traces.

Machichnus regularis. - The closely spaced, overlapping paired grooves are confidently assigned as gnawing (rasping) traces generated by small rodents (Pokines 2015). Rodents commonly gnaw on bone and antlers to obtain minerals from the material and to sharpen/shorten their ever-growing incisors (Haglund 1992; Patel 1994). These rodent-induced traces show that many mammoth carcasses were at least partially skeletonized prior to burial (Pokines 2015). The traces are on several well-articulated specimens, therefore skeletonization occurred while articulation was maintained. Because many of the rodent traces are on the lower portions of the *M. Columbi* remains near the paleosurface, even partial burial prior to skeletonization is not plausible for (at least) some of the specimens.

Brutalichnus brutalis. - The deep, arcuate grooves that removed the compact tissue of articular surfaces are interpreted as carnivore gnawing traces (Haynes 1980). The size of the gouges and the spacing between individual grooves is indicative of the cheek teeth of a large cat (Haynes 1983a, 1985; Pobiner 2008). The position of these structures on the *M. columbi* long bones provides additional evidence that some of the specimens were disarticulated and biogenically modified prior to burial.

Nihilichnus nihilicus. - Individual and sets of punctures are interpreted as the result of bites inflicted by a large carnivore, perhaps while the scavengers were attempting to dismember or transport the carcass (Haynes 1983a; Pobiner 2008). The spacing between indents on a single set indicates that one scavenging individual had spacing between dental cusps equal to 1.8 cm (Fig. 3.6A; Delaney-Rivera et al. 2009). The holes are distinct from invertebrate borings and foramen canals due to the irregular/triangular morphology, the jagged outer margins, lack of bioglyphs, and the cortical material that is pressed into the cancellous bone (i.e., compare Fig. 3.6 to Fig. 3.7; Martin and West 1995; Laudet and Antoine 2004; Britt et al. 2008; Ekdale and De Gibert 2010; Blackwell et al. 2012).

Cubiculum isp. - The size and morphology of the shallow borings on the mammoth fossils are consistent with the boring generated on a wild-hog skull by captive hide beetles (compare Figs. 3.7A-E to Fig. 3.7F). Additional borings of similar dimensions and morphology have been produced by confined dermestid beetles on bones in separate experiments (Kenneth Bader, personal communication, 2016). Trace fossils, such as these from WMNM, have been previously documented and interpreted as dermestid-beetle borings in other paleontological studies (e.g., Martin and West 1995; Hasiotis et al. 1999; Laudet and Antoine 2004; Britt et al. 2008; Bader et al. 2009; Saneyoshi et al. 2011; Pirrone et al. 2014b).

It is well known that consumption of vertebrate remains by hide (dermestid) beetles occurs during dry-decay, and dermestid larvae avoid humidity (Coe 1978; Coombs 1979; Schroeder et al. 2002; Lefebvre and Gaudry 2009; Woodcock et al. 2013). Accordingly, rainfall and humidity are the primary factors in the settlement and

development of dermestid beetles on corpses (Charabidze et al. 2014). Since the southern portion of the L1 assemblage rested directly upon river gravel within the channel, it can therefore be inferred that the dermestid beetles scavenged upon the mammoth corpses while the channel was dry. The possibility does remain that perhaps the animals perished while the channel was flooding just prior to becoming dry; however, because there is no evidence for drowning, we feel that this is not the most parsimonious explanation in light of these new observations.

Weathering and Root Traces

Because diagenetic mineral staining and sediment infill crosscuts the weathered bone surfaces in many instances (Fig. 3.8), it can be inferred that the WMNM mammoths have undergone subaerial exposure prior to burial. Behrensmeyer (1978) found Stage 1 can be achieved very rapidly, Stage 2 required at least two years of subaerial exposure, and Stage 3 weathering required no less than four years in the climate of modern Amboseli. Although the climate of central Texas during MIS4 is not directly analogous to the Behrensmeyer (1978) study, weathering of the WMNM assemblage at an order of magnitude faster would imply subaerial exposure for months at least.

The branching, sinuous furrows etched into the fossils are interpreted as root traces that occurred after burial (Mikuláš 1999; Montalvo 2002). The higher density of rooting of the upper fossiliferous layer relative to L1, in addition to the presence of root tissue in some of the furrows, suggests that much of the rooting is modern. However, because the fossils were entombed in a zone of active pedogenesis, presumably some of the furrows are attributed to early rooting activity shortly after burial. Crosscutting relationships between furrows can be used to determine the relative timing of individual

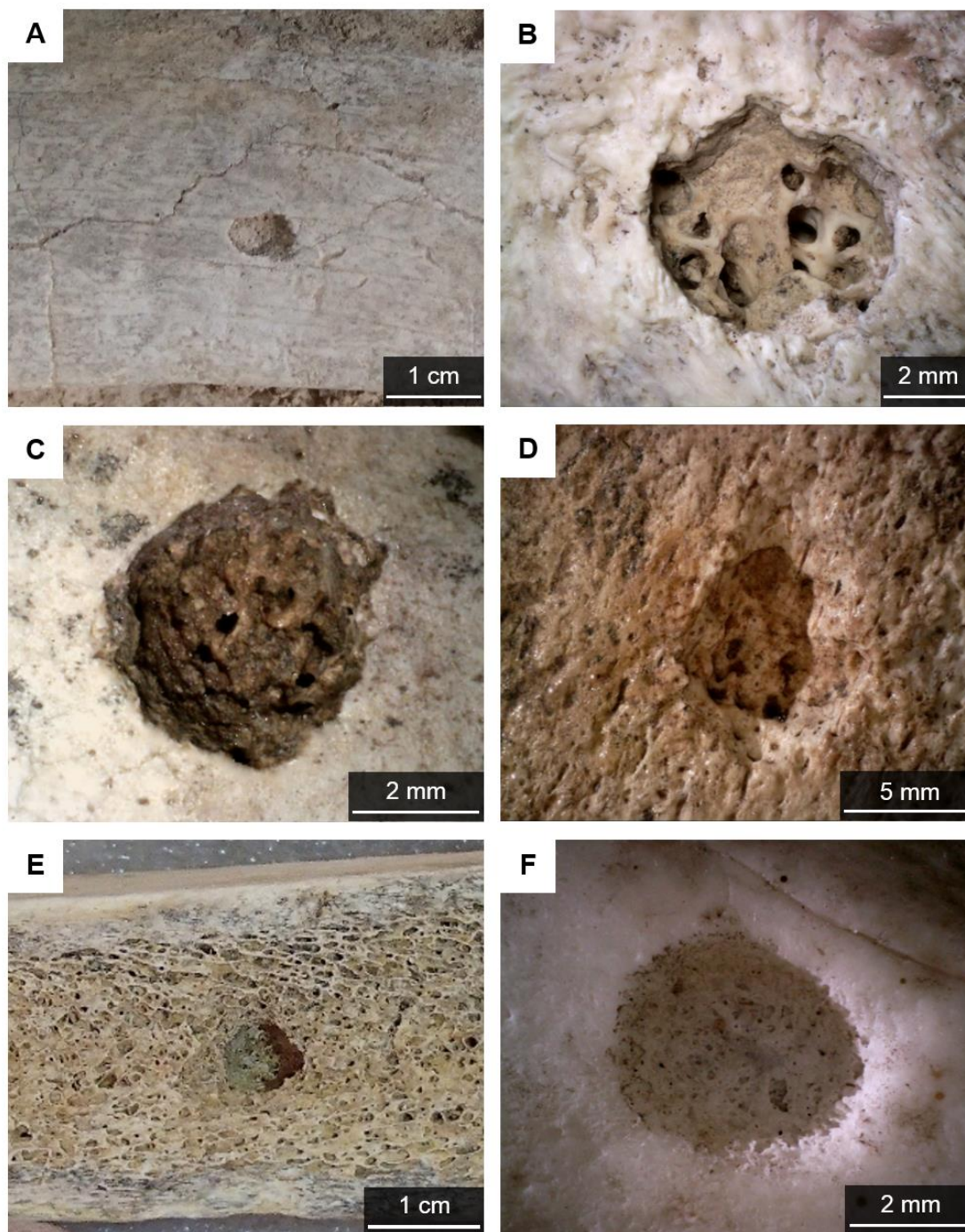


Figure 3.7. *Cubiculum isp.* on various skeletal elements. **A)** Slightly elliptical, hemispherical bore on *in situ* rib of mammoth W. **B)** Hemispherical boring on mammoth U phalanx (545-BU-MMC). **C)** Shallow bore on femoral articulation surface 761a-BU-MMC. **D)** Shallow bore on eroded long bone of mammoth D limb fragment (203-BU-MMC). **E)** Hemispherical bore in cancellous bone on the surface of a spiral fracture (20-BU-MMC). **F)** Comparative trace generated by captive hide beetles on a wild-hog skull (*Sus scrofa*). Note the similarities in size and morphology to Figs. 3.7A-E.

roots on single bones, but the unconsolidated nature of the paleontological site and shallow burial history make it difficult to differentiate early burial versus relatively recent root etching in the absence of root tissue.

Bone Fractures and Trampling

Photos published in 1981, as well as excavation photos archived at BU-MMC, show significant damage to freshly exposed elements (Naryshkin, 1981). Much of this damage can be attributed to post-burial lithostatic pressure of the overburden. Of the material found at WMNM, the camel shows the clearest evidence of compaction, with the skull reduced to less than 50% of its original height. Longitudinal fractures parallel to the grain of the bone can form at any time from Behrensmeyer Stage 1 on, and could thus be attributed to sediment compaction (Behrensmeyer 1978). The transverse fractures, which are perpendicular to the grain of the bone, occurred after the organic component of the bone has been destroyed and likely also post-date burial (Montalvo et al. 2015).

Alternatively, spiral fractures and stepped spiral fractures occur only when organic collagen is present in the bone (Andrews and Fernandez-Jalvo 1997). Such spiral and stepped spiral fractures could have occurred during a sudden flood and violent burial event as proposed by Fox et al. (1992), but many of the spiral fractures observed have eroded edges (Fig. 3.8C, D), suggesting that a duration of time had passed between the fracture and burial (Myers et al. 1980).

In an archeological context, spirally fractured bone is often attributed to humans (Dillehay 1992), but the WMNM fossils predate the presence of humans in North America (Waters et al. 2011). Another source for spiral fractures would be scavengers processing a carcass (Haynes 1983b); however, most spiral fractures at the site are not

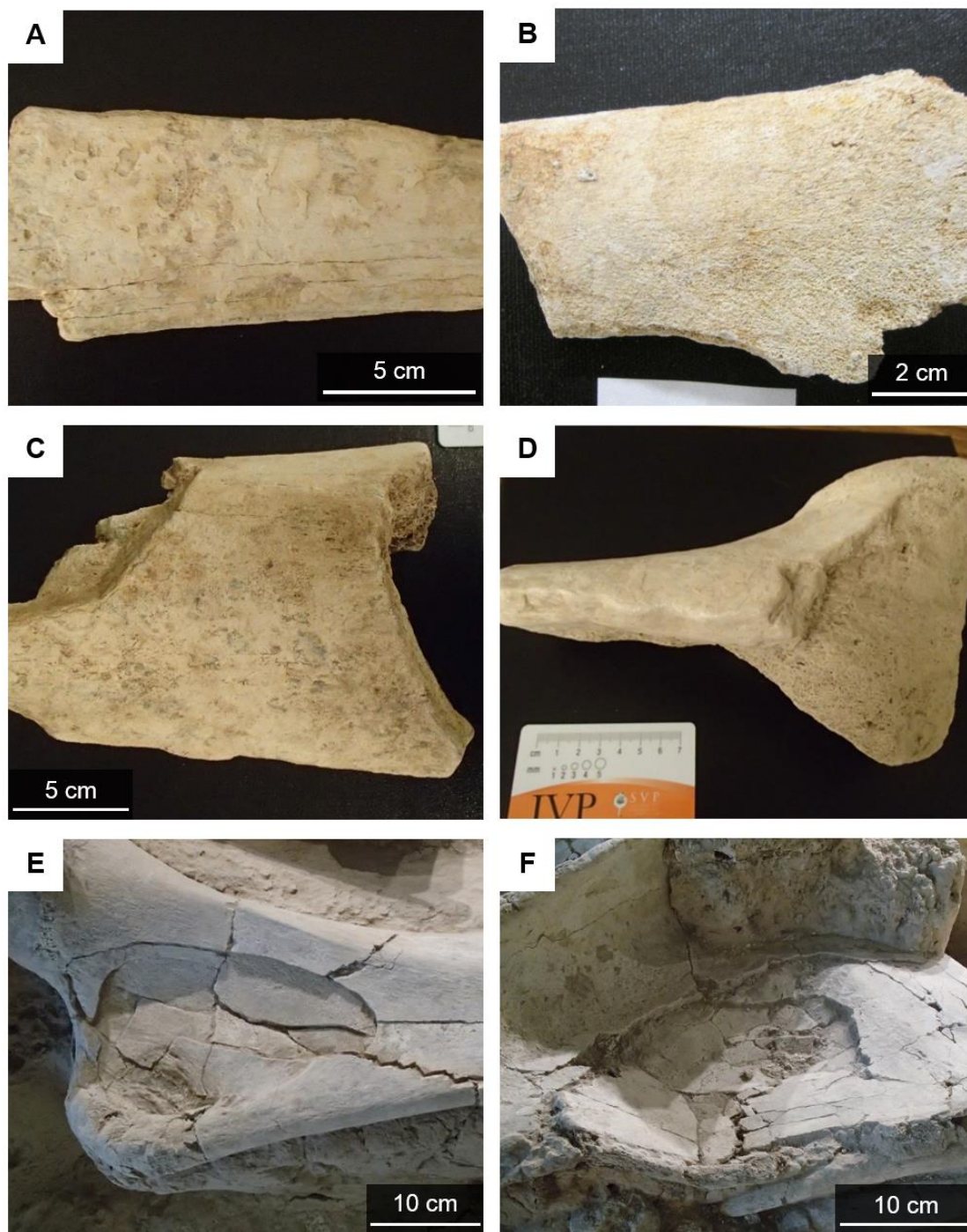


Figure 3.8. Weathering and fractures on WMNM fossils. **A)** Flaking layers of concentric cortical bone on fragment 210E-BU-MMC. **B)** Fibrous-texture weathering pattern on 646h-BU-MMC. **C)** Spiral fracture on bone fragment 204e-BU-MMC. The spiral fracture is on the bottom and has rounded edges. The top exhibits longitudinal and transverse fractures. **D)** Spiral fracture on bone fragment 206e-BU-MMC. The left is an example of Behrensmeyer (1978) Stage 2, and the right illustrates Stage 3. **E)** Stepped spiral fracture on *in situ* left femur of mammoth Q. **F)** Footprint-sized pattern of fractures on an *in situ* scapula of mammoth Q.

associated with other signs of scavenging. The remaining possibility is vertebrate trampling, and the scapula of the bull mammoth is likely additional evidence for trampling behavior recorded at the site (Fig. 3.8F; Behrensmeyer et al. 1986).

A Diminished Watering Hole

Many kill mechanisms have been put forward for the WMNM assemblage such as: drowning, quicksand, disease, electrocution from lightning, a meteor impact, freezing, and hunting (Naryshkin 1981; Fox et al. 1992; Haynes 1992). To date, drowning and rapid burial during a time of rising flood waters remains the most widely accepted mechanism of death, whereas the other scenarios have been generally disregarded/ruled out (Bongino 2007; Nordt et al. 2015).

We propose that a drought (opposed to a catastrophic flood) is a more parsimonious kill mechanism for particularly the L1 assemblage because: (1) A diminishing watering hole concentrating water-stressed fauna explains the high taxonomic diversity - particularly the aquatic organisms such as an alligator, freshwater turtles, and fish. (2) Migration to a distant water source explains the lack of infant *M. columbi* in the assemblage - when extant elephant herds travel to distant water sources during extreme droughts, the calves are often lost or separated and are subject to predation (Loveridge et al. 2006). (3) The death of a nearly complete herd would overwhelm the water-stressed scavengers and account for the articulated specimens and limited scavenging traces (Coe 1978; Haynes 1980, 1988). Small bone elements of *M. columbi* feet (e.g., phalanges, carpals, tarsals) and tails are uncommon in the WMNM assemblage, which would be expected of a large carcass that is partially dismembered. Haynes (1983a) divided the utilization of prey carcasses into three stages (light, medium,

and heavy), dictated by the quantity of available carrion for a given number of scavengers. During “heavy” utilization of carcasses (i.e., when carrion is limited), damage/consumption of bone is maximized, therefore vertebrate scavenging trace fossils are more common (Haynes 1985). A thanatocoenosis composed of at least 16 Columbian mammoths in a relatively small area would result in underutilization of prey carcasses, vertebrate scavenging marks on bone would be less abundant, and articulation could be maintained.

The lack of desiccation-related features in the sediment that would be characteristic of drought conditions, such as deep vertical mudcracks and mudcrack polygons, can be explained simply by the paucity of clay and abundance of silt, sand, and gravel sediments, which would not shrink and form desiccation features (cf. Nordt et al., 2015, their Figs. 4, 5 and 9 showing sediment types and reconstructed paleoenvironment conditions). Additionally, the climate proxies that were applied to the encasing paleosols (i.e., Nordt et al. 2015), which suggest the climate was relatively cool and wet, were developed on modern soils formed over periods of time at least 10^2 to 10^3 years and would not capture a short-term extreme drought (Nordt et al. 2006, 2007).

Moving forward, we suggest that the diminishing watering-hole hypothesis can be further tested through serial sampling/isotopic analysis ($\delta^{18}\text{O}$) of mammoth teeth from WMNM. Because mammoth teeth were continually growing and reflect the isotopic composition of the drinking water, the last layer of growth in the teeth would contain a $\delta^{18}\text{O}$ enrichment (relative to the rest of the teeth) if the mammoths were consuming water from a highly evaporated water source prior to death (Hoppe 2004).

Conclusions

This study contradicts the “conventional wisdom” held for the WMNM site, which has long maintained that there was no evidence for scavenging of mammoth carcasses. A corollary was that the animals were rapidly buried by a major flood (or series of floods). Certainly alluvial sedimentation ultimately buried the death assemblage, but new evidence of vertebrate and invertebrate scavenging casts light on dry-decay, partial skeletonization, and prolonged subaerial exposure prior to burial. Provided these new findings, along with the high taxonomic diversity of the site and the lack of mammoth calves, we propose that all of these observations can be simply explained by a prolonged drought at a diminished watering hole. Ongoing research of *M. columbi* teeth from the site can be used to evaluate if the mammoths were drinking from an evaporated water source prior to death.

Acknowledgments

We thank George Massey, Kenneth Bader, and Greg McDonald for guidance and helpful discussions. We also thank Anita Benedict for access to the BU-MMC collections and dermestid beetle colony, the National Park Service and Raegan King for providing access to the excavation pit, and Baylor University for research funds. This paper was greatly improved through the comments and suggestions provided by M. Gabriela Mángano, an anonymous associate editor, and two anonymous reviewers. NPS permit #WACO-2016-SCI-0001.

CHAPTER FOUR

Reply: The Waco Mammoth National Monument May Represent a Diminished Watering-Hole Scenario Based on Preliminary Evidence of Post-Mortem Scavenging

This chapter is published as: Wiest, L.A., Esker, D., and Driese, S.G., 2017. Reply: The Waco Mammoth National Monument may represent a diminished watering-hole scenario based on preliminary evidence of post-mortem scavenging, *PALAIOS*, v. 32, p. 1-1.

We sincerely welcome this discussion from Smith (2017) in response to our article regarding the Waco Mammoth National Monument (WMNM) that indicates the Columbian mammoth herd was subject to subaerial exposure and scavenging prior to burial, rather than being killed and buried in a single event (Wiest et al. 2016). Smith's comments do not dispute the methods or results in Wiest et al. (2016) but do highlight the inconsistencies between our conclusions and the previous understanding of the causative agents surrounding the fossil assemblage (Fox et al. 1992). We appreciate this opportunity to clarify and highlight the empirical basis for the interpretation in Wiest et al. (2016).

The major finding from our study is the preponderance of diverse bioerosive traces and weathering features that suggest dry-decay, skeletonization, and prolonged subaerial exposure prior to burial (Wiest et al. 2016, 2017). This is highly contrary to rapid and catastrophic burial, which has long been assumed as the kill mechanism for the Waco mammoths (Fox et al. 1992; Bongino 2007; Nordt et al. 2015). Drought remains a plausible and parsimonious explanation that can be quantitatively tested (cf. Hoppe 2004)—there is currently a robust serial sampling/isotopic analysis ($\delta^{18}\text{O}$) underway (see Wiest et al. 2016) on seven teeth from individual mammoths from WMNM.

Smith cites inability to link the stratigraphy of the lower portion of the site to the upper portion as evidence that both accumulations “are connected and that death and burial occurred during the same event”. For death and burial to occur contemporaneously, as Smith suggests, one must reject the findings of diverse vertebrate and invertebrate scavenging traces, which were documented at all stratigraphic levels (Wiest et al. 2016). We remain uncertain as to the empirical evidence or logic for rejection of these results particularly with the equivocal stratigraphic interpretation.

The interpretation of catastrophic burial of the mammoth herd appears to be a common belief rather than one bound by verifiable observations and reproducible data. A central argument posed by Smith is that the conclusions presented in Wiest et al. (2016) are inconsistent with the popular scenario of a 45-year-old female (mammoth M; see Table 1 in Wiest et al. 2016) and bull (mammoth Q) preserved in life position while attempting to hoist juveniles to safety (Fox et al. 1992). For our study, we meticulously examined these individuals, the cited literature, the original bonebed maps, and excavation photographs archived at the Baylor University Mayborn Museum; from this, we were unable to find any objective data to support rapid and fatal burial. Regardless, if we assume that the bull (Q) and juvenile (R) were killed and buried simultaneously during a mutual encounter, and that *Mammuthus* behavior was analogous to behavior of extant elephants (Haynes 1991), it is more probable that the bull perished while attacking the juvenile, rather than attempting to save its life (Sukumar 2003). However, a combination of: (1) the previously reported absence of many of the foot (phalanges, carpals, tarsals) and tail elements (Fox et al. 1992; Haynes 1992); (2) our findings that demonstrate skeletonization prior to burial (Wiest et al. 2016); and (3) the abundance of

overlapping mammoths in a relatively small area (Haynes 1992), suggest that the occurrence of associated juvenile bones on and around the tusks of the adults is more likely attributable to chance as opposed to any specific type of behavioral interaction.

The new ichnological and taphonomic data shift the plausible mechanism of demise for the Waco mammoths to drought instead of the long-held and untested assumption of a catastrophic landslide or flood. We believe that a deeper knowledge of paleoenvironments at WMNM is warranted, based on careful taphonomic and ichnological study, stable isotopic analyses from teeth, and integration with paleoclimatic records and models. Science moves forward based on data and reproducibility of results, rather than staid beliefs.

CHAPTER FIVE

Morphological Characteristics of Preparator Air-Scribe Marks: Implications for Taphonomic Research

This chapter is under review as: Wiest, L.A., Ferraro, J.V., Binetti, K.M., Forman, S.L., Esker, D.A, and Zechmann, B. Morphological characteristics of preparator air-scribe marks: implications for taphonomic research, *Plos One*.

Abstract

Bone modification provides insights into understanding human evolution and nonhuman taphonomic processes. Scientific analysis of bone modification often occurs on remains that have been previously excavated, prepared and archived. These preparation activities can potentially introduce additional marks to the fossil material that may not be readily differentiated as post-excavation damage. Recognizing preparation damage is often straightforward when crosscutting relationships with other taphonomic features can be observed - however, other occurrences, especially subtle and/or isolated traces, require further analysis to infer or falsify the relative timing and modifying agents. Specifically, the air scribe, a small pneumatic tool commonly used for preparation, can generate unintentional marks on bones that may resemble the morphology of surficial modification caused by carnivores. The aim of this study is to provide high-resolution, detailed morphological information by using light and scanning-electron microscopy (SEM) to aid investigators in assessing the hypothesis that a trace in question is derived from air-scribe preparation activities. The main diagnostic characteristic of air-scribe-induced damage is the occurrence of sequential, variously spaced, sub-millimeter scallop-like stepped bone removals. The morphology can grossly resemble some carnivore-

induced tooth damage. Contrary to marks produced by trampling, stone tools, and carnivores no continuous internal features, such as microstriations, were observed by SEM within air-scribe-produced grooves. Thus, the presence of continuous internal or associated sub-features can be used to falsify an air-scribe origin. A culmination of the morphological criteria presented herein, cross-cutting relationships with other surficial features (e.g., diagenetic discoloration, weathering textures), the pattern of occurrence, and an overall contextual framework for the assemblage is suggested for accurate identification of such traces. The ability to recognize or falsify air scribe preparator damage will allow analysts to confidently proceed with interpreting past biological and sedimentological interactions with animal remains.

Introduction

Bone surface modifications (traces/marks that cut or destroy hard osseous tissue) are critical for understanding human behavioral evolution and nonhuman taphonomic processes because they record past biological and sedimentological interactions with animal remains (Bunn 1981; Blumenschine and Selvaggio 1988; Cutler et al. 1999; Hasiotis et al. 1999; Njau and Blumenschine 2006; West and Hasiotis 2007; Britt et al. 2008; Domínguez-Rodrigo et al. 2010; McPherron et al. 2010; Ferraro et al. 2013; Holen et al. 2017; Sahle et al. 2017). Post-mortem carnivore processing, hominin butchering, and invertebrate colonization are ancient behaviors that are most readily inferred through study of the morphology of the resulting damage preserved on the bones (Haynes 1980; Potts and Shipman 1981; Martin and West 1995; Laudet and Antoine 2004; Mikuláš et al 2006; Blumenschine et al. 2007; Domínguez-Rodrigo and Barba 2007; Domínguez-

Solera and Domínguez-Rodrigo 2009; Longrich and Ryan 2010; Blackwell et al. 2012; Pante et al. 2012; Malassé et al. 2016; Njau and Gilbert 2016; Wiest et al. 2016). The recent discovery that tramping animals and biting crocodiles can produce linear marks that mimic hominid cutmarks highlights how descriptions and explanations of bone surface modifications can dramatically alter interpretations of ancient assemblages (Behrensmeyer et al. 1986; Sahle et al. 2017). Such descriptions and explanations of bone surface modifications also assist analysts in breaking equifinalities. The concept of equifinality is appropriate for bone modification studies, which often necessitates multiple working hypotheses on the origin of bone alteration and additional contextual data (Lyman 2004; Sahle et al. 2017; Ferraro et al. 2018).

Scientific analysis of bone modifications often occurs after the fossils have been excavated, prepared and archived. These excavation and post-excavation activities can potentially introduce additional marks to the fossil material that may or may not be readily differentiated as modern damage. In many instances, differentiating preparation damage from other marks is relatively straightforward. Such is generally the case when cross-cutting relationships can be applied in relation to other taphonomic features preserved on the bone (e.g., staining, root etching, weathering texture) to deduce the relative timing of the trace generation (Behrensmeyer 1978; Mikuláš 1999; Montalvo 2002; West and Hasiotis 2007; Fernandez-Jalvo and Andrews 2016; Wiest et al. 2016). However, other occurrences, especially subtle and/or isolated traces, require further analysis to infer the modifying agent. Specifically, the air scribe, which is a small pneumatic tool commonly used for preparation, can generate unintentional damage to skeletal elements that grossly resembles the morphology of surficial modification caused

by carnivore processing (cf. Fig. 3.1B and Fig. 3.2B). Diagnostic criteria for differentiating modern air scribe preparator damage is absent from the paleontological, ichnological, archaeological, and taphonomic literature. Furthermore, it is plausible that many archived specimens that were treated with pneumatic tools will persist further into the future than the knowledge of how they were prepared; some modern museums keep careful records of excavation and preparation techniques (including damage reports), but such record keeping is not universal (Anderson et al. 1994). Analysts working on collections that were archived prior to the advent of the air scribe should still consider the possibility of air-scribe damage as many collections are prepared long after the date of collection.

The aim of this study is to provide morphological information to aid investigators in assessing the hypothesis that modification in question is derived from air-scribe preparation activities. Although air scribes are commonly used in fossil preparation, and many workers inevitably encounter damage from air scribes during taphonomic research, this paper presents the only high-resolution investigation of the morphological characteristics of such damage.

Materials and Methods

The experimental air scribe-induced features were generated by a Chicago Pneumatic Air Scribe (see Ratkevich 1998) on non-diagnostic Pleistocene chelonian carapace fragments and mammalian bone remains from the Chalbi Basin, northern Kenya, which were exported from the country for destructive geochemical analyses (Ferraro et al. 2012, 2013). A variety of reasonable transverse speeds, approach angles, and downward pressures were applied to the air scribe with the objective of introducing a

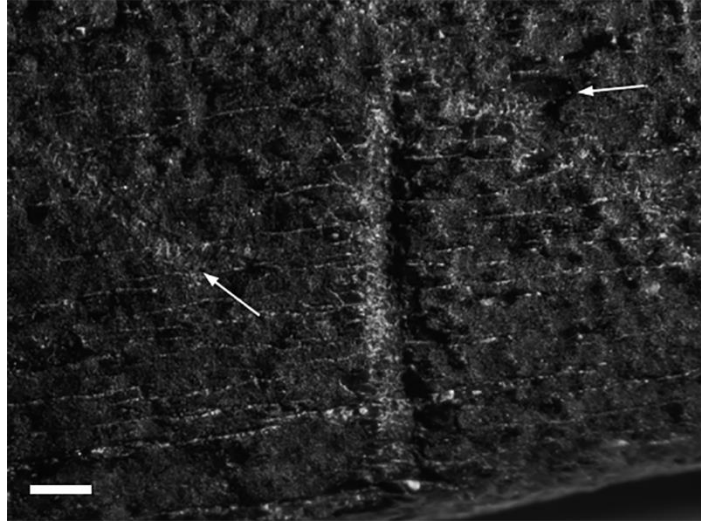


Figure 5.1. Archived bone fragment imaged with a digital camera. Sample was recovered from West Turkana, Kenya, and contains markings from air-scribe preparation techniques. Scale bar = 1 mm. Arrows indicate position of shallow grooves. Notice the similarities between these marks and the carnivore-induced tooth scores in Figure 5.2.

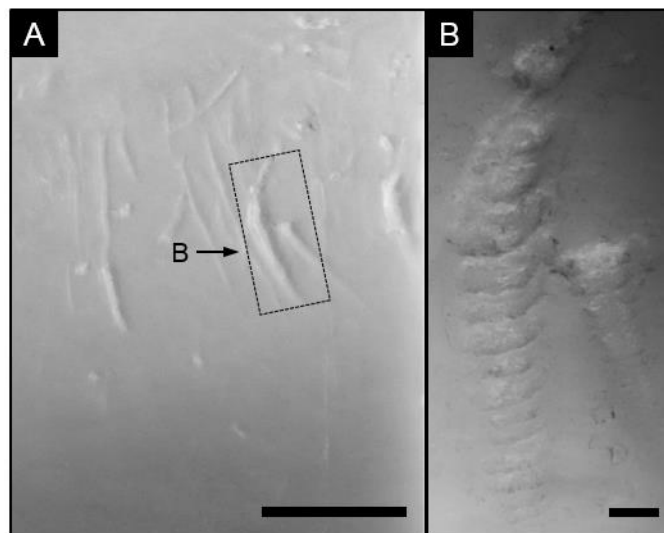


Figure 5.2. Carnivore-induced tooth scores and pits on bovine long bone (Sample 4-2) under a stereomicroscope. A) scale bar = 1 cm; B) scale bar = 1 mm. Notice the morphological similarity between the chatter marks highlighted in B and the accidental air-scribe damage depicted in Figure 5.1.

morphologically diverse range of markings. The experimental carnivore-induced bone surface modifications analyzed in this study were generated by providing feral pig (*Sus scrofa*) and domestic bovine (*Bos taurus*) long bones to domestic canines (*Canis lupus familiaris*). The experimental lithic-tool-induced marks were generated using basalt flakes, hammerstones, and anvils during ongoing butchery experiments with domestic goats (*Capra aegagrus hircus*).

Macroscopic bone surface modifications analyzed were examined and imaged under low-angle, polarized-LED illumination with limited background light. Visual inspection was conducted with the extended depth of field (EDOF) setting on a Dino-Lite Edge digital microscope (AM7915 Series) with DinoCapture 2.0 software (v. 1.5.26.C), and a stereo-microscope (SZX16, Olympus Corp., Tokyo, Japan). Scanning Electron Microscopy (SEM) images were taken of uncoated samples at low vacuum conditions either with a FEI Versa 3D scanning electron microscope (FEI, Hillsboro, OR, USA) or a Hitachi TM3030 Plus tabletop scanning electron microscope (Hitachi, Tokyo, Japan). All micrographs were taken with 15kV and at ~10mm working distance.

Results

Air-scribe marks

The experimental air-scribe marks are categorized in two classes as grooves (Figs. 5.1, 5.3: right column) and pits (Fig. 5.4: right column; see Pirrone et al. 2014 for definitions of general morphological terms). Air-scribe pits vary in diameter and depth (~mm scale), which is dependent on the pressure and duration of the application of the chisel tip to the material. The pits share a common, ‘rosette’-like morphology. This rosette appearance is caused by the repetitive removal of arcuate flakes that leave behind

sub-millimeter scallops (Fig. 5.4B, D). The individual scallops often have a flat base that cleaves along cortical lamellae boundaries. Scallops toward the center of the pit penetrate deeper bone layers, generating a crater-like overall morphology with a rosette-like crater wall (Fig. 5.4B, D).

Air-scribe grooves, similar to the air-scribe pits, also contain rough outer margins composed of variably-shaped, sub-millimeter, negative flake scars that result from the high-frequency reciprocating impacts of the bit (Fig. 5.3B, D, F). The gross morphology of the grooves (e.g., depth, sinuosity, etc.) varies dependent on the operator and is undiagnostic. The basal floor of the grooves varies from smooth (Fig. 5.3B) to scalloped and rough (Fig. 5.3D). Chatter-marked refers to the sequential arcuate ridges that are perpendicular to the long axis of the groove. Small-scale features that exhibit linear continuity (e.g., shouldering, microgrooves, etc.) within or associated with the air-scribe grooves were not observed for the samples.

Comparison to carnivore linear marks

The tooth scores (linear grooves) and the air-scribe grooves overlap in size (~ 1-2 mm) and depth (typically < 1 mm; Fig. 5.2). Traces produced by either mechanism can have a smooth internal floor (Fig. 5.3A, B), or a rough base with fine ridges perpendicular to the long axis (Fig. 5.3C-F). Unlike the marks produced by the carnivores, grooves produced by the air scribe have a sequential scalloping/cratering effect that generates an irregular outer margin (Fig. 5.3B, D, F). The air-scribe-induced damages does not exhibit any features that are continuous across the series of scallops, such as microgrooves, microstriations, or shouldering (cf. Fig. 5.3A, E; Fernandez-Jalvo and Andrews 2016).

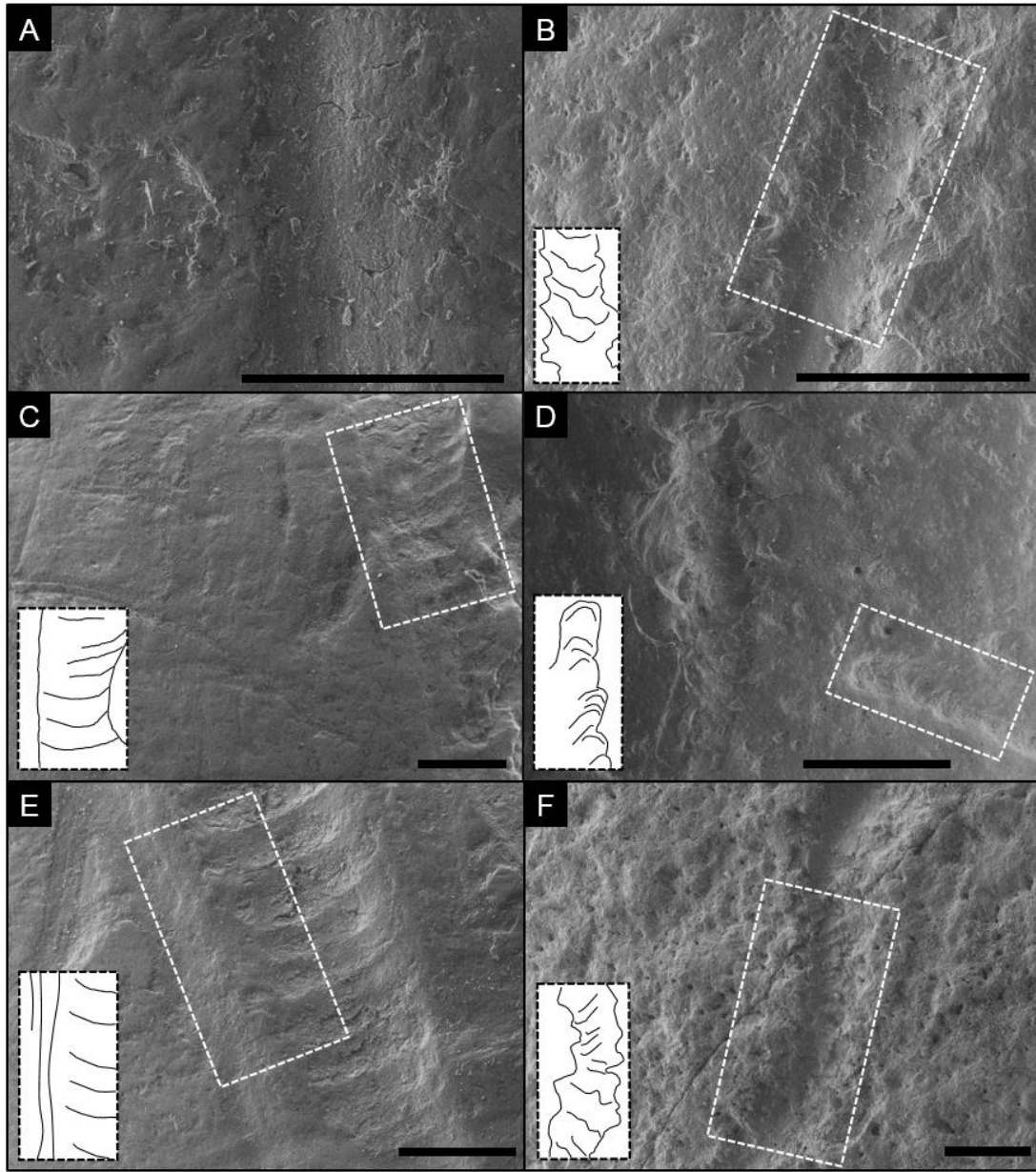


Figure 5.3: Comparison of carnivore-induced tooth scores (left column) and air-scribe-induced grooves (right column) under SEM. Insets are interpretive drawings of highlighted areas. A) Segment of a smooth tooth score with relatively smooth margins and faint, internal grooves exhibiting continuity on a bovine long bone; scale bar = 0.5 mm. B) Segment of a transition within an air-scribe groove from a chatter-like morphology (upper half) into a smooth-based groove on a fossilized tooth plate; scale bar = 1.0 mm; Notice the rougher margins in comparison to A. C) Shallow tooth score with chatter marks, a smooth left margin, and an irregular right margin on a bovine long bone; scale bar = 1.0 mm. D) shallow (lower left) and deep (top to bottom) air-scribe grooves on a fossilized tooth plate; scale bar = 1.0 mm. Notice the similarities between the chatter morphology of the lower-left mark and the scores depicted in C and E. Also note the relatively rougher margins. E) Tooth score with pronounced chatter markings and a long-axis-parallel, smooth left shoulder with through-going continuity on a bovine long bone; scale bar = 1.0 mm. F) sinuous air-scribe groove with faint chatter marks, rough margins, and an absence of through-going continuity on a fragment of a chelonian carapace; scale bar = 1.0 mm.

Comparison to carnivore pits

The tooth pits and air-scribe pits can also overlap in gross morphology and size (Fig. 5.4), often exhibiting a semi-circular shape with rough outer margins (Fig. 5.4, cf. left and right columns). The tooth pits and the air-scribe pits can crosscut multiple layers of cortical lamellae and result in the removal of material (Fig. 5.3). The pits generated by the air scribe have a ‘rosette’-like morphology that is generated as a series of steps down toward the center of the trace (Fig. 5.4 B, D). The tooth pits, on the other hand, do not exhibit the rosette morphology or sequential scalloping, but instead, are more irregular and have a flattened base (Fig. 5.4A, C; Fernandez-Jalvo and Andrews 2016). The tooth pits also have a relatively less-steep sidewall, and occasionally exhibit a raised margin (Fig. 5.4C), whereas the air-scribe marks are typically steeper and do not possess raised, shoulder-like margins (Fig. 5.4B, D).

Comparison to linear lithic marks

The air-scribe grooves are distinct from cutmarks and sedimentary abrasion (Potts and Shipman 1981; Behrensmeyer 1986). Specifically, microstriations and/or associated scratches were not observed with any of the air-scribe induced marks (Behrensmeyer 1986; Fernandez-Jalvo and Andrews 2016). The sequential, arcuate scallops, which are ubiquitous with the air-scribe marks are not observed in the linear lithic marks. Air-scribe damage also has a relatively rougher outer margin, which lacks any raised shoulders.

Comparison to lithic pits

The gross size and shape of the air-scribe pits can somewhat resemble percussion pits (compare Fig. 5.4B and 5C), but the experimental lithic-tool-induced damage differs

from the air-scribe pits and grooves by having internal and associated microstriae, which are not observed for the air-scribe marks (Fig. 5.5; Blumenschine and Selvaggio 1988). Additionally, the sequential, arcuate scallops are unique to the air-scribe marks and are not observed in the percussion pits.

Discussion

Morphological descriptions of air-scribe marks provide analysts with a means to potentially identify or falsify post-excavation damage that confounds bone surface modification studies. This has several important implications, as well as raises several questions:

Explanatory mechanisms

The differences in the morphologies between the air-scribe induced marks and the tooth pits and scores can be attributed to the different fracture mechanics responsible for the removal of material. Namely, the carnivore teeth introduce a relatively slow, static load on the bone surface, whereas the high-frequency reciprocating impacts of the air-scribe bit cause dynamic loading. Static vs. dynamic loading dictates the shape of the expelled particles (flakes), and thus influences the morphology of the resulting trace (Capaldo and Blumenschine 1994).

The experimental carnivore-induced and lithic-tool-induced traces were generated on fresh bone containing collagen (Fig. 5.2 and 5.5 respectively), whereas the unintentional and experimental air-scribe marks (Figs. 5.1, 5.3: right columns, and 5.4: right column) were produced on fully fossilized material. This difference in preservation inherently influences differences in the physical properties of the material (e.g. hardness,

texture, density), which may alter bone breakage on the macroscopic and microscopic scales (Andrews and Jalvo 1997).

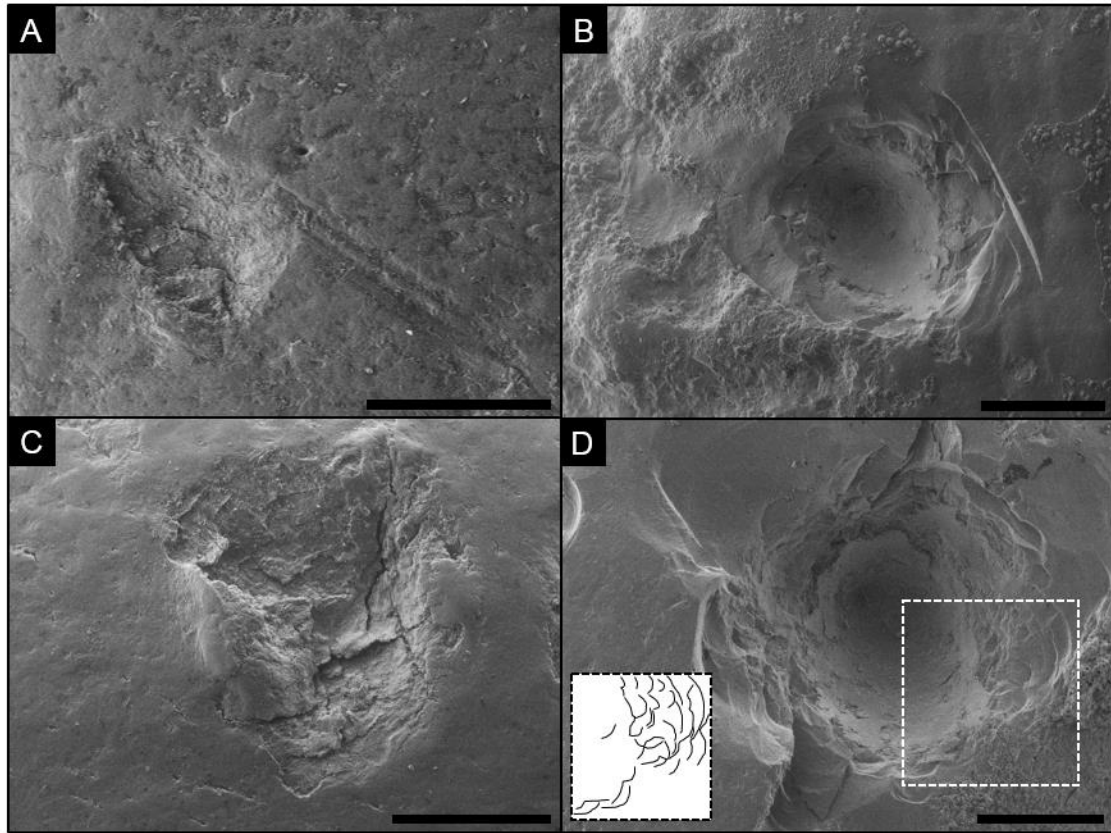


Figure 5.4: Comparison of carnivore-induced tooth pits (left column) and air-scribe-induced pits (right column) under SEM. Notice the rosette-like morphology of the pits depicted on the right. A) Shallow tooth pit with associated microgrooves (faint score) on a bovine long bone; scale bar = 1.0 mm. B) Shallow pit generated by an air-scribe on a fossilized mammalian fragment. Notice the sequential, stepwise scalloping that creates flat benches on the various layers of cortical lamellae; scale bar = 1.0 mm. C) tooth pit with raised margins on the left and right sides; scale bar = 1.0 mm. D) Somewhat deeper air-scribe-induced pit (relative to B) on a mammalian fragment; scale bar = 1.0 mm. Inset is interpretive drawing of highlighted area.

The use of SEM

The key criteria for differentiating air-scribe marks (e.g., small-scale scallops, rough outer edge, etc.) may be observed with a hand lens (10x) or low-power microscopy

(~10-40x), and identification does not necessarily require scanning electron microscopy. However, the SEM yields an effective method for imaging specifically the morphology of these traces (Bromage 1984, Boyde and Jones 1996). Glares, color variations, and limited depths of focus, which can induce artifacts, are the main limitations when light microscopy is applied. These complications were eliminated when SEM was used to evaluate the ultrastructure of air-scribe damage on bones. Furthermore, modern SEMs do not require coating of non-conductive samples, such as bones, with a fine layer of conductive metal (e.g. iridium, gold, palladium) or carbon, which can induce artifacts as well (Stokross et al., 1998, Golding et al., 2016). In low vacuum/variable pressure mode, as applied in this study, non-conductive samples, such as bones, can be imaged in the SEM in their native state (James, 2009, Miyazaki et al., 2012, Georgiadis et al. 2016, Zechmann 2018). However, the SEM does have limitations. The vacuum chambers of the SEMs have a finite size and limit the size of the sample that can be observed. Of the two SEMs used, the FEI Versa 3D SEM has the largest vacuum chamber and is capable of imaging bone fragments up to approximately 20 cm in length. The Hitachi TM3030 Plus tabletop SEM is limited to samples < 10 cm in length, in which case microscopy needs to be focused on the center region of the sample. Cutting the sample can circumvent SEM-based sample length limitations for studies if sample modification is acceptable. Often cutting the sample is ill advised or not practical for rare finds, in which case making a mold of the structure in question could allow one to still utilize an SEM approach (Bader et al. 2009).

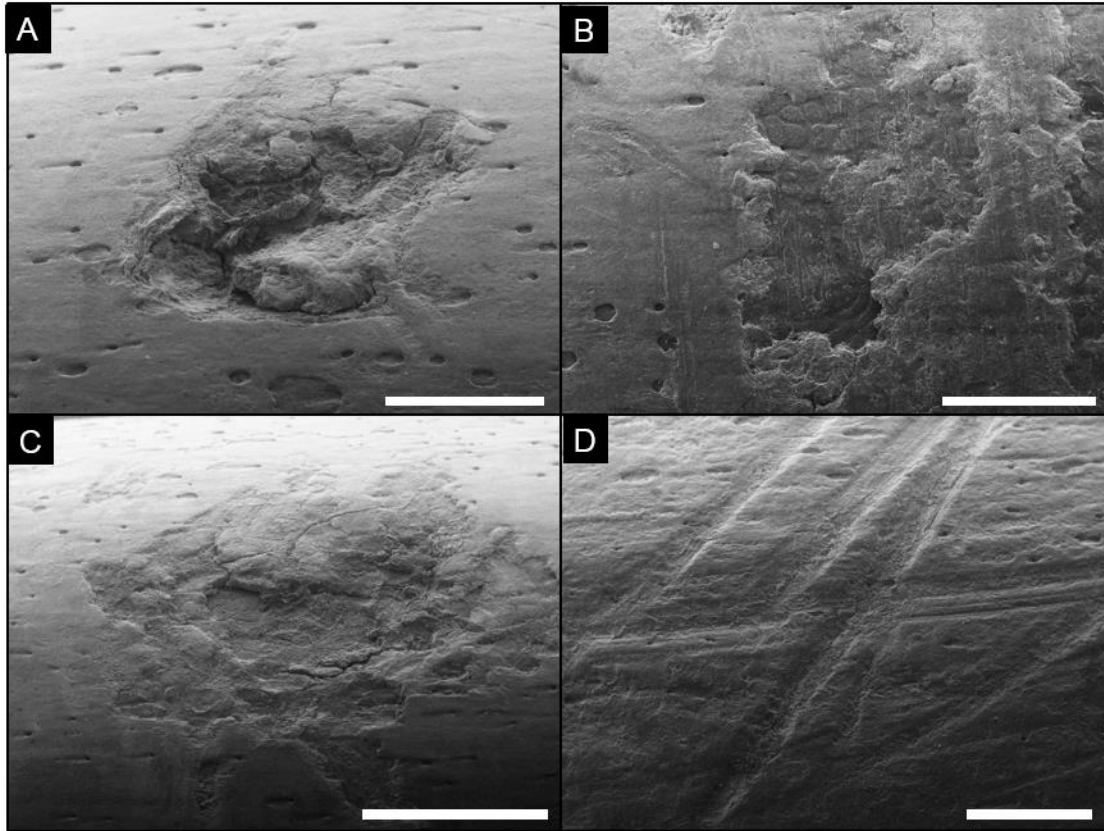


Figure 5.5: Experimental lithic-tool damage on goat bones under SEM. A) Percussion pit; notice the roughness and cracking that is not apparent on the air-scribe damage depicted in Fig. 5.4B,D; scale bar = 2 mm. B) Irregularly shaped percussion pit with abundant (vertically oriented) microstriations; scale bar = 2 mm. C) Percussion pit with associated microstriations and fine-scale fractures; scale bar = 1 mm. D) Multiple, crosscutting cutmarks with internal microstriations and smooth margins; scale bar = 2 mm.

Analytical issues

Ideally, color observations can be used in bone modification analysis for assessing when the trace in question was generated relative to burial and/or fossilization. In many cases crosscutting relationships with color heterogeneities provide insight into the relative timing for the origin of the trace, which then can be used to infer if is the damage is recent, for instance from preparation or excavation (Wieberg and Wescott 2008). However, in many assemblages, the outer and inner cortical bone coloration is not

different (e.g., bonebeds containing fossilized or unfossilized material that is mostly white). Under such a scenario, crosscutting relationships with color variations do not occur (O’Harra 1920). Thus, the detailed morphology of the imprint remains the most reliable criterion to infer if the trace in question is post-discovery or related taphonomy or bioerosion.

The experimental air-scribe marks described herein were generated by a single device used by a single operator. Other chisel tips and/or types of scribes may introduce a host of somewhat alternate morphologies. The size of a mark may be an unreliable criterion for diagnosing the origin, as this would be dependent on the size of the scribe or species/size of the carnivore.

The air-scribe-induced marks may be confused with carnivore-induced tooth scores or pits based on the gross morphology and similar size. Inadvertently attributing this preparation damage as carnivore modification would inflate frequencies of these marks in assemblages. Partitioning bone attributes to air-scribe-induced damage is important for frequency-based bone modification studies, particularly with a small sample size (e.g., Lokaklalei).

Conclusions

There are morphological differences between the traces generated by air scribes and natural agents of bone surface modification such as carnivores. Sequential, sub-millimeter scallops/craters are unique to the reciprocating impacts of the air-scribe. Conversely, the presence of linearly continuous sub-features (i.e., internal grooves, shoulders, microstriations), which are often observed in marks produced by carnivore modification, trampling, and lithic tools, can be used to falsify the hypothesis that a trace

in question was generated by an air-scribe. A combination of the morphological criteria presented herein, cross-cutting relationships with other surficial features (e.g., diagenetic discoloration, weathering textures), the distribution of the modification, and an overall contextual framework for the assemblage is suggested for the interpretation of such traces. The ability to recognize or falsify air scribe preparator damage will allow analysts to confidently proceed with interpreting past biological and sedimentological interactions with animal remains.

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CHAPTER SIX

Summary and Future Research

Ichnology provides a unique perspective to understand the ethology of the survivors in response to extreme environmental perturbations. Studying survival behaviors from the ancient past is important because it may one day help address some of the decisions regarding our current mass extinction.

Each of the findings presented herein raises further questions and curiosities that could be addressed by future research. The subsequent paragraphs are suggested research directions stemming from this work:

Chapter Two – what organisms did not experience the Lilliput effect during the aftermath of the K-Pg extinction? Discovering biota that were buffered from this phenomenon will aid in assessing the driving mechanisms behind the Lilliput effect. Future studies should focus on extending such datasets across different taxa and depositional environments, particularly from the continental realm, to better understand the spatial, temporal, and ecological context of this phenomenon. Trace fossils have great potential to yield such an archive, but body fossils, such as turtle remains and crocodilian teeth, should also be assessed.

Chapter Three – what other evidence exists to assess the drought hypothesis? There is currently a robust serial sampling/isotopic analysis underway on four teeth from individual mammoths from WMNM (Donald Esker, personal communication, 2018).

Other proxy data external to the site, such as speleothem analysis, could be used to evaluate the climate of the region for that particular time.

Chapter Four – how do megafauna behave when they are faced with a fatal drought? Do they actively disperse on the landscape, or remain concentrated until death? Scientific observations regarding current megafauna die-offs, such as the large concentration of wild horses around a depleted watering hole in Arizona during May 2018 (<https://www.cbsnews.com/news/horses-found-dead-southwest-drought-arizona-najavo-nation/>), could be used to link the behavioral aspects of such an event to the resulting taphonomic assemblage.

Chapter Five – how else can we better bound equifinality in bone modification studies? More experimental studies with a diversity of modifying agents are greatly needed.

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