6-2016

Taphonomy of a Lance Formation(Maastrichtian, WY) Dinosaur Bonebed with a Focus on Tooth Traces

Matthew A. McLain

Recommended Citation

McLain, Matthew A., "Taphonomy of a Lance Formation(Maastrichtian, WY) Dinosaur Bonebed with a Focus on Tooth Traces" (2016). *Loma Linda University Electronic Theses, Dissertations & Projects*. 410.
http://scholarsrepository.llu.edu/etd/410

LOMA LINDA UNIVERSITY
School of Medicine
in conjunction with the
Faculty of Graduate Studies

Taphonomy of a Lance Formation (Maastrichtian, WY) Dinosaur Bonebed with a Focus on Tooth Traces

by

Matthew A. McLain

A Dissertation submitted in partial satisfaction of
the requirements for the degree
Doctor of Philosophy in Earth Science

June 2016

Each person whose signature appears below certifies that this dissertation in his/her opinion is adequate, in scope and quality, as a dissertation for the degree Doctor of Philosophy.

, Chairperson

Leonard Brand, Professor of Biology and Paleontology

H. Paul Buchheim, Professor of Geology

Arthur Chadwick, Research Professor, Biology, Southwestern Adventist University

Stephen G. Dunbar, Professor of Biology

Ronald Nalin, Adjunct Assistant Professor of Geology

Kevin E. Nick, Associate Professor of Geology

ACKNOWLEDGEMENTS

There are a great many people that I should very much like to acknowledge as contributing to the completion of this project, but I would be remiss if I did not first thank my wife, Jessica McLain. She has been incredibly forbearing with me as I have worked countless hours on my dissertation and many more talking her ears off about my research. She has been supportive of my graduate studies and work, and I do not deserve to be married to someone as wonderful, thoughtful, loving, or caring as her. She has managed to work part time to help provide our necessary income during my graduate studies, and we have struggled together in having and raising two boys, Alaric and Cody. Through these stressful days she has always sought to encourage me, and I would not have been able to do this work without her constant support.

I am also deeply indebted to my undergraduate advisor and professor, John Whitmore. He worked hard to develop a strong geology program at Cedarville University. Through his guidance and the classes he and others taught at Cedarville, he was able to turn me from a kid who was obsessed with dinosaurs to a diligent and productive student of geology. His teaching, training, exhortation, and encouragement have been invaluable to me as I have been working on my PhD, and I cannot thank him enough for the time he invested in me.

Without Ken Coulson and his wife Beth, Jessica and I would have been lost and confused in the crazy world of southern California. They began to help us even before we moved out here from New York, and we have developed deep friendships that will last beyond our time together at Loma Linda. I spent many late evenings at the Coulson home discussing geology, paleontology, philosophy, and religion with Ken, and he has helped to keep me sane during my time in graduate school. Both he and Sarah Maithel have been close companions on trips to Geological Society of America conferences, and for that I am very thankful.

Ken and Beth also introduced Jessica and me to our church, the Anchor Bible Church of Redlands, which has helped us out in more ways than I would ever be able to explain. In the same manner that Loma Linda University has developed my abilities as a researcher, the Anchor Bible Church has greatly influenced my character, maturity, and faith as a person. Specifically, from the Anchor Bible Church, I would like to thank Todd Barnett for teaching me and giving me an opportunity to work part time so that Jessica could spend more time with the kids, Amee Thompson and her kids Neo, Trinity, and Niobe for watching my children on numerous occasions, and the rest of the church for their prayers and encouragement during this difficult, but rewarding, process.

On the scientific side of my life, my advisors Dr. Leonard Brand and Dr. Arthur Chadwick have given me great leadership in my research, writing, and teaching. Dr. Brand has encouraged my various research pursuits, and he has often guided me in what steps to take next as I sought to make my way through the confusing labyrinth of PhD coursework and studies. Additionally, he gave me the opportunity to greatly develop my skills as an educator in giving me the opportunity to teach the vertebrate paleontology class at Loma Linda University. Both he and Dr. Chadwick have helped me think through the complexities of the relationship between philosophy and science in a way that I would not currently understand without them. Dr. Chadwick has been a great guide in the field and has expanded my teaching ability by allowing me to teach some undergraduate students about dinosaurs and pterosaurs in the field. He was the one who first got me started on this particular project, and he has worked long hours for my benefit on several occasions during this project. For that I am incredibly grateful.

I also want to thank the members of my committee. As a committee, they have corrected my wrong thinking on scientific matters, and they have tested my abilities as a researcher, which has improved my scientific thinking and problem solving immensely. I want to thank Dr. Paul Buchheim for his very useful instruction in the field, and Dr. Kevin Nick for giving me the opportunity to teach mineralogy and for helping me understand making thin sections and using the XRD. I want to thank Dr. Ronald Nalin for not letting me off the hook in regards to understanding fluvial geology, and I am very thankful for Dr. Stephen Dunbar's insight into living organisms, which has helped me think through the paleobiology of dinosaurs.

Raúl Esperante, Andrew Farke, Howell Thomas, and Elizabeth Rega all assisted me in understanding the taphonomy of the bones I was studying, specifically the tooth traces (or lack thereof!). Without their help, I no doubt would have labeled many features as tooth traces that were in reality not made by a bite at all. I additionally want to thank Andrew Farke for allowing me to visit the collections in the Raymond Alf Museum on multiple occasions and for allowing us to search Hell Creek Formation bones in the collections for tooth traces. I also want to thank Dr. Luis Chiappe, Dr. Nathan Smith, and Maureen Walsh at the Los Angeles County Museum of Natural History for their help in identifying what bone of a tyrannosaurid HRS13997 was.

I am deeply indebted to two of my LLU colleagues, Dr. David Nelsen and Bethania Siviero. We worked together in the field and in the collections of SWAU on trying to understand the paleontology and especially taphonomy of these Lance

Formation bonebeds. David dug with me for two field seasons at Rose Quarry, and he was essential to aiding me in developing the field methods, excavating fossils, and trying to understand the depositional history of the Rose Quarry bonebed. Bethania and I have worked for many long hours on defining tooth trace criteria and distinguishing true tooth traces from other types of marks. I greatly appreciated our discussions on how to further research at the quarries, and I am confident she will do well in her dissertation work.

I must thank those besides David and Dr. Brand who helped me at Rose Quarry in digging up fossils and exposing the sedimentology of the site: Art Miller, Karin Covi, Brandon Marini, Katrina Marini, Michael Sprague, Jordan Oldham, Mark Guilliams, and other students including Kelby Carambot and Marcel Jackson. I am indebted to Rose Weeks for discovering Rose Quarry and to Dr. Keith Snyder, Ivan Snyder, and Karl Olson among others who did the preliminary work at the site. Without Keith and Ivan Snyder, I never would have been able to study HRS13997, the tooth-traced tyrannosaur bone which features largely in this dissertation, so I thank them for finding it and carefully gluing it. Along similar lines, I am grateful to Sabrina Illingworth for preparing the bone. I want to thank Dr. Kurt Wise and Pete Larson for visiting our site and providing helpful information on the geology of the Lance Formation. I also want to acknowledge Dominic Ombati in helping me with XRD preparation, Lance R. Pompe in teaching me to use ArcGIS, and Ranjan Fernando in sending me relevant papers. Finally, I want to thank Chris Griffin for his help in reading over portions of this manuscript, Elizabeth McLain in locating papers for me, Dr. Ryan Sinclair and Douglas Havens for help in 3D-printing a model of HRS13997, Elieze Strydom for help with registration and paperwork, Dr. Robert T. Bakker for helpful discussions on tyrannosaurid paleobiology and vertebrate paleontology in general, and my parents, Doug and Kristin McLain, along with my siblings Michael, Stephanie, and Elizabeth McLain, for encouraging me to pursue a dream that everyone seems to lose after they turn 10.

CONTENT

Chapter

Appendices

FIGURES

TABLES

ABBREVIATIONS

DW	Denticle Width
HRS	Hanson Research Station (Collection held at SWAU)
REE	Rare earth elements
RQ1	Rose Quarry 1
RQ1.5	Rose Quarry 1.5
RQ2	Rose Quarry 2
SEM	Scanning electron microscopy
SW	Striation Width
SWAU	Southwestern Adventist University
XRD	X-ray diffraction

ABSTRACT OF THE DISSERTATION

Taphonomy of a Lance Formation (Maastrichtian, WY) Dinosaur Bonebed with a Focus on Tooth Traces

by

Matthew A. McLain

Doctor of Philosophy, Graduate Program in Earth Science
Loma Linda University, June 2016
Dr. Leonard Brand, Chairperson

The Rose Quarry bonebed found in the Maastrichtian Lance Formation of eastern Wyoming possesses a complex blend of taphonomic signatures. Disarticulated, disassociated, fragmented bones of various states of abrasion from dinosaurs, turtles, and crocodilians are clustered together in a channelized sandstone unit. The mismatched taphonomic signatures of the bonebed suggest that it is a mixed assemblage, containing bones with different taphonomic histories that were washed together by a flood event. Sedimentological data, including the presence of large mud clasts in the bonebed, agree well with this hypothesis. The abundant breakage of the bones in the Rose Quarry bonebed is attributed mainly to trampling. This study highlights the striking variability possible in fluvial bonebeds, including differences in pre-burial history, depositional mechanism, subenvironment, and post-burial history.

Although only a few Rose Quarry bones show evidence of tooth traces, a similar nearby bonebed contained a tyrannosaurid metatarsal (HRS13997) that possessed numerous scores on the posterolateral surface near its ventral end. The presence of a *Knethichnus parallelum* tooth trace, the first known on a tyrannosaurid bone, allows for us to measure the widths of the striations left by the tooth denticles scraping along the bone’s surface. Comparison with theropod teeth from the Lance Formation leads us to conclude it was bitten by another tyrannosaurid, suggesting possible cannibalism in the species *Tyrannosaurus rex*.

CHAPTER ONE

INTRODUCTION

For the past 20 years, Southwestern Adventist University (SWAU) has been sending teams led by Art Chadwick to eastern Wyoming to uncover dinosaur fossils from the Lance Formation (Maastrichtian). Over 15,000 dinosaur bones have been collected, as well as remains from mammals and aquatic vertebrates such as crocodilians, turtles, bony fishes, and cartilaginous fishes, from what is conventionally considered an alluvial plain with fluvial systems (Robinson et al., 1996). Bones are usually well-preserved, but disarticulated. Even though elements from several species of dinosaurs have been discovered, the large majority of fossils come from the hadrosaur *Edmontosaurus*. Through the use of GPS technology coupled with GIS software, SWAU has created a three-dimensional reconstruction of their quarries without any of the surrounding rock. These reconstructions, coupled with observations from the field, have led Chadwick and his team to conclude that the bones in the Main Quarries are normally graded, with larger bones at the bottom grading up into smaller bones at the top of the bed (Weeks et al., 2015). Based on this data, it was suggested that this bonebed represents a massive submarine debris flow which sorted the skeletal elements of dinosaur carcasses. More recently, new quarries have been opened in different layers than the Main Quarries bonebed. Gar Ridge Quarry, Rose Quarry, and Ivarrest Quarry are all excavated out of fossiliferous sandstone deposits. In these three quarries, there are different taphonomic signatures and taxic abundances than in the Main Quarries. In Rose Quarry, there are very few bones of the hadrosaurid dinosaur *Edmontosaurus*, and the bones show varying preservation states not found in the Main Quarries. Because of the drastically different nature of the Rose Quarry bonebed when compared to the well-studied Main Quarries bonebed, I determined to analyze the sedimentology, taphonomy, and paleontology of Rose Quarry in order to arrive at a taphonomic history and depositional model for its origin.

In the process of studying the taphonomy of the Rose Quarry bones, I found marks on the bone surfaces which were difficult to interpret. Although many of these marks initially appeared to be tooth traces left by bites from crocodilians and theropod dinosaurs, it became clear that more robust criteria were needed in order to verify which marks were from teeth, and which marks had other origins. Bethania Siviero, David Nelsen, and I began a process of studying supposed tooth traces in the bones from the Main Quarries and Rose Quarry held at SWAU. We compared these marks to descriptions in the literature. Our refined tooth trace criteria will be described in an upcoming publication and are also presented in a different format in Appendix C.

While digging in June of 2015, Keith and Ivan Snyder stumbled upon a tyrannosaurid long bone from a currently unexcavated dinosaur bonebed in sandstone. Although this bone was not found in Rose Quarry, it was valuable for me to study as a part of my dissertation because it possessed numerous, well-preserved tooth traces on its surface. Through analysis of these tooth traces and the literature, I determined that these bites were made by a *Tyrannosaurus rex,* which may mean that this is an example of tyrannosaurid cannibalism, probably scavenging rather than predation. Such a discovery is helpful to understanding the taphonomy of Rose Quarry and the other Hanson Ranch quarries, and to understanding the paleobiology of tyrannosaurids – important constituents of Maastrichtian ecosystems.

Geologic Setting

The Lance Formation is a Maastrichtian quartz sandstone unit with accessory siltstone and mudstone beds. In North and South Dakota it overlies the Fox Hills Formation (Upper Cretaceous) and is overlain there and in Wyoming by the Fort Union Formation (Paleocene) (Lloyd and Hares, 1915). The contact between the Lance Formation and Fort Union Formation is the Cretaceous – Paleogene (K-Pg) boundary. At Dogie Creek in Wyoming, the K-Pg is characterized by the presence of a boundary clay containing hollow goyazite spherules overlain by a smectitic layer containing shocked quartz and an iridium anomaly (Bohor et al., 1987). This boundary is characterized by a fern spore spike and a last appearance datum (LAD) for all but one palynomorph taxon (Bohor et al., 1987). Analysis of drill cores from the Green River basin indicate that the Lance Formation is at least 2,500 feet thick. The Lance Formation is typically interpreted as fluvial strata deposited on an alluvial plain, including both meandering and braided river deposits (Robinson et al., 1996). Paleocurrent studies have indicated that the predominant flow direction was from the west with the suggested sediment provenance being the Wyoming-Idaho thrust belt (Montgomery and Robinson, 1997). The Lance Formation has been studied in cores from the Green River basin because it is a porous hydrocarbon reservoir (Montgomery and Robinson, 1997; Robinson et al., 1996). The Maastrichtian Lance Formation of Wyoming is thought to be equivalent with the Hell Creek Formation of Montana (Johnson et al., 2002) as is the Laramie Formation of Colorado (Lloyd and Hares, 1915). For a discussion of fluvial processes and deposits, see Appendix A.

Paleontology

The word “dinosaur” was first coined by Sir Richard Owen in 1842 to describe the incredibly large fossil reptiles that had been discovered in the previous years: *Iguanodon*, *Megalosaurus*, and *Hylaeosaurus* (Owen, 1842). The term is usually translated as “terrible lizard”, but a more accurate translation that expresses Owen’s meaning in the current vernacular would be “fearfully great (or awesome) lizard”; he named them such as he was motivated by their immense size and majesty (Torrens, 2012). In these first three genera of dinosaurs discovered, the two major dinosaurian groups can already be found (Figure 1). *Iguanodon* and *Hylaeosaurus* belong to the order Ornithischia (“bird-hipped”), which contains the major subdivisions of Ornithopoda, Thyreophora (Stegosauria + Ankylosauria), and Marginocephalia (Ceratopsia + Pachycephalosauria) (Butler et al., 2008; Weishampel, 2004). *Megalosaurus*, on the other hand, belongs to the order Saurischia (“lizard-hipped”) which includes the major subdivisions Sauropodomorpha, the long-necked dinosaurs, and Theropoda, the bipedal typically carnivorous dinosaurs (Holtz and Osmólska, 2004). It is commonly believed that certain dinosaurs from the group Maniraptora, which includes the taxa Dromaeosauridae, Troodontidae, Oviraptorsauridae, Caenagnathidae, and Therizinosauria, within the suborder Theropoda evolved into birds during the Mesozoic. Ergo, Aves is phylogenetically nested within Theropoda and Dinosauria (Padian and Chiappe, 1998; Xu et al., 2009). Non-avian dinosaur fossils have only been found in Mesozoic rocks from the Carnian of the Triassic system (dated at 237-228.4 Ma) to the Maastrichtian of the Cretaceous system (dated at 72.1-66 Ma) (Gradstein et al., 2012).

Upper Cretaceous dinosaur bonebeds of North America are dominated by the remains of hadrosaurs and ceratopsians. Accessory herbivores in these Upper Cretaceous, North American bonebeds include other ornithischians such as ankylosaurs, pachycephalosaurs (Sullivan, 2006), and non-hadrosaur ornithopods (Loeuff, 2012) and the saurischian ornithomimosaurs, therizinosaurs, oviraptorids (Loeuff, 2012; Zanno and Makovicky, 2010), caenagnathids (Longrich et al., 2013), and sauropods (only in the *Alamosaurus* fauna of the Southwestern USA) (Lehman, 1987). Carnivores found in the same layers include troodontids (however, at least some troodontids may have been omnivorous (Holtz et al., 1998)), dromaeosaurs, tyrannosaurs (Barsbold, 1974; Loeuff, 2012) and the tooth genus *Paronychodon* (Carpenter, 1982). Juvenile dinosaurs and dinosaur eggshells are rare in the Lance Formation, as they are worldwide, but have been found (Carpenter, 1982). Although small ornithischians (less than 100 kg) are present in the Upper Cretaceous, they are less diverse and abundant than the large hadrosaurs and ceratopsians (Evans et al., 2013b). Because this distribution differs drastically in comparison to modern mammal communities, this disjunction in diversity has been attributed to lower preservation potential of smaller dinosaurs (Evans et al., 2013b). Non-dinosaurian constituents of these strata include azhdarchid pterosaurs, crocodilians, turtles, small mammals, fish, and various invertebrate taxa (Witton and Naish, 2008). Fossil tracks of a hadrosaur, non-avian theropods (including the ichnospecies *Saurexallopus zerbsti* and possible tyrannosaurid tracks), birds, and invertebrates have been reported in the Lance Formation (Lockley et al., 2004).

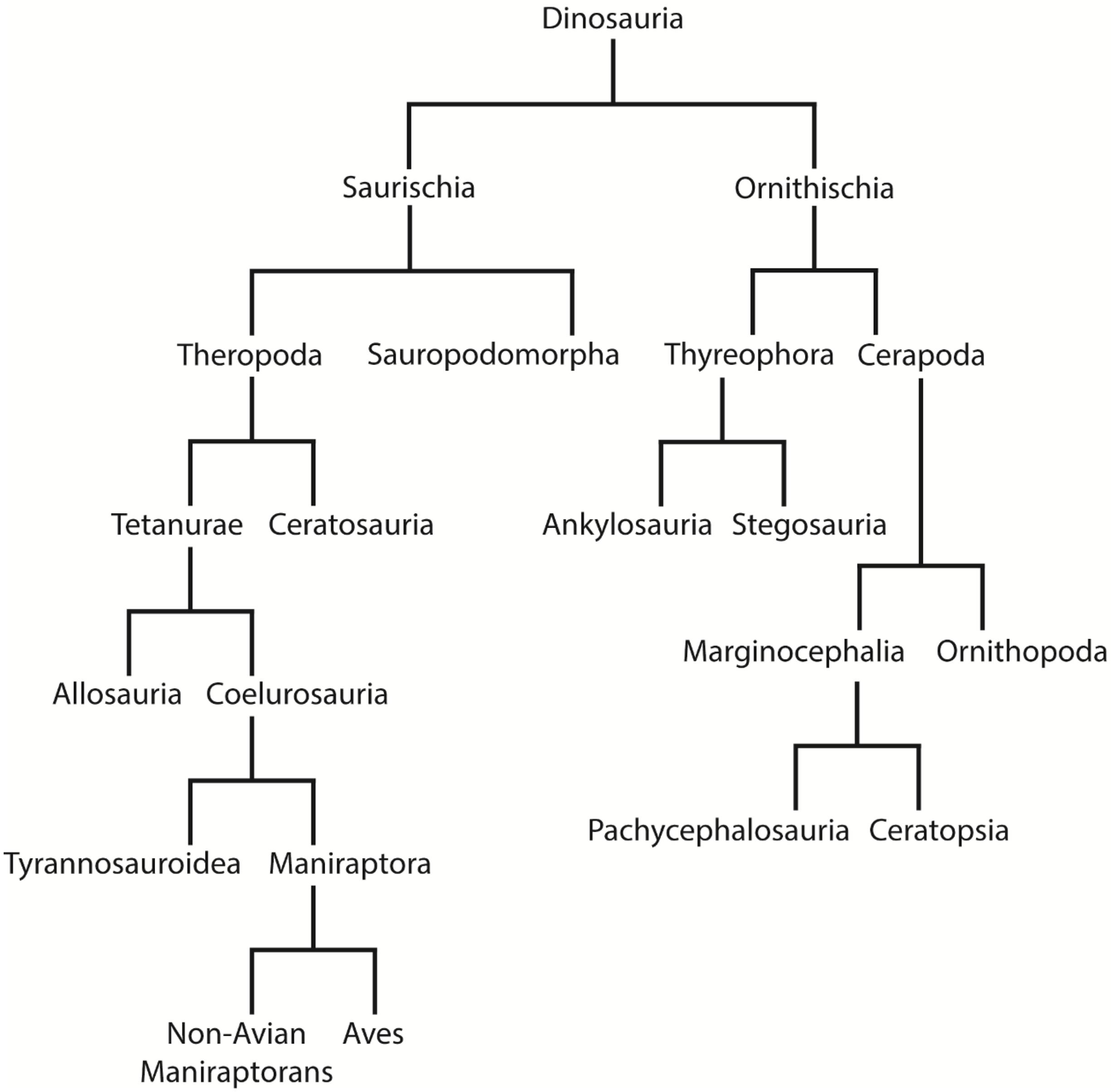

Dinosauria
Saurischia
Ornithischia
Theropoda
Sauropodomorpha
Thyreophora
Cerapoda
Tetanurae
Ceratosauria
Ankylosauria
Stegosauria
Marginocephalia
Ornithopoda
Allosauria
Coelurosauria
Pachycephalosauria
Ceratopsia
Tyrannosauroidea
Maniraptora
Non-Avian Maniraptorans
Aves

Figure 1. Simplified cladogram of Dinosauria adapted from Butler et al. (2008) and Holtz and Osmólska (2004).

The Hanson Ranch Quarries of the Lance Formation (Maastrichtian) of Eastern Wyoming include representative species of most of these taxa. The main constituent of the quarries, representing over 90% of the bones discovered in the past 15 years, is the hadrosaur *Edmontosaurus annectens*. Hadrosaurs are characterized by their duck-like beaks and their large batteries of cheek teeth. Interestingly, several other Upper Cretaceous hadrosaur-dominated bonebeds are known from the Western United States (Varricchio and Horner, 1993). *Triceratops horridus*, the famous three-horned ceratopsian, is the second most commonly found dinosaur from the quarries. A few skulls and skull fragments of *Pachycephalosaurus wyomingensis*, a pachycephalosaur, have been found in the area. Pachycephalosaurs are obligate bipedal dinosaurs with thickened skull roofs. Nodosaurid – armored ankylosaurs without tail clubs – osteoderms have also been found. The majority of theropod fossils found in the quarries are teeth. Abundant teeth as well as some other bones are known for two tyrannosaur taxa: *Tyrannosaurus rex* and *Nanotyrannus lancensis*. A partial skull assigned to *N. lancensis* has also been discovered, but is as of yet undescribed. Evidence of smaller carnivores comes in the form of troodontid teeth, including at least one tooth of the species *Pectinodon bakkeri*, and dromaeosaur teeth assigned to the genus *Dromaeosaurus*, but probably better assigned to *Acheroraptor* (Evans et al., 2013a). A single metatarsal of a possible ornithomimosaur was found in 2010. Some teeth, assigned to the coelurosaur genus *Richardoestesia* have been discovered (however, Larson and Currie (2013) suggest that *Richardoestesia*-like teeth from outside the Dinosaur Park Formation, Oldman Formation, or Aguja Formation should be labeled as cf. *Richardoestesia*). Occasional mammal (multituberculate and metathere) teeth have been found in the quarries, but as of yet no pterosaur fossils have been discovered. Crocodilian (*Brachychampsa* and *Borealosuchus*) and turtle (predominantly trionychids) fossils are common in the deposits, as are gar scales. Several shark, ray, and skate teeth, as well as bivalves and gastropods, have also been discovered in the quarries.

Taphonomy

It is fitting in the introduction to briefly discuss some of the important terms used in this taphonomic study. For a fuller discussion of taphonomy, including a more detailed discussion of the taphonomic signatures described here, please see Appendix B: A Guide to Taphonomy.

Taphonomy concerns everything that happens to an organism from the moment it dies until it is uncovered as a fossil. One of the most important factors to consider in taphonomic analysis of a bonebed is whether bones are autochthonous (in place), parautochthonous (transported within environment), or allocthonous (significantly transported). Fossils can be inspected for taphonomic signatures that hint at their history before burial. Notable taphonomic signatures for consideration include: 1) articulation – well-articulated specimens suggest rapid burial; 2) orientation – specimens oriented in a certain direction suggest a transport direction; 3) abrasion – heavy abrasion on bones suggests transport, but a lack of abrasion does not necessarily rule out that transport has taken place; 4) weathering – bones exposed to the elements before burial will show different weathering signatures depending on how long they were exposed and to what climatic factors; 5) bioerosion – bones can be bored by invertebrates or bitten by predators, scavengers, and/or gnawing rodents; and 6) trampling – bones that have been trampled may show trampling marks and/or trampling notches.

CHAPTER TWO

SOLVING TAPHONOMIC JIGSAW PUZZLES: COMPLEX TAPHONOMIC SIGNATURES IN A RECENTLY DISCOVERED LANCE FORMATION (MAASTRICHTIAN) DINOSAUR BONEBED, WYOMING

Abstract

The uppermost Cretaceous (Maastrichtian) Lance Formation is one of the most productive of the dinosaur-bearing formations of the western United States, yielding well-known dinosaur genera such as *Tyrannosaurus*, *Triceratops*, *Edmontosaurus*, and *Pachycephalosaurus*. On a ranch in eastern Wyoming, multiple fossil quarries have been excavated at several sites in close proximity and are collectively termed the Main Quarries. However, the recently discovered Rose Quarry site differs significantly from the Main Quarries in its lithology, present taxa, and state of fossil preservation. Abundant, yet fragmentary, disarticulated and disassociated bones and teeth are contained within a channelized sandstone unit along with mud clasts. The vertebrate fossils of Rose Quarry possess varying abrasion states suggesting a mixed assemblage, with some bones also possessing tooth traces and trampling marks. We present a depositional model for the Rose Quarry bonebed in which a flood mixes bones already present in the channel or from an older bonebed with bones from the floodplain that had been bitten, trampled, and broken. This study illustrates that striking variability is possible between fluvial bonebeds, and that this variability is influenced by pre-burial and post-burial factors, as well as depositional subenvironment and mechanisms.

Introduction

Significance

Bonebeds, defined as single sedimentary strata with a bone concentration that is unusually dense relative to adjacent lateral and vertical deposits (Behrensmeyer, 2007), provide us with extraordinary glimpses into ancient ecosystems and the paleobiology of extinct taxa including trophic relationships, behavior, ontogeny, and intraspecific variation (Brinkman et al., 2007; Manzig et al., 2014; Ryan et al., 2001; Wang et al., 2014). Consideration of the taphonomy and sedimentology of vertebrate bonebeds *in situ* is extremely important to understanding the depositional history of the fossils of interest. In particular, reconstructing the general depositional environment can prove essential to providing a larger context to detailed paleontological observations. Approximately half of all bonebeds recorded in the ETE Bonebed Database are in fluvial paleoenvironments, particularly in the Cretaceous where 61% of bonebeds are interpreted as fluvial (Behrensmeyer, 2007). As a result, numerous studies have looked at how the remains of organisms are transported, concentrated, and buried in fluvial systems (e.g., Aslan and Behrensmeyer, 1996; Behrensmeyer, 1975, 1982, 1988; Smith, 1993; Voorhies, 1969).

Many Upper Cretaceous dinosaur bonebeds are interpreted as fluvial deposits, but a simple designation of an assemblage as fluvial masks the possible depositional complexities present in many dinosaur bonebeds. This is especially a concern in light of a recent study by Moore (2012) in which he concludes that isotaphonomy should not be assumed even for bonebeds of similar facies without other evidence. The sharp contrast in bonebed characteristics that can occur within the same fluvial paleoenvironment is illustrated well in two recently discovered bonebeds from the Lance Formation

(Maastrichtian) of eastern Wyoming. The first bonebed discovered was quarried in several locations and is collectively referred to as the Main Quarry bonebed. Bones in this assemblage are disarticulated and disassociated, but are typically unbroken and very well-preserved, showing essentially no abrasion or weathering. The large majority of bones come from the hadrosaur *Edmontosaurus*, and they are normally graded in a mudstone. Weeks et al. (2015) concluded that this 1 m thick, matrix-supported bonebed represents a debris flow deposit. Another bonebed, found lower stratigraphically and less than a kilometer away, is drastically different in its lithology, sedimentology, present taxa, and taphonomy. This bonebed, called the Rose Quarry bonebed, occurs at the base of a fine-grained, trough cross-bedded sandstone, and it contains almost no identifiable hadrosaur material. Instead, the majority of the fossils come from turtles, ceratopsids (cf. *Triceratops*), and crocodilians. Although the bones are disarticulated and disassociated as in the Main Quarry bonebed, the bones in the Rose Quarry bonebed vary in preservation from being very well-preserved to unidentifiable bone gravel. In addition, field excavations yielded abundant broken bones – in stark contrast to the whole bones found at the Main Quarry bonebed. As we excavated this new site, we were surprised by the great differences between two Lance Formation bonebeds separated only by a small ravine and less than a dozen meters in stratigraphic thickness.

We thus sought to determine the depositional history of the Rose Quarry bonebed in order to understand why it is so different than the Main Quarries bonebed. Namely, we needed to determine what processes were involved in depositing the bones and sediment, and what was the cause for the abundant bone breakage. We suspect that the Rose Quarry bonebed is a mixed assemblage, containing bones with varying taphonomic histories.

Through analysis and interpretation of the taphonomic and sedimentological data of the Rose Quarry bonebed, we seek to not only explain the depositional history of this bonebed, but also to provide clues that can help other researchers describe and interpret fluvial bonebeds, especially the problem of abundant bone breakage.

Geologic Setting

The Lance Formation of North Dakota, South Dakota, and Wyoming is one of several dinosaur-bearing formations from western North America, and is thought to be equivalent with the Hell Creek Formation of Montana (Johnson et al., 2002). Both of these Maastrichtian formations are composed primarily of quartz sandstone with accessory siltstone and mudstone beds. In Wyoming, the Paleocene Fort Union Formation overlies the Lance Formation, which in turn overlies the Meeteetse Formation in the Wind River and Bighorn Basins and the Fox Hills Sandstone in the Powder River Basin (Connor, 1992; Lloyd and Hares, 1915). The contact between the Lance Formation and the Fort Union Formation is the Cretaceous – Paleogene (K-Pg) boundary.

The Lance Formation is typically interpreted as fluvial strata deposited on an alluvial plain that incorporates both meandering and braided river deposits (Robinson et al., 1996). Paleocurrent studies have indicated that the predominant flow direction was from the west with the Wyoming-Idaho thrust belt as the suggested provenance of the sediment (Montgomery and Robinson, 1997).

The site of interest is on a cattle ranch in the eastern flank of the Powder River Basin in Niobrara County of eastern Wyoming. This site has yielded over 15,000 vertebrate fossil bones during its nearly twenty years of excavation. There are several distinct bonebeds on the ranch, spread over an area greater than 1 km^2. The Main Quarry bonebed, exposed at six locations (North Quarry, South Quarry, Southeast Quarry, Teague Quarry, West Quarry, and Neufeld Quarry), is roughly 1 m thick and consists of normally graded isolated bones in a fissile mudstone. Most work over the past fifteen years has occurred at the Main Quarries. However, new bonebeds in sandstone units on the same ranch have recently been explored. One such bonebed (Rose Quarry), which outcrops at the top of a small hill, was discovered in 2011 (see Figure 2). Fossils from Rose Quarry are typically found at the base of the bed along with iron concretions and large mud clasts. The base of this sandstone unit shares an erosional contact with an underlying fissile mudstone unit rich in fragmentary plant fossils.

Stratigraphy within the Lance Formation has been notoriously difficult (Connor, 1992), and the same is true for local stratigraphy on the ranch as “most apparent horizons are diagenetically altered beds that are not reliably traceable over distance” (Weeks and Chadwick, 2011). However, Weeks and Chadwick (2011) were able to trace a 2 m thick seismite bed continuously for up to a kilometer in outcrop across several locations. They deduced that there are three fossiliferous horizons beneath this seismite datum (Figure 3). One is 15 m below the seismite bed and corresponds to Gar Ridge Quarry, a typical microvertebrate site (Eberth et al., 2007b). The next fossiliferous horizon is 29 m below the seismite bed and corresponds to the Main Quarries. The third fossiliferous horizon is 38 m below the seismite bed, and it appears to correspond to Rose Quarry. If the stratigraphy is correct, then Rose Quarry is stratigraphically distinct from the mudstone bonebed excavated at the Main Quarries and the sandstone bonebed excavated at Gar Ridge Quarry.

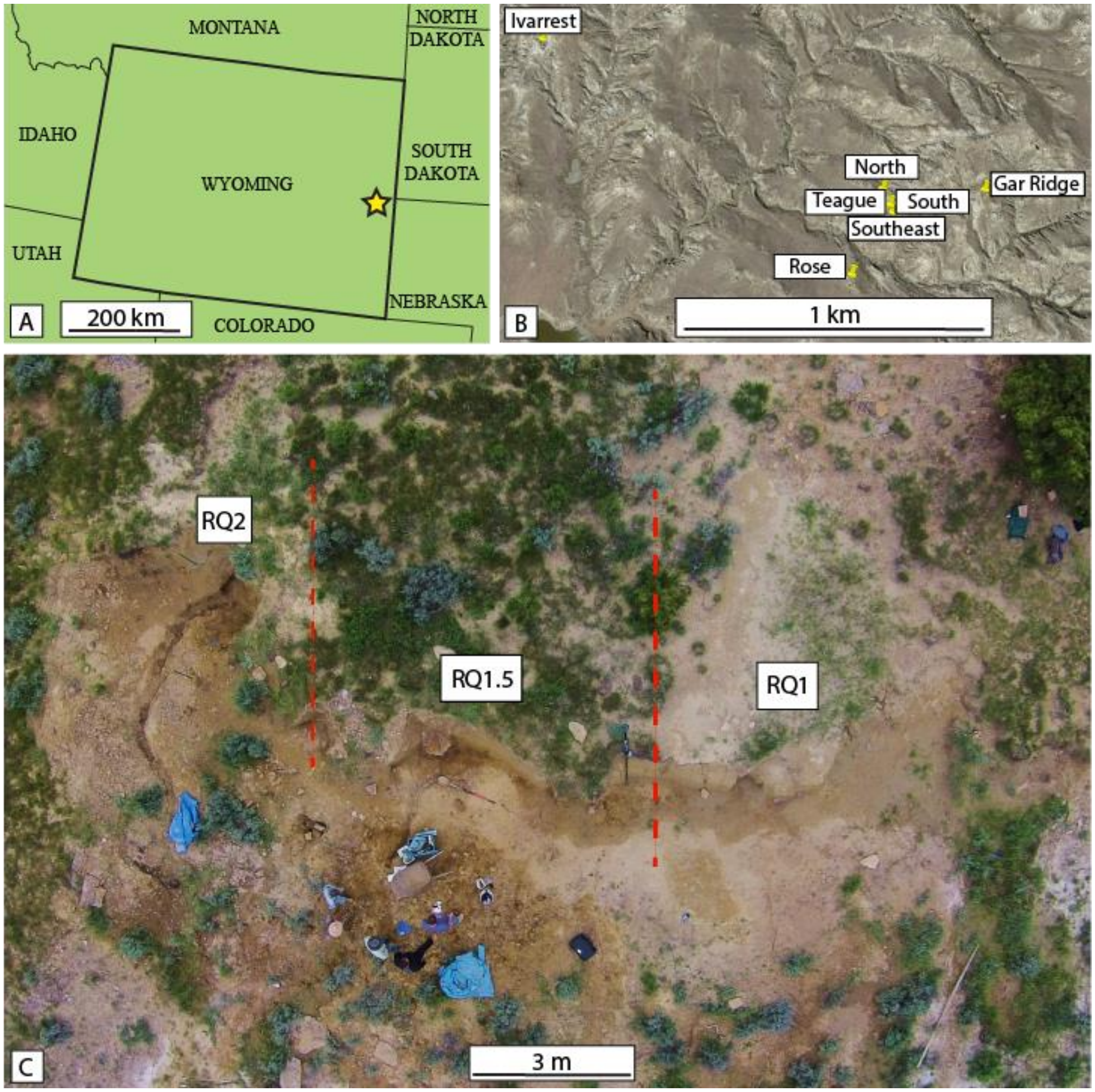

MONTANA
NORTH DAKOTA
IDAHO
WYOMING
SOUTH DAKOTA
UTAH
NEBRASKA
A
200 km
COLORADO
B
Ivarrest
North
Gar Ridge
Teague
South
Southeast
Rose
1 km
RQ2
RQ1.5
RQ1
C
3 m

Figure 2. Location of Rose Quarry. **A)** Map of Wyoming with the study site indicated by a star. **B)** Location of Rose Quarry on the ranch in comparison to other quarries. **C)** Locations of the sub-quarries: Rose Quarry 1 (RQ1), Rose Quarry 1.5 (RQ1.5), and Rose Quarry 2 (RQ2), with the boundaries between them delineated with a dashed red line. Image B modified from Google Earth, Data: SIO, NOAA, U.S. Navy, NGA, and GEBCO. Image C taken aerially as a single capture by a drone.

Hadrosaur bonebeds are common throughout the Upper Cretaceous of the western United States (Varricchio and Horner, 1993). In the Main Quarries, the majority of bones (>90%) have been assigned to the hadrosaur *Edmontosaurus annectens*. Accessory taxa found in this mudstone bonebed include the dinosaurs *Triceratops horridus*, *Pachycephalosaurus wyomingensis*, *Thescelosaurus neglectus,* Nodosauridae indet., *Tyrannosaurus rex*, *Nanotyrannus lancensis* – considered by some authors to be a juvenile *Tyrannosaurus rex* (Carr, 1999; Holtz, 2001), *Pectinodon bakkeri*, Dromaeosauridae indet., *Richardoestesia* sp., the crocodilians *Brachychampsa* and *Leidyosuchus*, multiple turtle taxa, multiple mammal taxa including multituberculates, gar, sharks, batoid skates, gastropods, bivalves, angiosperms, and conifers.

The bonebed excavated at Rose Quarry is dominated by turtle, crocodilian, and ceratopsid (cf. *Triceratops*) remains. Unlike the Main Quarries, hadrosaur fossils appear to be uncommon. Gar scales are abundant, and teeth from theropods, crocodilians, and skates are common. Remains of nodosaurids, *Pachycephalosaurus*, and *Thescelosaurus* have been found, but are rare. Plant material is rare in the sandstone beds of Rose Quarry. However, plant material is common in the mudstone layer below, as well as within the mudstone clasts found within the bonebed horizon.

The differences in prominent taxa, sedimentology, and bone fragmentation between the Main Quarries and Rose Quarry prompted further investigation of this new site. Through extensive study of the paleontology, taphonomy, and sedimentology, we sought to explain the taphonomic and depositional history of this bonebed.

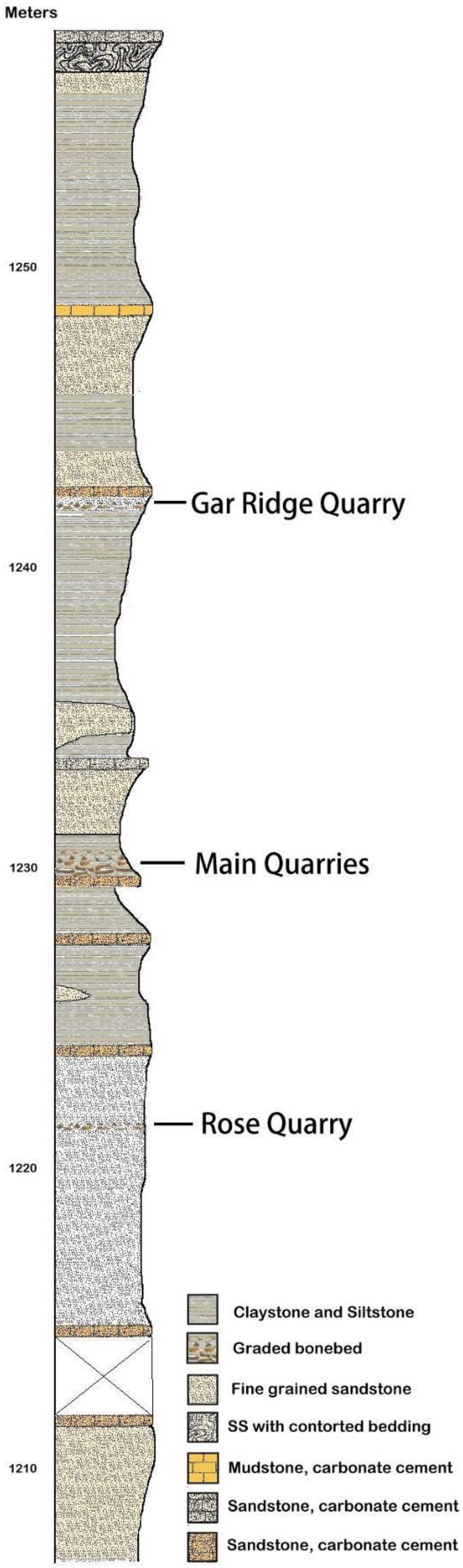

Meters
1250
Gar Ridge Quarry
1240
Main Quarries
1230
Rose Quarry
1220
1210
Claystone and Siltstone
Graded bonebed
Fine grained sandstone
SS with contorted bedding
Mudstone, carbonate cement
Sandstone, carbonate cement
Sandstone, carbonate cement

Figure 3. Stratigraphic column of the Hanson Ranch Quarries. Figure adapted from Weeks and Chadwick (2011). SS stands for sandstone.

.

Methods

Field Methods

Field research was conducted every June from 2011-2015. During each season, a team of three to five people worked at Rose Quarry. For each fossil discovered, an identification card was created. The cards contained a unique field number, tentative taxonomic assignment, description and tentative assignment of the skeletal element, discoverer's name, and the page number of the field book which contained a more detailed description. In our field notebooks, we recorded the specimen field number, skeletal and taxonomic assignment, relevant sedimentologic and taphonomic features in and around each fossil, and a sketch of the specimen including length and width measurements. While the fossil was still in place, we recorded its location using a Magellan Z-Max RTK (real-time kinematic) GPS rover with at least three points recorded for every catalogued specimen with sub-centimeter measurement accuracy. After the bones were cleaned, photographs of the bones were combined with their GPS coordinates to create a digital aerial map of the quarry with the matrix removed. Small, unidentifiable bone fragments and turtle shell fragments under 3 cm in diameter were not given specific field numbers, but their locations were marked by a single GPS point each. These specimens were collected in bags marked with the name of their particular sub-quarry. Additional observations of sedimentologic and taphonomic features in the Rose Quarry were recorded, sketched, and photographed with centimeter scales. In conjunction with the excavation and study of fossils, we conducted facies analysis on the Rose Quarry bonebed and its associated layers (Figure 4) utilizing the fluvial facies codes from Miall (1978 as listed in Miall, 1982). We used a Brunton compass to determine paleocurrent

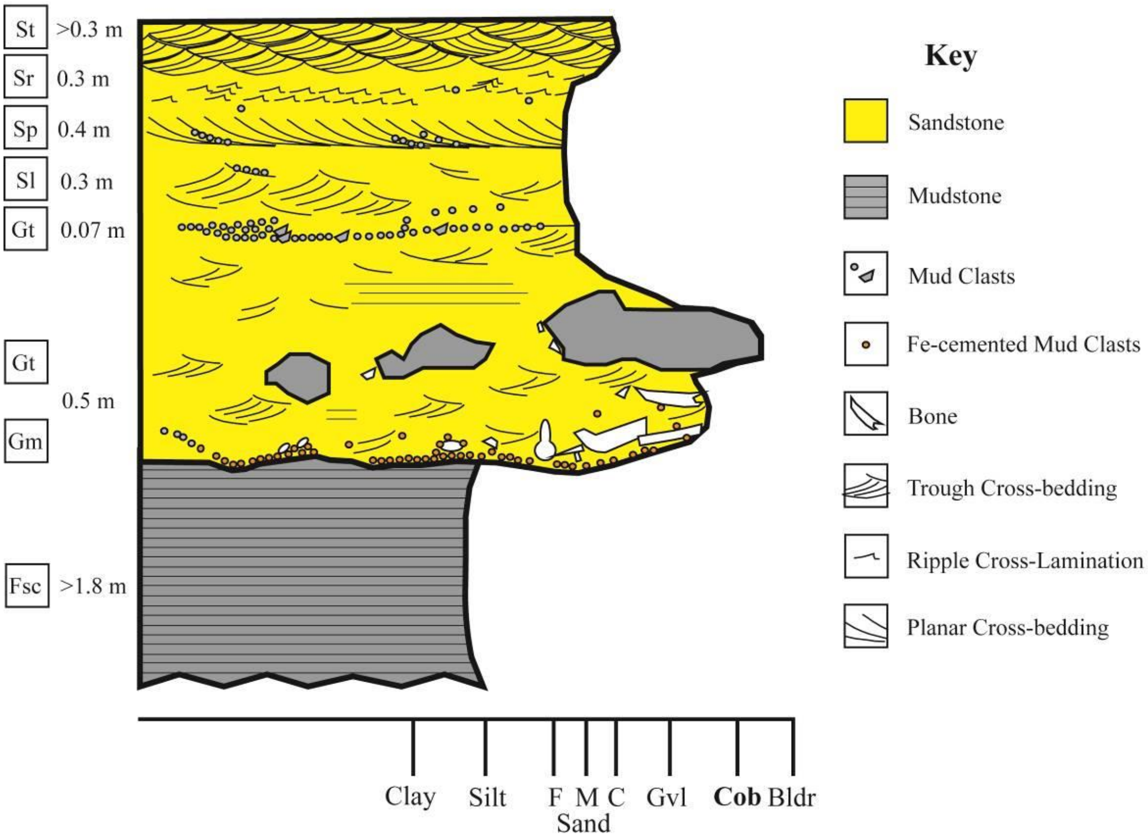

St >0.3 m
Sr 0.3 m
Sp 0.4 m
Sl 0.3 m
Gt 0.07 m
Gt
0.5 m
Gm
Fsc >1.8 m
Clay
Silt
F M C
Sand
Gvl
Cob Bldr
Key
Sandstone
Mudstone
Mud Clasts
Fe-cemented Mud Clasts
Bone
Trough Cross-bedding
Ripple Cross-Lamination
Planar Cross-bedding

Figure 4. Generalized stratigraphic column of the units and facies at Rose Quarry. Miall (1977) fluvial facies codes are listed on the far left (see Table 6 for descriptions of the facies codes). See text for unit descriptions. Abbreviations: Bldr, boulder; C, coarse sand; Cob, cobble; F, fine sand; M, medium sand.

directions from dip-azimuth measurements of cross-beds.

To better understand the extent of the bonebed, we dug exploratory pits extending laterally from Rose Quarry along the hill at approximately the same elevation as the bonebed. At each pit, beginning well above where we expected the bonebed to be, we excavated until we encountered the underlying mudstone unit. After we flattened and cleaned the walls of the pits, we took notes, measurements, and pictures of the visible layers. After exposing the layers, we utilized the GPS rover to mark distinctive stratigraphic surfaces that could help trace the architecture of the bonebed including the top of the mudstone unit underlying the bonebed (TML) and the top of a concretion-rich layer associated with the bonebed (TCL). We also exposed large vertical sections along multiple areas within Rose Quarry – Rose Quarry 1 (RQ1) and Rose Quarry 2 (RQ2) – and recorded elevations for TML and TCL with the GPS rover. We also photographed Rose Quarry aerially with a DJI Phantom 2 Vision Plus drone loaned from Cedarville University.

Lab Methods

After fossils were collected in the field, they were taken to Southwestern Adventist University (SWAU) to be prepared. At the SWAU fossil collections, I (MM) analyzed all prepared bones for abrasion, weathering, breakage/fragmentation, tooth traces, and trample marks. Only a subset of the excavated bones had been prepared (619 of 1,652), but we believe that this sample is representative of the quarry. As we dug, every bone was collected, and then bones were packed into boxes the same evening of their collection. SWAU workers prepared bones box by box, so that there was no particular preference as to which bones were prepared first. I used the criteria and categories from Ryan et al. (2001) to classify abrasion (Table 1), weathering (Table 1), and breakage/fragmentation (Table 2) on the Rose Quarry bones and teeth. Tooth traces on the bones were analyzed according to methods we developed (manuscript in preparation), which are modified from existing criteria in the literature (Binford, 1981; Njau and Blumenschine, 2006; Pobiner, 2008; Pobiner et al., 2007), and the traces were identified as belonging to one of four categories: pits, punctures, scores, or furrows. I identified trample following Fiorillo (1984, 1989). Trample marks are sets of shallow, subparallel scratches on the surface of bones thought to be caused by small grains of quartz or feldspar dragging along the surface of a bone when it is stepped on (Behrensmeyer et al., 1986; Fiorillo, 1984, 1989). The mineral grains are most likely pressed between the bone and the trampler's foot (Fiorillo, 1987). I also searched the Rose Quarry for a second kind of trampling bone modification occurring on oblique fracture angles called a trampling notch (Blasco et al., 2008). I recorded all taphonomic information on the bones at SWAU in a Microsoft Excel 2013 spreadsheet.

We used Adobe Illustrator CS5 to measure orientations of 335 bones (257 in RQ1 and 78 in RQ2) on the digital Rose Quarry map. We only measured orientations of bones that had one axis that was obviously longer than any other. In order to plot the data as rose diagrams, we utilized the free software PAST v. 3.08, a paleontological statistics software package (Hammer et al., 2001). Bone orientation significance was statistically analyzed with a Rayleigh's test.

Table 1. Abrasion and weathering definitions from Ryan et al. (2001).

Taphonomic Criterion	Stage 0	Stage 1	Stage 2	Stage 3
Abrasion	Fossil has a pristine surface and shows no signs of abrasion.	Broken edges of the fossil are rounded and the surface is polished.	Broken and unbroken edges of the fossil are well-rounded, surface is well-polished, and the original texture is still discernible.	All edges of the fossil are extremely well-rounded, the surface is very well-polished, and processes are simply bumps.
Weathering	No cracking or flaking on fossil surface.	Fossil surface has cracks that are parallel or sub-parallel to the internal fibrous structure of the bone. Long bone ends in good condition.	Parallel or sub-parallel cracks are starting to penetrate into the marrow cavities of long bones, flaking occurs on the surface at these cracks, and the ends of long bones are either deeply eroded or missing.	Large chunks of the outer laminated bone have entirely flaked away, and the remaining surface is highly cracked and flaking.

Table 2. Fracture type definitions adapted from Ryan et al. (2001).

Fracture Type	Description
Collection	Fracture made during collecting or preparing a specimen.
Longitudinal	Break parallel to the long axis of a bone, which can be due to desiccation or be a modified compression fracture.
Spiral (Green)	Breaks occurring at angles not perpendicular to the bone's long axis. The breaks are often saw-toothed, and they indicate breakage prior to fossilization.
Transverse (Compression)	Bone appears to be crushed. The pattern can include multiple stepped cracks, but the cracks are parallel to each other. These are usually attributed to sediment deformation, but they may indicate trampling.
Indeterminate	The fracture cannot be easily placed into another category.
"Straight"	An indeterminate fracture that is very straight.
Shear	A fracture created by biting through a bone diagnosed by the presence of a tooth trace at the break. This is distinguished from chewing.

Results

Sedimentology

Directly beneath the Rose Quarry bonebed is a fissile, gray mudstone rich in plant fossils (Miall code Fsc) including amber, but lacking in vertebrate fossil material. The contact between the mudstone unit and the bonebed is uneven with irregularities on the cm-scale. We could not measure the full thickness of the mudstone unit as its lower contact is covered, but the greatest thickness observed is 1.8 m.

The bonebed proper (~0.5 m thick) can be split into two sub-units, each differentiated by a separate facies. The lower sub-unit (Miall code Gm), which we referred to as the concretion layer, contained abundant, well-rounded, generally spherical, gravel-sized mud clasts heavily cemented by iron oxides (hematite and goethite), fossil gar scales, and fossil bones and teeth. The fabric of the lower sub-unit is clast-supported. Where major excavation has occurred, the lower bonebed sub-unit lies directly above the mudstone, separated by an erosional contact, but toward the south the bonebed is thinner, higher in elevation, and resting on sandstone. Within the lower subunit, the bones are sometimes imbricated. The upper bonebed sub-unit facies (Miall code Gt) has considerably fewer gravel-sized mud clasts but instead contains very large, subangular to subrounded, mud clasts, some of which are over 0.7 m in diameter, and wider horizontally than vertically (Figures 5 and 6). Small bones are occasionally found in this upper sub-unit, often adjacent to the large mud clasts. The large mud clasts sometimes touch the contact with the underlying mudstone or rest directly on bones (Figure 6B). No vertebrate fossils have been found within the large mud clasts, but plant fossils are common. The matrix of the bonebed is very fine to fine, trough cross-bedded to planarbedded, sandstone (Figure 5A). Thin section analysis and XRD of sandstone samples from the bonebed show that roughly half of the grains are quartz, with abundant feldspars (including potassium feldspar), chlorite, and accessory micas and pyroxenes. Volcanic and metamorphic rock fragments, plant fragments, and small bone fragments were also noted in the thin sections. Hematite and goethite cement is common in the sandstone. The upper sub-unit contains fewer small mud clasts than the lower. In some places, the upper portion of the upper sub-unit contains coarser, medium sand. Paleocurrent direction, as read from the occasional cross-beds in and near the bonebed, is west to east.

A discontinuous layer, or sometimes two layers, of gray, subrounded to rounded, gravel-sized mud clasts overlies the bonebed unit in most locations (Figure 5B), varying in thickness from 10-70 mm (Miall code Gt). In some locations, imbrication is visible in these small mud clasts. These mud clasts differ from those in the bonebed in that they are never iron-cemented and they seem to lack fossil plant material. Trough cross-bedded sandstone (0.21-0.3 m thick), very similar in structure to the sandstone of the upper portion of the bonebed, overlies the mud clast layer. Where the small mud clast layer is absent, the two trough cross-bedded sandstone intervals essentially represent a continuous unit (Miall code Sl).

Overlying this trough cross-bedded sandstone is another sandstone unit (~0.4 m thick) consisting of a large planar cross-set facies with tangential foresets often covered in mud drapes (Miall code Sp, Figure 5B). Occasional ripples and gravel-sized mud clasts are present in this unit. Directly above this unit is a sandstone facies with unidirectional ripple cross-laminations (0.2-0.3 m thick) also often containing mud drapes (Miall code Sr, Figure 5C). Overlying the rippled sandstone and capping the Rose Quarry hill is a

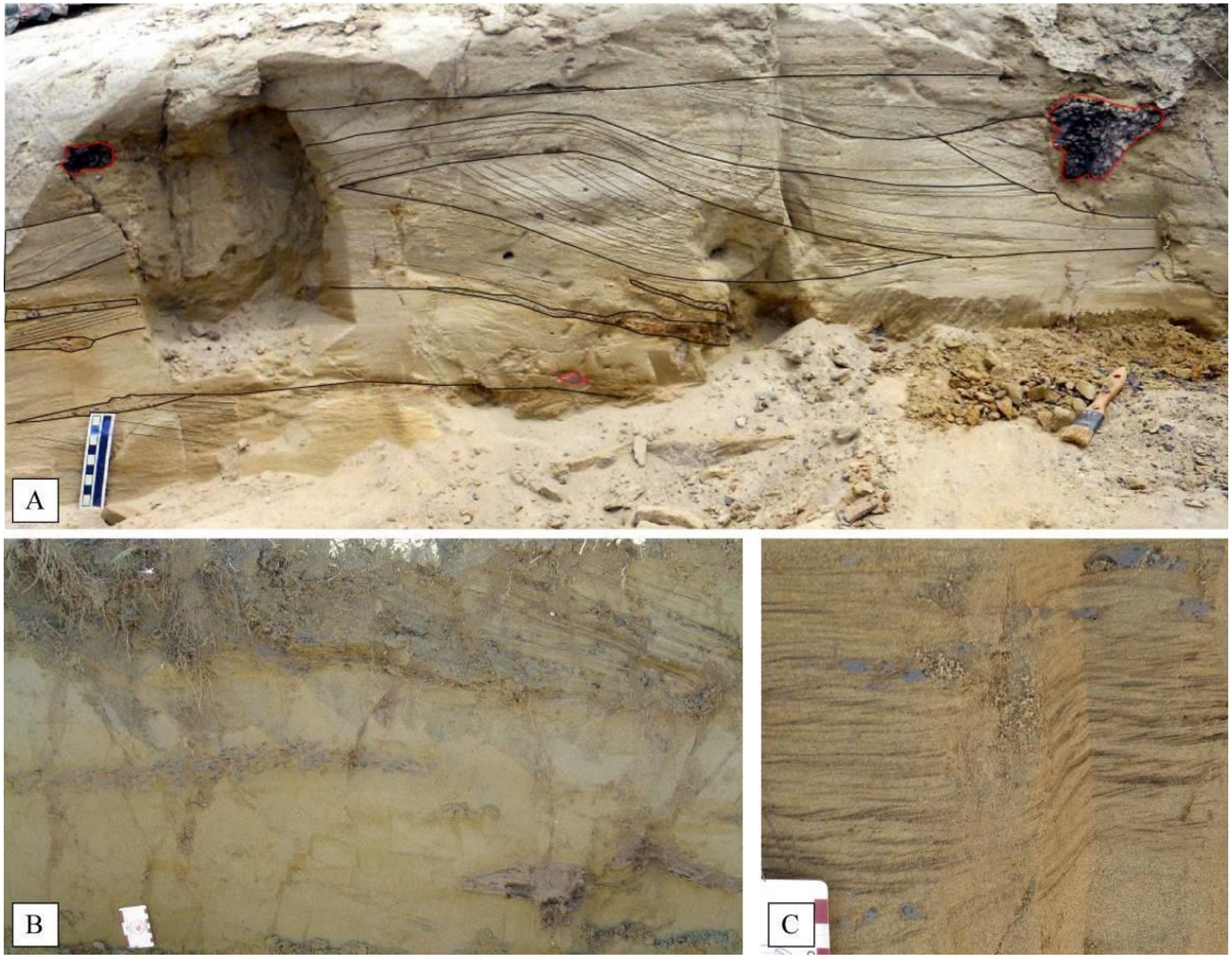

A
B
C

Figure 5. Sedimentology of Rose Quarry. **A)** A cross-section of Rose Quarry 1 exposed roughly perpendicular to paleocurrent direction, overlain with line drawings delineating the cross-sets and outlining the mud clasts. **B)** Several structures exposed in cross-section including (from bottom to top): large mud clasts, a small mud clast layer (indicated by a white arrow), and tangential cross-beds. Faint trough cross-bedding can be seen in the sandstone surrounding the large mud clasts. **C)** Unidirectional ripple cross-lamination with occasional small mud clasts about 1.3 m above the base of the bonebed. The wall is cut such that the left and right sides are parallel, and the middle is a surface nearly perpendicular to the other two faces.

hard, heavily weathered and eroded layer of dark brown, trough cross-bedded sandstone facies (>0.3 m) (Miall code St).

Taxon and Element Identification

To date, 1,652 bones have been collected from Rose Quarry, but only 619 have been prepared and are available for study in the collections. Nevertheless, we suspect that the 619 prepared bones are a good representative of the fossils found in the quarry as the proportions of the various prepared bone types and taxa are similar to those identified in the quarry in one season. A quarter of the studied specimens are unidentifiable bone fragments, and another 2% are long bone fragments (Table 3). The majority of the identifiable fossils are whole or fragmented turtle carapaces and plastrons.

Thirty-nine percent of the 619 skeletal and dental elements cannot be identified to a particular taxon other than that most are from archosaurs, assuming Testudines is outside of Archosauria whether in Archosauromorpha or Parareptilia (Lee, 2013), and the large ones are no doubt from dinosaurs (Table 4). Just over a third (37%) of the elements are from turtles, but that high percentage is due to the large number of individual turtle scutes. Eleven percent of the elements, mainly frill fragments and teeth, come from ceratopsids (cf. *Triceratops*), and another 5% of the elements, mostly teeth, are from crocodilians (*Brachychampsa* and *Borealosuchus*). Beyond the other taxa listed, only four definitive bones from hadrosaurids (cf. *Edmontosaurus*) have been identified from Rose Quarry, including two teeth and a partial ilium. Hadrosaurids are present in Rose Quarry, but they seem to make up a very small percentage of the identifiable material. This differs drastically from the nearby hadrosaurid-dominated Main Quarries bonebed.

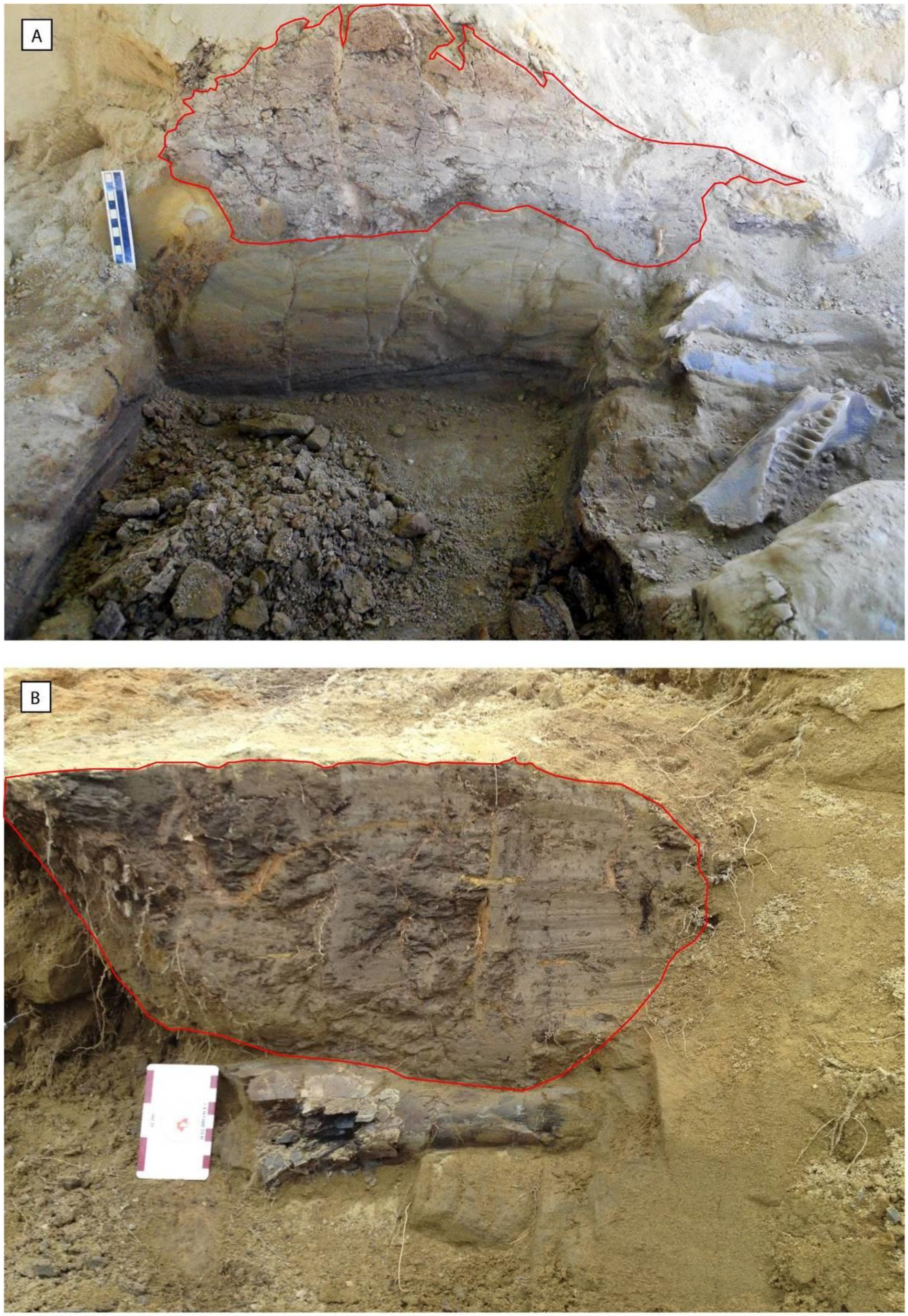

A
B

Figure 6. Large mud clasts in Rose Quarry. **A)** A large, angular mud clast (outlined in red) is slightly stratigraphically above the bonebed. **B)** A large mud clast (outlined in red) rests on top of a limb bone fragment.

Table 3. Rose Quarry skeletal elements.

Type of Bone	Number	Percent of Total
Bone Fragments	152	25%
Long Bone Fragments	12	2%
Turtle Shell Pieces	220	36%
Crocodilian Scutes	11	2%
Nodosaur Osteoderms	3	<1%
Ceratopsid Frills and Horns	38	6%
Skull Fragments	15	2%
Vertebrae	39	6%
Ribs	29	5%
Pectoral and Forelimb Elements	17	3%
Pelvic and Hindlimb Elements	5	<1%
Tendons	6	1%
Teeth	72	12%
Total	**619**	**100%**

Table 4. Rose Quarry present taxa.

Taxon	Number	Percent of Total
Archosauria indet.	242	39%
Actinopterygii	3	0%
Testudines	228	37%
Crocodylia	33	5%
Theropoda indet.	15	2%
Tyrannosauridae	15	2%
Dromaeosauridae	8	1%
Ceratopsidae	66	11%
Hadrosauridae	4	1%
Nodosauridae	3	1%
Pachycephalosauridae	1	<1%
Thescelosauridae	1	<1%
Total	**619**	**100%**

Bonebed Architecture

GPS measurements of the concretion and bone-rich layer and of the underlying mudstone layer show that the layer is in contact with the mudstone layer where the majority of the bones are concentrated, but that perpendicular to paleocurrent orientation, the concretion and bone layer raises in elevation, instead occurring immediately above a sandstone unit. The layer thins out in this direction as it raises before finally pinching out and disappearing.

There is a large concentration of bones visible in both RQ1 and RQ2 in aerial view (Figure 7). Very little excavation had occurred in RQ1.5 until the summer of 2015. Surprisingly, fossils were very sparse until we dug farther back into the sandstone and found a dense concentration of bones, resembling the situation in RQ1 and RQ2. Fossils become sparser as the layer pinches out to the south.

Taphonomy

Most fossils in Rose Quarry are disarticulated and disassociated, including turtle shell remains, which normally consist of individual scutes or scute fragments. However, a few whole turtle carapaces and plastrons have been found, as well as one articulated turtle carapace and plastron. Recently discovered paired theropod ischia represent the only articulated dinosaur remains found in Rose Quarry.

Concerning the bonebed in aerial view (Figure 7), the orientation data for RQ1 (Figure 8A) reveals a preferred orientation of the bones in a west-east direction (mean of 97.4°), which agrees with the paleocurrent data. This preferred direction is significant (Rayleigh $z_{3.281}$, P= 0.037). A rose diagram for the bones in RQ2 (Figure 8B) appears to show a preferred orientation (mean of 174.7°) perpendicular to the bones in RQ1, but there is no statistical support for this interpretation (Rayleigh $z_{1.264}$, P= 0.283).

Of the 619 bones and teeth studied, 68% (419 specimens) showed stage 1 abrasion (Figure 9), which corresponds with the subangular sedimentological category used for rock and mineral grains (Ryan et al., 2001). Fourteen percent (90 specimens) were not abraded (stage 0), and another 15% (91 specimens) had stage 2 abrasion. Only eight specimens (1%) were stage 3, and we were unable to determine the abrasion stage on 11 specimens.

Concerning these same 619 fossils, the majority (86%, 534 specimens) showed no signs of weathering – stage 0 (Figure 10). We were unable to assign another 6% (35 specimens) to a weathering category. Of the remaining 8%, the majority were stage 1 (40 specimens), while only four were stage 2 and three were stage 3. Three bones in Rose Quarry were lacking cortical surface altogether, which could be due to a high degree of weathering followed by transport.

Almost every bone in Rose Quarry possesses at least one broken edge. In fact, complete bones or teeth made up only 1% of the 619 specimens studied (Figure 11A). The majority of broken bones and teeth (62%, 374 specimens) have only one kind of break per specimen; however, many fossils (34%, 205 specimens) possess two kinds of breaks per specimen (Figure 11B). An additional 26 specimens (4%) have three kinds of breaks per specimen, and two bones have four kinds of breaks per specimen. Indeterminate breaks are the most common break type no matter how many breaks the specimen has (Table 5). Collection breaks are typically the second-most common, however bones with three kinds of breaks have fewer collection fractures than transverse,

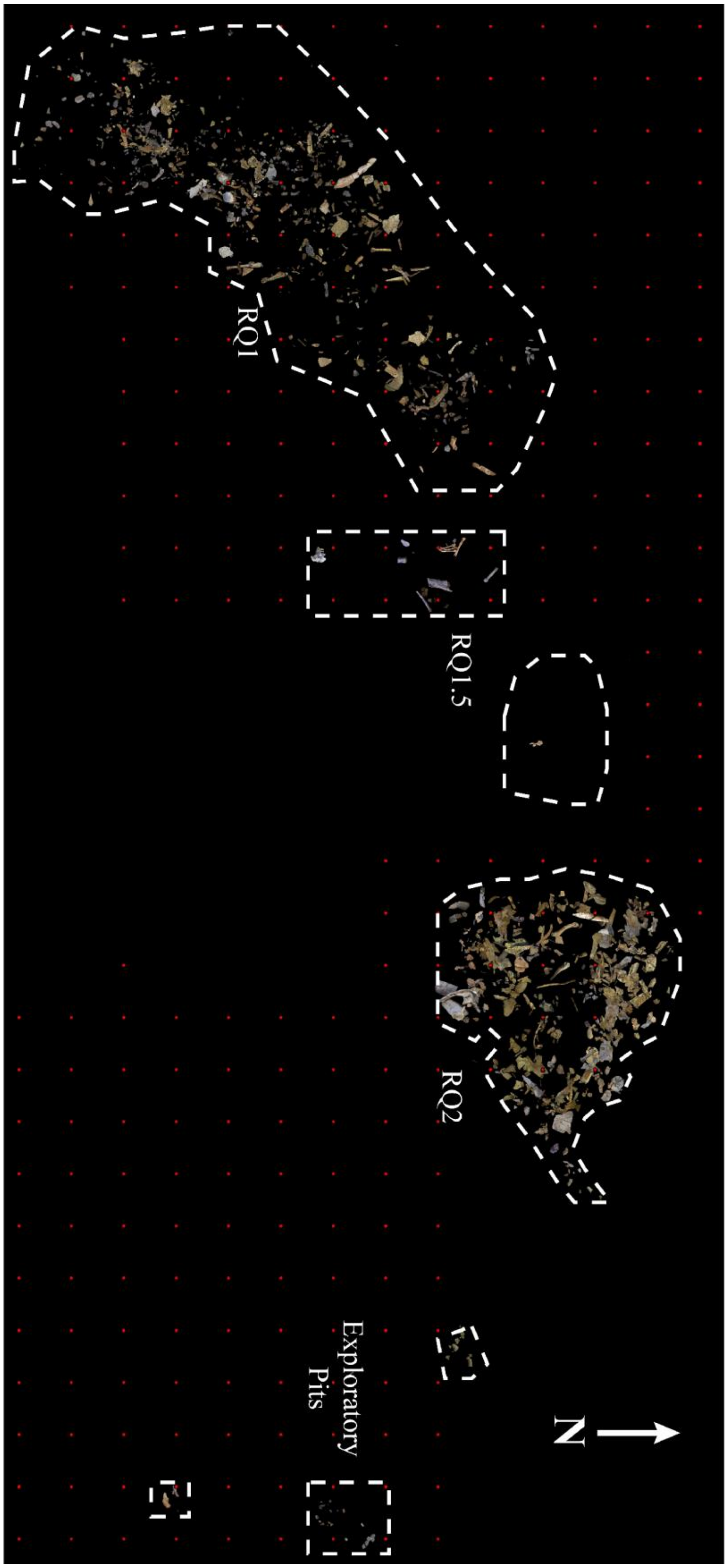
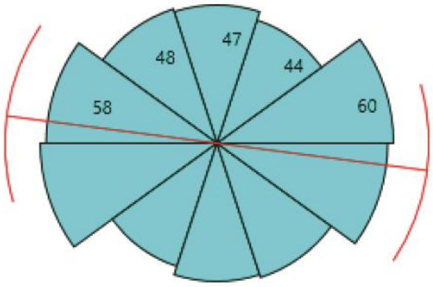
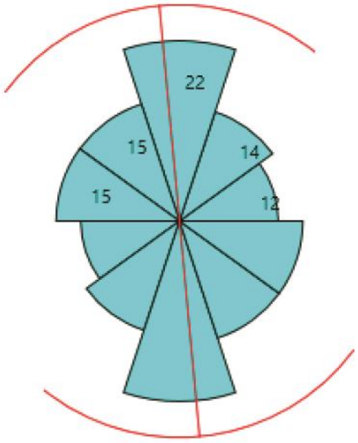

RQ1
RQ1.5
RQ2
Exploratory Pits
N

Figure 7. Aerial view of the bones in Rose Quarry. Excavated areas are outlined with a dashed line. All bones excavated between 2012 and 2015 are included. Red dots are on 1 m centers.



A



B

Figure 8. Rose diagrams for Rose Quarry bone orientation representing the alignments of bones with long axes in RQ1 (**A**) and RQ2 (**B**). Red line indicates the mean with the arc showing the 95% confidence interval on the mean.

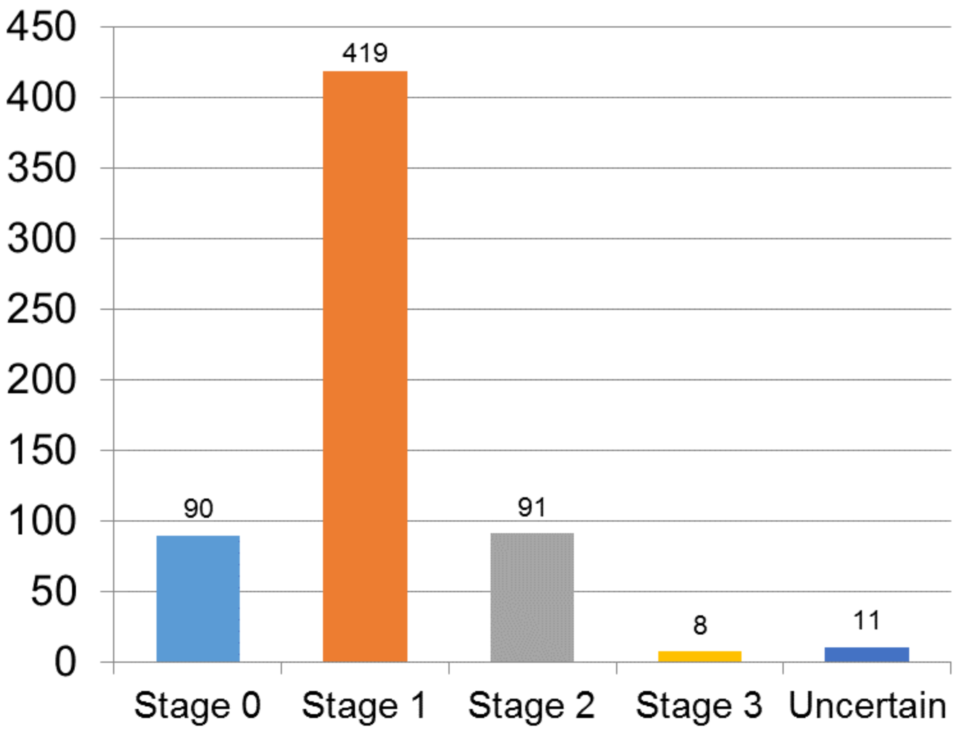

450
400
350
300
250
200
150
100
50
0
419
90
91
8
11
Stage 0
Stage 1
Stage 2
Stage 3
Uncertain

Figure 9. Abrasion of Bones in Rose Quarry. The bar graph of abrasion states includes 619 bones and teeth from the Rose Quarry bonebed.

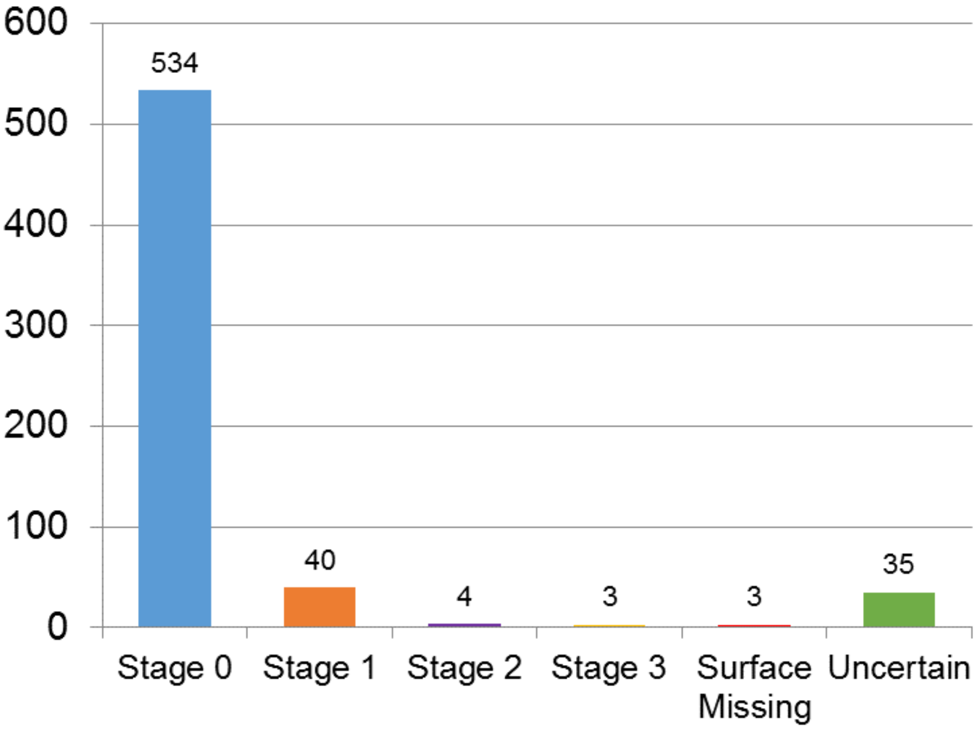

600
500
400
300
200
100
0
534
40
4
3
3
35
Stage 0
Stage 1
Stage 2
Stage 3
Surface Missing
Uncertain

***Figure 10*.** Weathering of Bones in Rose Quarry. The bar graph of weathering states includes 619 bones and teeth from the Rose Quarry bonebed.

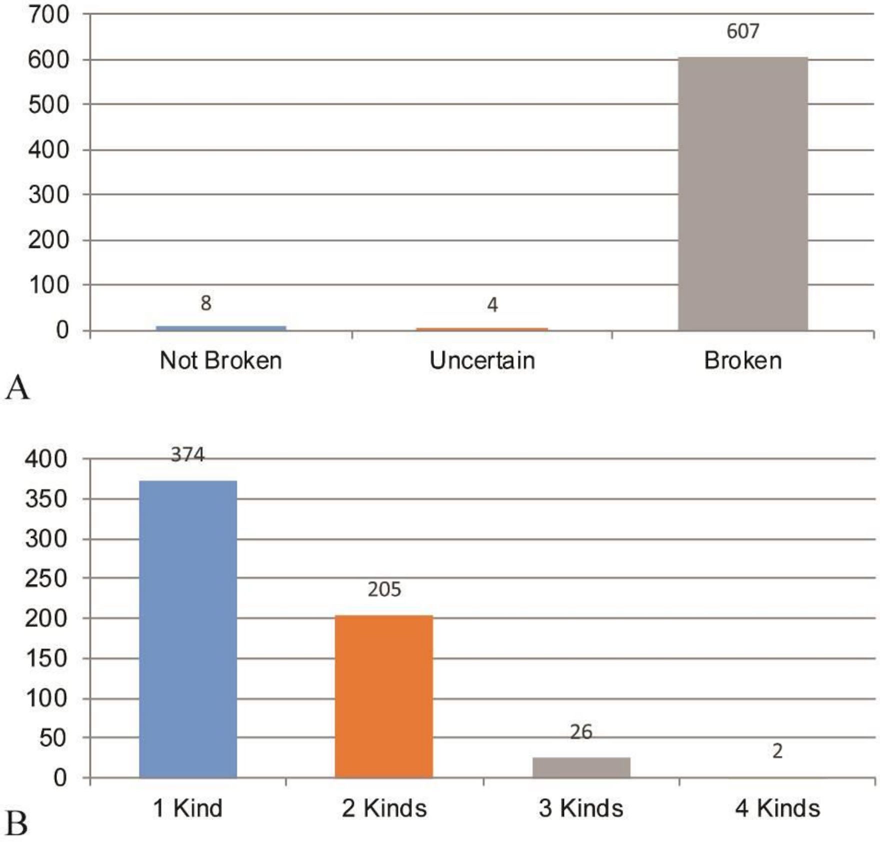

700
600
500
400
300
200
100
0
607
8
4
Not Broken
Uncertain
Broken
A
400
350
300
250
200
150
100
50
0
374
205
26
2
1 Kind
2 Kinds
3 Kinds
4 Kinds
B

Figure 11. Bone breakage in Rose Quarry. Two bar graphs displaying bone breakage in 619 bones and teeth from the Rose Quarry bonebed. **A)** Presence or absence of breaks. **B)** The number of break types per specimen.

Table 5. Number and type of fractures present on Rose Quarry bones.

Fracture Type	1 Type Present	2 Types Present	3 Types Present
Collection	22	94	9
Longitudinal	0	11	11
Spiral	2	34	12
Transverse	9	57	20
Indeterminate	334	179	25
"Straight"	7	37	1
Shear	0	1?	0

spiral, or longitudinal. Transverse and spiral fractures are relatively common, but longitudinal breaks appear to be rare in Rose Quarry bones.

Tooth traces are present on some bones from Rose Quarry (Figure 12), however they appear to be rare. Definite tooth traces are present on 1% (7 bones) of the 546 bones studied (excluding teeth), while another 3% (17 bones) show possible tooth traces, and 5% (28 bones) are doubtful. It is important to note, however, that the percentage of non-tooth-traced bones could be inflated because of the large number (n = 220) of small turtle shell fragments, each of which is counted as a separate bone. Pits, scores, and furrows can be found on bones from this site.

Rose Quarry fossils showing trampling marks and trampling notches account for a very small percentage of the total bones (Figure 13). Of the 546 bones (excluding teeth), only 3 (<1%) bones show definite trample marks/notches, while another 12 (2%) have possible trample marks/notches, and 9 (2%) have doubtful trample marks/notches. An example of a bone with trampling marks is HRS19067 (Figure 14A). HRS15840, a ceratopsid frill fragment, shows an incredibly jagged edge due to the presence of trampling notches (Figure 14B).

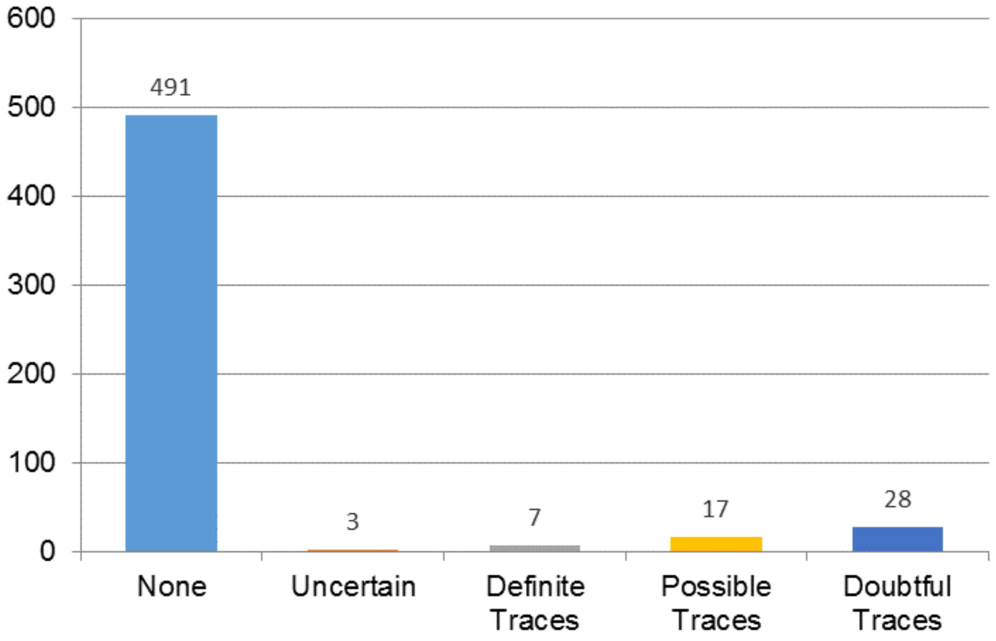

600
500
400
300
200
100
0
491
3
7
17
28
None
Uncertain
Definite Traces
Possible Traces
Doubtful Traces

Figure 12. Tooth traces in Rose Quarry. Bar graph of tooth traces on 546 Rose Quarry bones. Teeth are not included in these results.

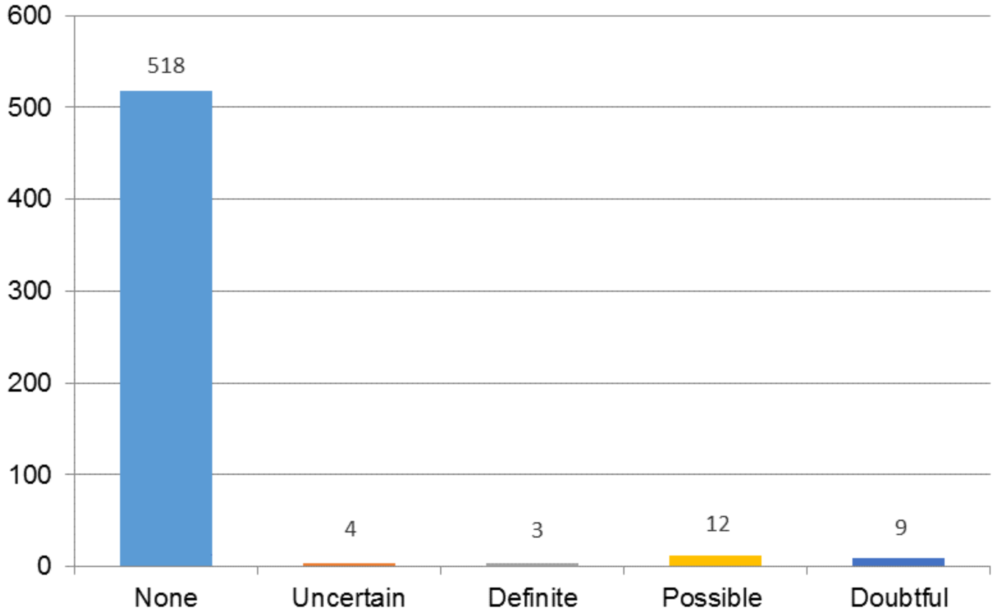

600
500
400
300
200
100
0
518
4
3
12
9
None
Uncertain
Definite
Possible
Doubtful

***Figure 13*.** Trampling marks and notches in Rose Quarry. Bar graph displaying the amount of bones possessing trampling marks and notches among 546 Rose Quarry bones studied. Teeth are not included in the count.

Discussion

Depositional Environment

We believe that the bones are concentrated as a lag at the base of a fluvial channel. The overall geometry of the bonebed is very channel-like, with the thickest portion found at the lowest elevation and pinching out as the bottom of the concretion layer rises in elevation to the south. The highest density of bones, and all of the large bones, are concentrated at the lowest elevation along with abundant mud clasts. As the layer pinches out to the south (toward the channel bank), the bones diminish in size and density. In addition, the trough cross-bedding and gravel-sized mud clasts are indicative of fluvial environments. Erosion of the hill has removed the opposite bank, which does not allow us to determine the total width of channel with any degree of certainty.

Taphonomic Considerations

That Rose Quarry is a mixed assemblage is evidenced in that the bones and teeth fall into three main abrasion categories: two-thirds of the fossils have stage 1 abrasion, one-sixth show no abrasion, and another sixth show stage 2 abrasion. This suggests different depositional histories for each of the abrasion categories. The stage 2 group could represent bones and teeth that had been in the channel for a longer period of time than stage 1 or stage 0 bones. Stage 1 and stage 0 specimens may have collected in the channel during a high energy event. Although it is tempting to assume that stage 1 elements came from farther away than stage 0 elements, there is not a direct relationship between greater transport distance and higher abrasion states, and bones in a fluvial environment that are stationary may be abraded more than those that are transported as they get “sand-blasted” (Aslan and Behrensmeyer, 1996; Behrensmeyer, 1990), which could also be the case with the stage 2 bones. The degree of abrasion is a function of many factors including the type of bone, duration of exposure, mode of sediment transport, nature of the bed, and the way in which the grains impact the bone surface (Thompson et al., 2011). Despite the uncertainties associated with the various causes of abrasion, the fact that three separate abrasion signals are found in Rose Quarry suggests separate taphonomic pathways before final burial of the bones.

The majority of Rose Quarry bones do not show weathering, and so must have disarticulated and then been buried within a year as evidenced by modern observations of bone weathering (Behrensmeyer, 1978). Additionally, the presence of small, rounded mud clasts around the bones and teeth suggest that they entered the channel from the floodplain in an event that had the strength to rip up mud and transport it, as well as the bones (Zeigler et al., 2005). Mud clasts are common constituents of other fluvial vertebrate bonebeds (Rogers, 1990; Zeigler et al., 2005). At this time, we cannot determine how quickly the channel filled up with sediment, or whether all of this was deposited in a single event or multiple events. We suspect that the layer of small mud clasts found above the largest mud clasts is another lag deposit, which may be eroding into the earlier flood deposit that generated the bonebed. The large mud clasts, in contrast, probably represent bank collapses followed by some transport, which would be expected to occur during a high energy flood. Interestingly, small bones are sometimes found adjacent to these large mud clasts stratigraphically higher than the bonebed lag. It is possible that as these large mud clasts were dragged by traction during a flood, they exhumed some of the bones from the lag and pushed them higher stratigraphically.

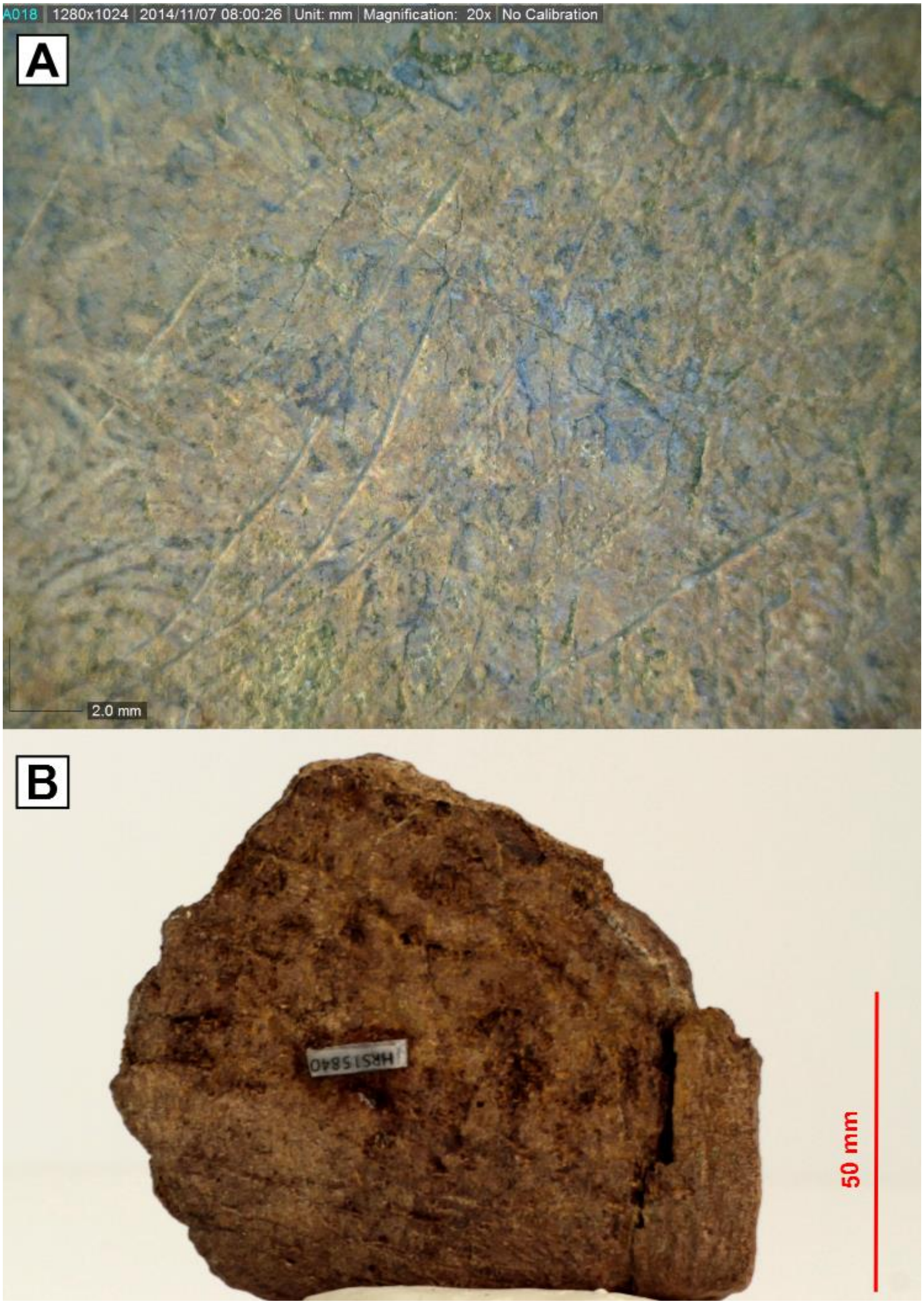

A018
1280x1024
2014/11/07 08:00:26
Unit: mm
Magnification: 20x
No Calibration
A
2.0 mm
B
HRS15840
50 mm

Figure 14. Evidence of trampling in Rose Quarry. **A)** Trampling marks on a Rose Quarry bone (HRS19067) at 20x magnification. **B)** A ceratopsian frill fragment (HRS15840) from Rose Quarry showing possible trampling notches along its jagged profile.

The other taphonomic peculiarity that must be addressed in order to understand the depositional history of this bonebed is the abundant fracturing. Almost all bones found in the Rose Quarry bonebed are fractured, and fractures often occur on multiple sides of the same bone. Collection breaks are not due to a taphonomic process in the past, so they should be excluded from a discussion of break origins. However, only 22 of the 619 bones possessed solely collection breaks, so removing those specimens does not significantly impact the overall picture. The large majority of these fractures cannot be post-depositional breaks as fragmented bones are not in association with their respective pieces from which they broke away. Such breaks must have occurred prior to deposition, and the different pieces were probably separated from each other by hydraulic transport. Fracturing was not likely caused by prolonged exposure prior to burial since weathering is very rare in bones from Rose Quarry, and although most bones show some abrasion, few are heavily abraded. The small number of longitudinal fractures found on Rose Quarry bones, thought to be related to desiccation (Ryan et al., 2001), agrees with the lack of weathering. Some fractures may be a result of biting from predators/scavengers, however, there are no clear instances of a bite-induced fracture in these bones. Notable among the tooth-traced bones is HRS15710, which appears to have a large puncture on its surface (Figure 15). This puncture was probably made by a tyrannosaur tooth as no other carnivorous animals from the Lance Formation have teeth large enough to leave such a trace. This trace fits the description of a puncture as specified by Pobiner (2008), in that it is an oval mark with its long axis no more than three times the length of the short axis, characterized by the crushing of the cortical bone into the damaged feature. Interestingly, the edges of this trace (Figure 15C) appear to show regrowth. If this observation is correct, then this suggests the bitten animal survived the bite before dying at a later time. It is possible that this mark may not be a puncture, but that it is instead a type of pathology; nevertheless, we feel that the overall morphology and the cracks that seem to radiate out from the trace suggest it is a puncture trace in the process of healing. One could imagine a harder bite breaking through a bone, but the small percentage of tooth-traced bones (1-8%) at Rose Quarry suggests that biting is not the origin of the abundant breaks, and it agrees well with Fiorillo’s (1991) statement that tooth-traced bones typically make up 0-4% of bones in a dinosaur bonebed.

This leaves two possibilities as the cause of the abundant fractures: (1) breakage due to trampling and (2) breakage due to transport. Trampling has been implicated in other sites where bone fragmentation has occurred, such as the *Eotyrannus* site in the Lower Cretaceous Wessex Formation of the Isle of Wight (Hutt et al., 2001), bonebeds from the Upper Cretaceous Two Medicine Formation in Montana (Rogers, 1990), the Snyder quarry bonebed from the Petrified Forest Formation of the Chinle Group in New Mexico (Zeigler et al., 2005), and the Danek Bonebed from the Upper Cretaceous Horseshoe Canyon Formation of Alberta (Bell and Campione, 2014). Trampling marks and notches are present on a few of the bones from Rose Quarry, but they are very rare. This would seem to rule out trampling as a cause for much of the bone breakage; however, trampling does not necessarily have to leave scratches or notches on bones. Fiorillo (1989) noted that highly weathered bones do not show trample marks after they have been trampled. There are some possible instances of significant weathering at Rose Quarry, but most bones do not show weathering. Severe abrasion could destroy


A
B
C
A077 | 1280x1024 | 2014/11/07 13:04:08 | Unit: mm | Magnification: 20x | No Calibration

Figure 15. A punctured long bone fragment (HRS15710). **A)** Puncture shown in side view (indicated by arrow). **B)** Puncture shown in plan view (indicated by arrow). **C)** Puncture at 20x magnification.

evidence of trample marks, but it is unlikely that stage 1 abrasion would destroy all traces of trample marks. In fact, some of the bones we noted as possessing or possibly possessing trample marks showed stage 1 abrasion. Because trampling marks are caused by quartz and feldspar grains on the foot of a trampler dragging along the surface of the bone, an absence of sand-sized grains of quartz and feldspar could preclude the formation of trample marks on bones even if they were trampled. This is not an unlikely scenario as many of the bones were probably sitting on a floodplain before they were incorporated into the channel during a flood event or bank collapse. Since floodplains consist of very fine-grained sediment, it is possible that many bones could be trampled without coming into contact with abundant sand-sized grains (Rogers, 1990). Since sand is still present on floodplains and could be carried for a distance on a trampler's foot, it is no surprise that there are a few instances of trampling marks in Rose Quarry.

Another possible cause of extensive bone breakage at Rose Quarry is hydraulic transport. Breakage of bones during hydraulic transport has not been documented, except in an experiment where small rabbit bones were flushed into a model burrow (Woodruff and Varricchio, 2011). Many researchers find significant bone breakage in hydraulic transport unlikely (Behrensmeyer, 1991; Eberth et al., 2007a). However, Ryan et al. (2001) suggested that a high energy event broke and fragmented *Centrosaurus* skeletal elements prior to their deposition. The occurrence of a high energy flood seems likely during the formation of the Rose Quarry bonebed due to the abundant mud clasts and the erosional contact with the underlying mudstone. In the absence of actualistic experiments on bone breakage and fragmentation in fluvial systems, we suggest that most of the bone breakage at Rose Quarry was due to trampling, and that perhaps the fragmentation was amplified during transport.

Depositional Model

In order to arrive at a depositional model for the Rose Quarry bonebed, it is necessary to combine the various taphonomic and sediementological observations. Because the Rose Quarry bonebed appears to be a mixed assemblage, then not all of the specimens that were buried together share the same taphonomic history. Additionally, it is not certain that all of the animals died at the same time. Nevertheless, it seems that at least some dinosaur, crocodilian, and turtle carcasses were exposed in a muddy floodplain-like area (Figure 16). There, the carcasses were scavenged by carnivorous animals (probably theropods and crocodilians) and some bones were trampled by large dinosaurs. These processes, as well as decay, contributed to disarticulation. Trampling in an environment characterized by fine sediment may have led to abundant breakage of dinosaur bones without the presence of abundant trampling marks. Bones showing stage 2 abrasion likely entered the channel via bank collapse or from reworking as the channel cut through an older bonebed. These stage 2 abrasion bones were in the channel for some time before the flooding event occurred, which may have brought the other bones into the channel from the floodplain. It is unclear why some bones were abraded while others were not, but further study with SEM may yield some answers (see Thompson et al., 2011). It seems likely that the large mud clasts were ripped from the bank during flood conditions. As expected for a fluvial deposit, the large and dense materials – bones and gravel-sized, rounded mud clasts – are concentrated at the base of the channel forming a lag deposit. Decay of organic matter within the small mud balls led to iron migration and the formation of pyrite during diagenesis, which later oxidized to hematite and goethite, forming the concretions and concretion layer.

Zeigler et al. (2005) suggested four criteria that would be indicative of a fluvial bonebed which originated from a catastrophic flood: (1) bone and wood are aligned, (2) elements show a moderate degree of hydrodynamic sorting, (3) mud rip-up clasts are present, and (4) no weathering or abrasion of material. The Rose Quarry bonebed has mud rip-up clasts, some of which are very large in size (up to 1 m in diameter), and RQ1 has bones aligned parallel with the paleocurrent direction as expected in a fluvial setting with strong currents (Behrensmeyer, 1990). The lack of significant orientation in RQ2 may be due to the large density of bones confined to a small area during deposition (Figure 7) or the presence of eddies or a bank collapse blockage. However, there does not appear to be any obvious hydrodynamic sorting of elements in Rose Quarry, and there are instances of abrasion and weathering among the bones. All four criteria apply well to a situation in which the organisms are killed and buried by a catastrophic flood, but the situation in Rose Quarry is more complicated as this flood mixed newer, less abraded elements with skeletal elements that had been in the channel for some time. The presence of trough cross-beds and planar beds of fine to medium sand containing large mud intraclasts, suggests a flow velocity from 0.6 to >1 m/s (Southard and Boguchwal, 1990, fig. 8).

Conclusions

Analysis of the sedimentology and taphonomy of the Rose Quarry bonebed has yielded several observations that are pertinent to the study of fluvial bonebeds. First, the processes that generate bonebeds in fluvial environments are likely to create mixed assemblages through the combining of terrestrial and aquatic fauna, allochthonous and autochthonous remains, and recently dead and time-averaged remains. Second, flooding appears to be important to the formation of fluvial bonebeds. Although bones can be transported and can accumulate through other processes, floods provide an opportunity to collect and bury the large amounts of bones necessary for the generation of a bonebed. Third, study of the Rose Quarry bonebed provides an example among other fluvial bonebeds of how to distinguish between pre-channel and post-channel taphonomic histories. Fourth, the complexity of the Rose Quarry bonebed, especially in contrast to the situation found at the Main Quarries bonebed, which is located in close stratigraphic and geographic proximity, helps us understand that bonebeds with striking variability in taphonomic features can exist in the same general vicinity and paleoenvironment. Variability in fluvial bonebeds is due to a number of features including pre-burial history, depositional mechanism, subenvironment, and post-burial history. Future studies of fluvial bonebeds should take into account the large variability possible in order to better describe their depositional history.

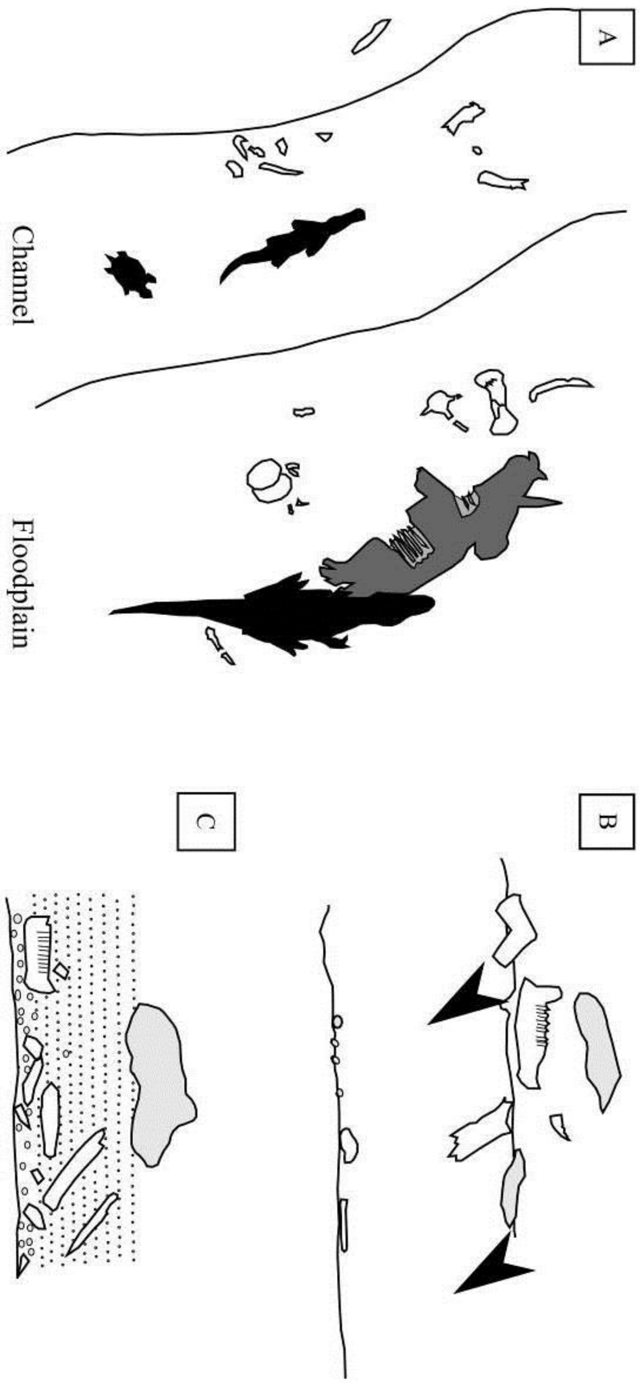

A
Channel
Floodplain
B
C

Figure 16. Depositional model for the Rose Quarry bonebed in three stages. **A)** (In plan view) Scavenging and trampling of dinosaur carcasses occurs while some bones have already entered the channel. **B)** (In cross-sectional view) A flood event brings floodplain bones into the channel along with rip-up mud clasts. **C)** (In cross-sectional view) The fossils and mud clasts are buried together.

CHAPTER THREE

TYRANNOSAUR CANNIBALISM: A CASE OF A TOOTH-TRACED TYRANNOSAUR BONE IN THE LANCE FORMATION (MAASTRICHTIAN), WYOMING

Abstract

A recently discovered tyrannosaur 4th metatarsal (HRS13997) from the uppermost Cretaceous (Maastrichtian) Lance Formation is heavily marked with several long grooves on its cortical surface all concentrated on the bone's distal end. The bone was found at the surface near a thin bonebed within a sandstone unit. The grooves on the surface are interpreted as scores made by theropod teeth. At least ten separate scores are visible, of varying width. In addition, the tooth ichnospecies *Knethichnus parallelum* (Jacobsen and Bromley, 2009), which consists of a series of parallel grooves often leading away from an initial groove, is found at the end of the score nearest the widest end of the bone. Through analyzing the striation width of the *Knethichnus parallelum* trace, we determined that the biter was a *Tyrannosaurus rex*, suggesting this may be an example of cannibalism. This is the first description of tyrannosaurid cannibalism in the Lance Formation and the first *Knethichnus parallelum* and *Linichnus serratus* found on a tyrannosaurid bone.

Introduction

Cannibalism has been observed in many extant carnivorous animal taxa (Polis, 1981). It is not surprising then, that examples of cannibalism would turn up in the fossil record. The most famous example of non-avian dinosaur cannibalism for many decades was a specimen of the Triassic theropod *Coelophysis bauri* (AMNH FR 7224), which was thought to show an adult specimen with juvenile *Coeleophysis* bones in its rib cage. However, Nesbitt et al. (2006) determined that these small bones were not from a *Coelophysis* but a crocodylomorph. Rogers et al. (2003) provided good evidence for cannibalism in the abelisaurid theropod *Majungasaurus crenatissimus* (formerly *Majungatholus atopus*) from Madagascar. Concerning tyrannosaurid theropods, Jacobsen (1998) determined that tyrannosaurid bite traces on tyrannosaurid bones from the Dinosaur Park Formation of Alberta might be evidence for cannibalism, but since there are at least two tyrannosaurid taxa known from that formation, *Gorgosaurus* and *Daspletosaurus*, there are other plausible explanations for these traces. Hone and Tanke (2015) described a *Daspletosaurus* skull from the Dinosaur Park Formation showing tyrannosaur bite traces, some of which they concluded were a result of feeding, but whether the biter was a *Daspletosaurus* or a *Gorgosaurus* could not be determined. However, Longrich et al. (2010) noted several *Tyrannosaurus rex* bones from the Hell Creek Formation of Montana that had large tooth scores, and attributed these bite traces to *Tyrannosaurus rex* feeding due to the large width of the scores as there are no other very large predators in the Hell Creek Formation.

In June of 2015, we discovered a large theropod bone fragment (HRS13997, Figure 17) attributable to Tyrannosauridae in a previously unexplored sandstone dinosaur-bearing bonebed in the Maastrichtian Lance Formation of the Powder River Basin in eastern Wyoming. Clustered on one end of the bone, we observed a series of subparallel scratches perpendicular to the long axis of the bone (Figure 18). The scratches were determined to match descriptions of tooth scores found in the literature, having length to width ratios of greater than 3:1 and U or V-shaped cross sections (Binford, 1981; Njau and Blumenschine, 2006; Pobiner, 2008; Pobiner et al., 2007). Also observed on the bone were one example each of the ichnotaxa *Knethichnus parallelum* (Jacobsen and Bromley, 2009) and *Linichnus serratus* (Jacobsen and Bromley, 2009) located in close proximity to one another (Figures 18 and 19). The *Knethichnus parallelum* trace is caused by the denticles on a serrated tooth dragging along the surface of a bone (Jacobsen and Bromley, 2009) as demonstrated by actualistic experiments on Komodo dragon (*Varanus komodoensis*) feeding behavior (D'Amore and Blumenschine, 2012). Striation widths on a *Knethichnus parallelum* trace can be equal or smaller than the denticle width from the biter's tooth, but never larger (D'Amore and Blumenschine, 2012). If the fauna of the formation in question is well known, as is the case with the heavily studied Lance Formation, then denticles on the teeth from the present carnivorous taxa can be compared to the *Knethichnus parallelum* trace to look for a match.

Methods

After excavation, HRS13997 was prepared at Southwestern Adventist University (SWAU) and photographed with a Canon Mark II 5D camera and an electronically coupled turntable. This allows for a 3DVR image of the bone to be created, which is available for viewing at http://fossil.swau.edu. The scratches on the bone were carefully observed and photographed using a Dino-Lite microscope. The widths of the striations on the *Knethichnus parallelum* were measured and compared to denticle widths on theropod teeth obtained from nearby Lance Formation quarries. HRS13997 was compared to tyrannosaurid material from the Los Angeles County Museum of Natural History for identification purposes.


Ventral
Dorsal
Anterior
Medial
Posterior
Lateral
CM

Figure 17. A tooth-traced tyrannosaurid metatarsal (HRS13997). Specifically, HRS13997 is a tyrannosaurid right metatarsal IV, shown here in anterior, medial, posterior, and lateral views. The fossil was photographed on a turntable with the dorsal side on the table surface. Tooth traces can be seen on the posterior and lateral surfaces. Photograph by SWAU from http://fossil.swau.edu.

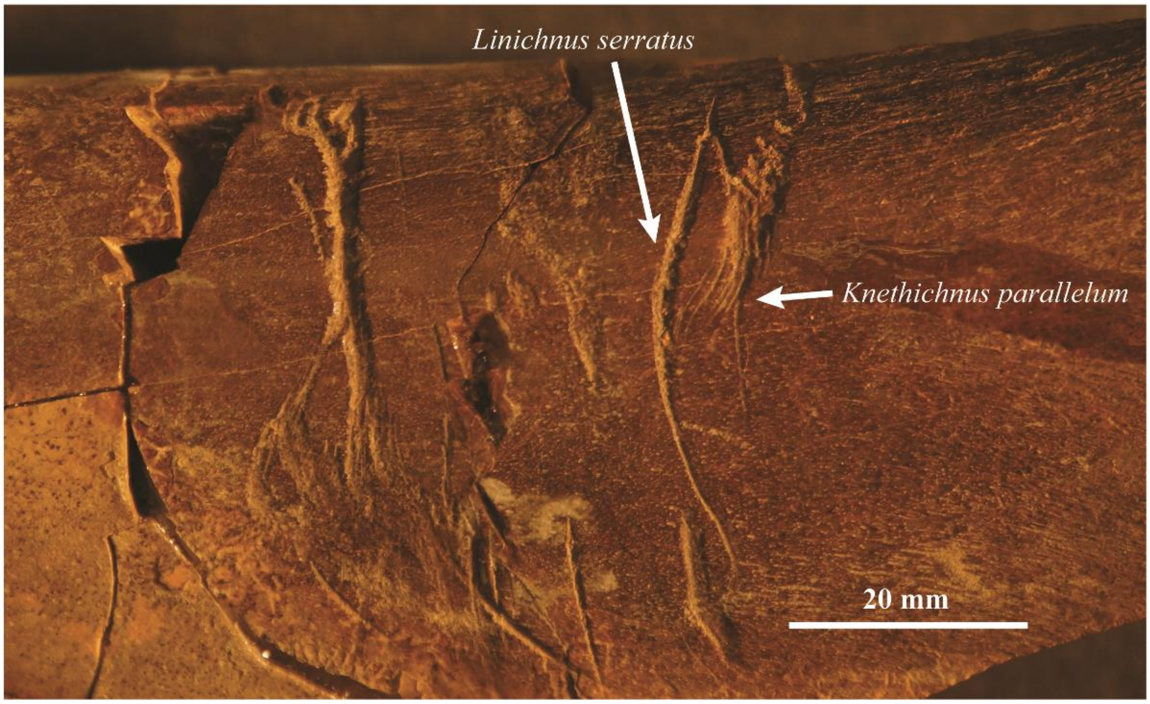

Linichnus serratus
Knethichnus parallelum
20 mm

Figure 18. Scores on the surface of HRS13997. Abundant scores cover the distal end of the posterior-lateral surface of this bone, with most scores directed perpendicular to the long axis of the bone. The *Knethicnhus parallelum* and *Linichnus serratus* traces are labeled.


Knethichnus parallelum
Linichnus serratus
2 mm

Figure 19. *Knethichnus parallelum* and *Linichnus serratus* traces on HRS13997. Photographed with a Dino-Lite microscope.

Results

HRS13997 is a tyrannosaurid right 4th metatarsal. This is evidenced by the flattened region on the medial surface that is the contacting surface with the distinctive 3rd metatarsal of tyrannosaurids, which narrows to a point medially (Holtz, 2004). Both the proximal and distal ends of HRS13997 are broken, resulting in a length of 280 mm for the remaining bone. In addition to the fractures at the distal and proximal ends, there is a section of the shaft that is missing, which exposes the bone's hollow core. HRS13997 shows no signs of weathering, although it does show stage 1 abrasion, following the definition from Ryan et al. (2001).

Tooth scores are located on the distal end of this bone. The scores have a U-shaped cross-section and the grooves vary in width from .6 mm to 6 mm. The most proximal trace is made of three separate scores which merge into a single score, the deepest trace on the bone. Distal to this trace is the *Linichnus serratus* trace and the *Knethichnus parallelum* trace, which cuts across an earlier score (Figure 18). Posterior to these traces is an assortment of small, shallow scores. The striation width (SW) of the *Knethichnus parallelum* on HRS13997 is 3 striations per 2 mm.

Discussion

Measurements of denticle width (DW) on theropod teeth from the Lance Formation (Table 6) compared with the striation width (SW) of 3 striations per 2 mm on the *Knethichnus parallelum* trace on HRS13997 demonstrate that the DW of most Lance Formation theropods is too small to have created the SW on HRS13997. In fact, we found that only the DW on teeth of *Tyrannosaurus rex* was large enough to have made

Table 6. Denticle widths of various Lance Formation theropods.

Taxon	Denticles Per 2 mm	Denticles Per 2 mm	Reference
	Our Measurements	Literature	
Acheroraptor	5 to 6		
Dakotaraptor		7 to 9	DePalma et al. (2015)
Pectinodon	4		
Tyrannosaurus	3	3.7-3.8*	Smith et al. (2005)
Nanotyrannus	4 to 5		

*(Smith et al., 2005) did not distinguish between *Tyrannosaurus* and *Nanotyrannus* teeth. Additionally, they measured denticles per 5 mm, so these have been scaled down to denticles per 2 mm.

the observed SW.

Due to the fact that this bone must have been bitten more than once in the same location and that the scores are perpendicular to the long axis of the bone, it seems likely that these marks are feeding traces. If these feeding traces on a *Tyrannosaurus* bone are from a *Tyrannosaurus*, then this would be excellent evidence for tyrannosaur cannibalism, either scavenging or predation. Before we can reach this conclusion, however, we must address some other possibilities.

These long grooves are certainly tooth scores. Not only do they match the description of scores provided in the literature, but the presence of both *Linichnus serratus* and *Knethichnus parallelum* confirm that these marks were made by ziphodont teeth. Even though the SW on the *Knethichnus parallelum* most closely matches the DW of *Tyrannosaurus rex* teeth, it is possible that there is another carnivorous varanid or theropod with large denticles that we have yet to find in the Lance Formation. Indeed, a large dromaeosaur was recently discovered in the Hell Creek Formation (DePalma et al., 2015), although those authors concluded that the DW of *Dakotaraptor* (17-20 denticles per 5 mm) was different than that of *Tyrannosaurus*. Even though the possibility exists that there may be another predator, the simplest explanation is that these tooth traces were left by *Tyrannosaurus rex*.

Since HRS13997 appears to be from a small Maastrichtian tyrannosaur, one could possibly assign the fossil to the contentious taxon *Nanotyrannus lancensis* (Bakker et al., 1988). Although some researchers consider *Nanotyrannus lancensis* to be a valid species (Currie, 2003; Larson, 2013; Schmerge and Rothschild, 2016), the majority of paleontologists view it as a skeletally immature *Tyrannosaurus rex* (Brusatte et al., 2016; Brusatte et al., 2010; Carr, 1999; Carr and Williamson, 2004; Holtz, 2001, 2004; Longrich et al., 2010). Since the debate is ongoing, we cannot yet rule out the possibility that this is interspecific feeding rather than cannibalism. Even if *Nanotyrannus* is discovered to be a distinct taxon, this find is still remarkable as it demonstrates a larger tyrannosaurid feeding upon a smaller tyrannosaurid, a discovery which gives us great insight into paleoecology and tyrannosaurid paleobiology.

Several studies have been conducted to determine whether tyrannosaurids were capable of biting deeply into bone. Tyrannosaurids have wider and longer teeth than most other theropod dinosaurs (Farlow et al., 1991). *Nanotyrannus* and juvenile tyrannosaurids have teeth that are serrated and labiolingually-compressed (ziphodont) as in other theropods, but *Gorgosaurus*, *Daspletosaurus*, *Albertosaurus*, *Tarbosaurus*, and *Tyrannosaurus* all have incrassate maxillary and dentary teeth (Holtz, 2001, 2004, 2008) that are considerably thicker labiolingually such that the labiolingual width is sometimes even thicker than the mesiodistal length (Bakker et al., 1988; Holtz, 2004). However, even in *Nanotyrannus,* juvenile tyrannosaurids, and non-tyrannosaurid tyrannosauroids such as *Dryptosaurus* and *Eotyrannus* the cross-sectional diameter is still greater labiolingually than in other theropods with crowns of the same height (Holtz, 2004). Tyrannosaurids have more obvious heterodonty than other large carnivorous theropods in that their premaxillary teeth are considerably smaller than their maxillary (or lateral) teeth (Holtz, 2004). The premaxillary teeth of tyrannosaurids and *Eotyrannus* possess D-shaped cross-sections (Hutt et al., 2001). Although the premaxillary teeth of tyrannosauroids differ significantly in morphology from the rest of their dentition, there does not appear to be any significant difference in the average denticle densities on either the mesial or distal carinae when compared to those of the dentary or maxillary teeth (Smith et al., 2005). Bakker et al. (1988) suggested that the posterior maxillary teeth may have been used to crack open bones. Erickson et al. (1996) estimated the bite force of a *Tyrannosaurus rex* tooth at 6,410–13,400 N based on experimental attempts to replicate observed *Tyrannosaurus rex* bite marks in a *Triceratops* pelvis (Erickson and Olson, 1996). Meers (2002) used functional and ecological data from extant carnivorous animals to infer the bite force of *Tyrannosaurus rex*, which he concluded was between 183,000–235,000 N (7,600–9,800 N on average at a single tooth). A more recent analysis by Bates and Falkingham (2012) utilized the computational engineering technique of multi-body dynamic analysis, and they arrived at even higher bite forces of between 35,000 and 57,000 N at a single posterior tooth, by far the highest bite force of any known animal. Bates and Falkingham (2012) also studied the bite force of a juvenile *Tyrannosaurus rex*, which they concluded was only 2,565–4012 N at a single posterior tooth. This weaker bite for young *Tyrannosaurus rex* combined with their lower, longer snouted skulls and smaller body size may suggest niche partitioning between adult and juvenile *Tyrannosaurus rex*, such that adults focused on large prey and juveniles attacked smaller prey. Henderson (2002) found the skull of *Tyrannosaurus rex* to be the strongest out of the seventeen theropod skulls he analyzed, which represented most of the various theropod groups, and this agrees well with the incredibly strong bite forces suggested for *Tyrannosaurus rex* above.

That some tyrannosaurids ate bone is supported by the discovery of two large coprolites attributed to carnivorous dinosaurs, one from the Maastrichtian Frenchman Formation of Saskatchewan, Canada that contained 30–50% bone fragments (Chin et al., 1998), and another from the Campanian Dinosaur Park Formation of Alberta, Canada which preserved undigested muscle tissue as well as bone fragments (Chin et al., 2003). Both of these coprolites must have come from tyrannosaurs as there are no other carnivorous animals found in those deposits that could produce feces of that size. Additional evidence for bone ingestion in tyrannosaurids comes from acid-etched hadrosaurid vertebrae found in association with a partial skeleton of the tyrannosaurid *Daspletosaurus* (Varricchio, 2001). Finally, tyrannosaurid teeth occasionally show irregular spalled surfaces which are caused by tooth contact with food, probably bones, although it is difficult to determine whether this contact was intentional or not (Schubert and Ungar, 2005).

Potential prey for tyrannosaurids would include the animals that are fossilized in deposits with them including dinosaurs such as ceratopsians, pachycephalosaurs, hadrosaurs, thescelosaurids, ankylosaurs, ornithomimosaurs, therizinosaurs, oviraptorosaurs, dromaeosaurids, troodontids, and other tyrannosaurids. In addition to dinosaurs, other vertebrates including pterosaurs, crocodilians, turtles, squamates, lissamphibians, and various mammal taxa are known from deposits containing tyrannosaurids. Of these various animals, there is evidence of tyrannosaurid predation on ceratopsians, hadrosaurs, ornithomimosaurs, and dromaeosaurids. Erickson and Olson (1996) described abundant tyrannosaurid tooth punctures on a *Triceratops* pelvis, and a similar situation was described by Fowler and Sullivan (2006) of a ceratopsid pelvis from the Kirtland Formation bearing tyrannosaurid tooth-traces. A remarkable discovery of a *Triceratops* supraorbital horn with a healed break was attributed to a tyrannosaur bite by Happ (2008) because of tooth punctures on the horn and scores on the squamosal of the associated skull, which is suggestive of predatory behavior in *Tyrannosaurus rex*. Rothschild (2015) has noted tyrannosaurid bite traces on *Triceratops* occipital condyles, although he did not attribute these bites to feeding, but instead to play behavior. A hadrosaurid tibia from Coahuila, Mexico shows several tyrannosaurid bite traces (Rivera-Sylva et al., 2012) and a humerus from the hadrosaurid *Saurolophus* shows many punctures and scores made by the premaxillary teeth of the tyrannosaurid *Tarbosaurus* (Hone and Watabe, 2010). That tyrannosaurids predated upon hadrosaurids rather than simply scavenging their carcasses is evidenced by two remarkable finds: a *Tyrannosaurus rex* tooth found lodged in a hadrosaurid caudal centrum, surrounded by healed bone growth (DePalma et al., 2013), and a partially-healed pathology on a sample of hadrosaurid skin associated with a skull showing healed bone around tooth score traces thought to be caused by a large tyrannosaurid (Rothschild and Depalma, 2013). An interesting discovery of tooth-traced gastralia from Mongolia demonstated that *Tarbosaurus* fed on the large, bizarre ornithomimosaur *Deinocheirus* (Bell et al., 2012). Additionally, Jacobsen (2001) described a very rare example of a dromaeosaurid (*Saurornitholestes*) dentary that appears to have been bitten by a small tyrannosaurid.

There are also several examples in the fossil record of tyrannosaurid tooth traces on tyrannosaurid bones. Tyrannosaurid face-biting due to intraspecific aggression has been suggested in the literature as a cause for tyrannosaurid skulls possessing tyrannosaurid tooth traces (Peterson et al., 2009; Tanke and Currie, 1998). Peterson et al. (2009) used the Extant Phylogenetic Bracket – a technique usually reserved for inferring the morphology of soft tissues in fossil organisms (Witmer, 1995) – to infer such behaviors could have occurred in tyrannosaurids, since intraspecific face biting can be found in the only two extant archosaur groups: crocodilians (Peterson et al., 2009) and birds (Blanco et al., 1997). Face-biting behavior in tyrannosaurs was also suggested to explain a tyrannosaurid left dentary (TMP 1996.05.13) with a tyrannosaurid tooth lodged in it from the Dinosaur Park Formation; however, Bell and Currie (2010) were unable to determine whether the bite occurred ante- or postmortem, nor could they discern whether the biter was the same species as the victim (two tyrannosaurid species are known from the Dinosaur Park Formation: *Daspletosaurus sp.* and *Gorgosaurus libratus*).

A skull and mandible from a skeletally immature specimen of the tyrannosaurine *Daspletosaurus sp.* (TMP 1994.143.0001) from the Dinosaur Park Formation of Dinosaur Provincial Park, Alberta, Canada appears to show both healed, premortem tooth traces and postmortem tooth traces on the mandible, all made by another tyrannosaurid (Hone and Tanke, 2015). The authors attributed the premortem traces to intraspecific combat and the postmortem traces to scavenging. However, the authors were unable to determine if the scavenging was cannibalistic because of the presence of two tyrannosaurid species in the Dinosaur Park Formation, as in the case of TMP 1996.05.13 noted above. According to Hone and Tanke (2015), the definite postmortem bite trace on the dentary was probably made by a tooth from the maxilla or non-anterior dentary of a tyrannosaurid because tyrannosaurid premaxillary teeth are more closely spaced.

Longrich et al. (2010) described four specimens of *Tyrannosaurus rex* (UCMP 137538, MOR 1126, MOR 920, and MOR 1602) from the Hell Creek Formation of Montana that possess tooth scores made by a large, predatory animal. UCMP 137538 is an isolated theropod pedal phalanx attributed to *Tyrannosaurus rex* because of its large size and provenance. Five furrows – called gouges by Longrich et al. (2010) – mark the proximal end (four on the dorsal surface and one on the ventral surface). Another pedal phalanx, MOR 1126, this time from a partial skeleton, also possesses tooth traces, this time in the form of furrows and scores with at least one containing denticle striae. MOR 920 is a left humerus that was found as part of an associated, skeletally mature *Tyrannosaurus rex* skeleton featuring several scores on its posterior surface. The final specimen (MOR 1602) they described was an isolated right metatarsal III missing the proximal half of its shaft. Two scores can be found on the medial surface. All of these tooth traces are attributed by the authors to feeding rather than fighting because the bites would have been difficult to inflict on a live animal, as three of the examples are from the feet. Additionally, at least one of the specimens (MOR 1126) was bitten more than once, and the score on MOR 1602 runs across the bone’s articulation with metatarsal II. None of the bites showed any evidence of healing, which confirms that they must have been bitten shortly before, at, or after death. These tooth scores are smaller in width than others previously attributed to *Tyrannosaurus* (Erickson and Olson, 1996), which led Longrich et al. (2010) to suggest they were made by juvenile or sub-adult *Tyrannosaurus* individuals (these authors consider *Nanotyrannus* to be a juvenile *Tyrannosaurus rex*).

The authors reason that because they only studied a relatively limited sample of tooth-marked bones, cannibalism must have been common in *Tyrannosaurus*.

Our discovery is also suggestive of cannibalism in *Tyrannosaurus rex*. Assuming *Nanotyrannus* is actually a young *Tyrannosaurus rex*, then this is an example of a larger *Tyrannosaurus* biting the foot of a smaller individual. That the tooth traces represent feeding rather than some other biting behavior is supported by four lines of reasoning. First, it would be very difficult for a tyrannosaurid to bite the foot of another living individual in some sort of intraspecific combat scenario. Indeed, there appear to be multiple bites in the same area, which further increases the unlikeliness of such a situation. Second, these scores are perpendicular to the long axis of the bone, which might be expected for a feeding trace, as scores are often perpendicular to the long bone axis (Pobiner et al., 2007). Third, all of these marks are examples of scores, where the teeth are dragging along the surface of the bone, rather than pits or punctures. This means that the animal was scraping its jaw along the foot, not just simply biting it as might be expected in a combat scenario. Fourth, the three scores in cluster 1 begin as separate traces, but then join together to form a single score. This suggests that the animal is turning its head as it is biting, probably to scrape off some flesh from the bone. Additionally, the close spacing of these teeth is indicative of the premaxillary teeth, which were probably used in scraping flesh off of bones (Hone and Tanke, 2015), as opposed to the larger, less closely spaced, more robust maxillary teeth. The combination of all of these factors suggests that the biter was indeed feeding on the other individual’s foot. It is possible, especially considering that the rest of the skeleton is unknown, that this could have been a very unusual combat situation as animals are known to very peculiar things, but we think the best explanation is that this is an example of feeding.

It cannot be determined whether the larger *Tyrannosaurus* killed the smaller *Tyrannosaurus*. Such events are difficult to determine in the fossil record even when multiple skeletons are involved, which means it is essentially impossible to determine if such an event took place from this single, broken metatarsal! However, considering that it would be difficult for a larger *Tyrannosaurus* to reach its jaws low enough to bite a smaller individual's foot suggests that these bites were made after the smaller individual was already lying on the ground. Additionally, there would not have been a great deal of meat attached to the metatarsals, which suggests this may be a scavenging scenario where the larger tyrannosaurid is attempting to get even the smallest bits of meat off of an already picked-over carcass.

Since it has been demonstrated that tyrannosaurids could and did eat bones (Chin et al., 1998; Varricchio, 2001), it is unclear why the larger tyrannosaurid did not simply swallow the smaller individual's foot or at least this metatarsal whole. There does not appear to be any evidence of etching by digestive processes on HRS13997 as has been noticed in other bones ingested by tyrannosaurids (Varricchio, 2001). For whatever reason, it appears that this *Tyrannosaurus* individual preferred to nip flesh off of the metatarsal rather than swallowing it whole.

Conclusions

The discovery of HRS13997, a fourth metatarsal from a small tyrannosaurid, in the Lance Formation of Wyoming, possessing *Tyrannosaurus* tooth scores on its surface, seems to be further evidence for cannibalistic behavior in this large theropod. Although cannibalism is a likely explanation for these tooth scores, it is also possible that a *Tyrannosaurus rex* was feeding upon a different, smaller species of tyrannosaurid, possibly the contentious taxon *Nanotyrannus lancensis*. Even if this bone does come from a separate species, this particular fossil does present us with new insights into tyrannosaur feeding behavior. It appears that at least on this occasion, a tyrannosaurid stripped flesh off of a bone rather than swallowing the bone whole, even when very little flesh was present. Additionally, the tooth traces on HRS13997 were probably made by the premaxillary teeth of *Tyrannosaurus rex*, which suggests that tyrannosaurids utilized different portions of their dentitions for different purposes. This find represents the first instance of tyrannosaurids feeding on tyrannosaurids in the Lance Formation, as well as the first instance of *Knethichnus subparallelum* and *Linichnus serratus* on a tyrannosaurid bone. It is possible that further excavations at the location of HRS13997's discovery may lead to uncovering of more material from this small scavenged tyrannosaurid.

CHAPTER FOUR

CONCLUSIONS

Detailed taphonomic, paleontological, and sedimentological work at Rose Quarry in the Lance Formation (Maastrichtian) of eastern Wyoming has led to the development of a taphonomic and depositional model for this distinct bonebed. The presence of conflicting abrasion signatures within the bonebed suggests that the site represents a mixed assemblage. That the majority of the bones show at least stage 1 abrasion agrees well with the sedimentological data, in that the bonebed was created by unidirectional flowing water transporting sediment. Trough cross-bedding and horizontal bedding in this channelized sandstone along with the presence of transported large mud clasts and bones indicates rapidly moving water. I suggest that a flood mixed bones from the floodplain with those already in the channel, which accounts for the mixed abrasion signatures. During this high energy event, overbank collapses resulted in large mud clasts that were deposited in the channel sands in conjunction with the bones which were transported via traction. The heavily fragmented nature of almost every Rose Quarry bone is probably not due primarily to breakage during transport, but rather, trampling prior to transport. The reason for the lack of abundant trample marks in this scenario is that bones were trampled in a muddy floodplain setting where there were not enough sand grains present to result in numerous trample marks. The scenario accounts for the peculiarities of Rose Quarry when compared to the Main Quarries, and this study highlights the variability possible in fluvial bonebeds, the importance of floods in generating fluvial bonebeds, and the process for distinguishing between pre-burial and post-burial taphonomic histories.

Although there are few tooth traces present on the Rose Quarry bones, a nearby bonebed yielded a tyrannosaurid metatarsal possessing abundant tooth traces made by a *Tyrannosaurus rex*. This may suggest cannibalism in *Tyrannosaurus rex*, although the bone may belong to the contested genus *Nanotyrannus lancesis*. The close spacing of the scores on the metatarsal suggests that the biter was stripping off flesh with its premaxillary teeth. Tyrannosaurids appear to have been the apex predators in Maastrichtian dinosaur communities as preserved in locations such as Rose Quarry, and this discovery sheds light on their paleobiology, namely their carnivory and feeding techniques.

There are several future research projects that could be conducted in association with the Rose Quarry bonebed. I hope to soon analyze rare earth element (REE) traces in bones from Rose Quarry of varying preservation states to see if I can understand the different sources for the mixed assemblage that makes up this bonebed. REEs are taken up quickly after burial, so any bones that were buried and then later reworked and buried in the Rose Quarry bonebed would possess differing REE signatures from bones that were buried for the first time at the Rose Quarry site. In conjunction with this project, I am interested in studying the abrasion of Rose Quarry bones under scanning electron microscopy (SEM), as Thompson et al. (2011) determined that fresh, weathered, archaeological, and fossil bones all showed varying abrasion features under SEM. More work could certainly be done on the turtles found in Rose Quarry as to why some shells are articulated whereas others are not. Finally, further excavation at the site of HRS15997’s discovery could potentially yield more bones belonging to that tyrannosaurid, which might give us a clearer glimpse into tyrannosaurid paleobiology.

REFERENCES

Allison, P. A., 1986, Soft-bodied animals in the fossil record: the role of decay in fragmentation during transport: Geology, v. 14, p. 979-981.

Allison, P. A., and Briggs, D. E. G., 1991, Taphonomy of nonmineralized tissues, *in* Allison, P. A., and Briggs, D. E. G., eds., Taphonomy: Releasing the Data Locked in the Fossil Record: New York, New York, Plenum Press, p. 25-70.

Aslan, A., and Behrensmeyer, A. K., 1996, Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork River, Wyoming: *Palaios*, v. 11, no. 5, p. 411-421.

Bakker, R. T., Williams, M., and Currie, P. J., 1988, *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the Latest Cretaceous of Montana: *Hunteria*, v. 1, no. 5, p. 1-30.

Barsbold, R., 1974, Saurornithoididae, a new family of small theropod dinosaurs from Central Asia and North America: Palaeontologia Polonica, v. 30, p. 5-30.

Bates, K. T., and Falkingham, P. L., 2012, Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics: *Biology Letters*, v. 8, p. 660-664.

Behrensmeyer, A. K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya: *Bulletin of the Museum of Comparative Zoology*, v. 146, no. 10, p. 473-578.

-, 1978, Taphonomic and ecologic information from bone weathering: *Paleobiology*, v. 4, no. 2, p. 150-162.

-, 1982, Time resolution in fluvial vertebrate assemblages: *Paleobiology*, v. 8, no. 3, p. 211-227.

-, 1988, Vertebrate preservation in fluvial channels: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 63, p. 183-199.

-, 1990, Bones, *in* Briggs, D. E. G., and Crowther, P. R., eds., *Palaeobiology: A Synthesis*: Oxford, Blackwell Scientific Publications, p. 232-235.

-, 1991, Terrestrial vertebrate accumulations, *in* Allison, P. A., and Briggs, D. E. G., eds., *Taphonomy: Releasing the Data Locked in the Fossil Record*: New York, NY, Plenum Press, p. 291-335.

-, 2007, Bonebeds through time, *in* Rogers, R. R., Eberth, D. A., and Fiorillo, A. R., eds., *Bonebeds: Genesis, Analysis, and Paleobiological Significance*: Chicago, Illinois, The University of Chicago Press, p. 65-101.

Behrensmeyer, A. K., Gordon, K. D., and Yanagi, G. T., 1986, Trampling as a cause of bone surface damage and pseudo-cutmarks: *Nature*, v. 319, p. 768-771.

Bell, P. R., and Campione, N. E., 2014, Taphonomy of the Danek Bonebed: a monodominant *Edmontosaurus* (Hadrosauridae) bonebed from the Horseshoe Canyon Formation, Alberta: *Canadian Journal of Earth Sciences*, v. 51, p. 992-1006.

Bell, P. R., and Currie, P. J., 2010, A tyrannosaur jaw bitten by a confamilial: scavenging or fatal agonism?: *Lethaia*, v. 43, p. 278-281.

Bell, P. R., Currie, P. J., and Lee, Y.-N., 2012, Tyrannosaur feeding traces on *Deinocheirus* (Theropoda:?Ornithomimosauria) remains from the Nemegt Formation (Late Cretaceous), Mongolia: *Cretaceous Research*, v. 37, p. 186-190.

Binford, L. R., 1981, Patterns of bone modifications produced by nonhuman agents, *Bones: Ancient Men and Modern Myths*: San Diego, CA, Academic Press, Inc., p. 35-86.

Blanco, G., Traverso, J. M., Marchamalo, J., and Martínez, F., 1997, Interspecific and intraspecific aggression among Griffon and Cinereous Vultures at nesting and foraging sites: *Journal of Raptor Research*, v. 31, no. 1, p. 77-79.

Blasco, R., Rosell, J., Peris, J. F., Cáceres, I., and Vergès, J. M., 2008, A new element of trampling: an experimental application on the Level XII faunal record of Bolomor Cave (Valencia, Spain): *Journal of Archaeological Science*, v. 35, no. 6, p. 1605-1618.

Boggs, S., Jr., 2012, *Principles of Sedimentology and Stratigraphy*, Upper Saddle River, New Jersey, Prentice Hall.

Bohor, B. F., Triplehorn, D. M., Nichols, D. J., and Hugh T. Millard, J., 1987, Dinosaurs, spherules, and the "magic" layer: A new K-T boundary clay site in Wyoming: *Geology*, v. 15, p. 896-899.

Brand, L. R., Esperante, R., Chadwick, A. V., Porras, O. P., and Alomia, M., 2004, Fossil whale preservation implies high diatom accumulation rate in the Miocene-Pliocene Pisco Formation of Peru: *Geology*, v. 32, no. 2, p. 165-168.

Brand, L. R., Hussey, M., and Taylor, J., 2003, Decay and Disarticulation of Small Vertebrates in Controlled Experiments: *Journal of Taphonomy*, v. 1, no. 2, p. 69-95.

Brinkman, D. L., Eberth, D. A., and Currie, P. J., 2007, From bonebeds to paleobiology: Applications of bonebed data, *in* Rogers, R. R., Eberth, D. A., and Fiorillo, A. R., eds., *Bonebeds: Genesis, Analysis, and Paleobiological Significance*: Chicago, IL, The University of Chicago Press, p. 221-263.

Brusatte, S. L., Carr, T. D., Williamson, T. E., Jr., T. R. H., Hone, D. W. E., and Williams, S. A., 2016, Dentary groove morphology does not distinguish '*Nanotyrannus*' as a valid taxon of tyrannosauroid dinosaur. Comment on: "Distribution of the dentary groove of theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988": *Cretaceous Research*, v. *In Press*, p. 1-6.

Brusatte, S. L., Norell, M. A., Carr, T. D., Erickson, G. M., Hutchinson, J. R., Balanoff, A. M., Bever, G. S., Coiniere, J. N., Makovicky, P. J., and Xu, X., 2010, Tyrannosaur paleobiology: new research on ancient exemplar organisms: *Science*, v. 329, p. 1481-1485.

Buffetaut, E., and Suteethorn, V., 1989, A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: Remarks on the taphonomic and palaeoecological significance of such associations: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 73, no. 1-2, p. 77-83.

Butler, R. J., Upchurch, P., and Norman, D. B., 2008, The phylogeny of the ornithischian dinosaurs: *Journal of Systematic Paleontology*, v. 6, no. 1, p. 1-40.

Carpenter, K., 1982, Baby dinosaurs from the Late Cretaceous Lance and Hell Creek Formations and a description of a new species of theropod: Contributions to Geology, University of Wyoming, v. 20, no. 2, p. 123-134.

Carr, T. D., 1999, Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria): *Journal of Vertebrate Paleontology*, v. 19, no. 3, p. 497-520.

Carr, T. D., and Williamson, T. E., 2004, Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America: *Zoological Journal of the Linnean Society*, v. 142, p. 479-523.

Chin, K., Eberth, D. A., Schweitzer, M. H., Rando, T. A., Sloboda, W. J., and Horner, J. R., 2003, Remarkable preservation of undigested muscle tissue within a Late Cretaceous tyrannosaurid coprolite from Alberta, Canada: *Palaios*, v. 18, no. 3, p. 286-294.

Chin, K., Tokaryk, T. T., Erickson, G. M., and Calk, L. C., 1998, A king-sized theropod coprolite: *Nature*, v. 393, p. 680-682.

Collinson, J. D., 1978, Alluvial sediments, *in* Reading, H. G., ed., *Sedimentary Environments and Facies*: New York, Elsevier, p. 15-60.

Connor, C. W., 1992, The Lance Formation - petrography and stratigraphy, Powder River Basin and nearby basins, Wyoming and Montana: *U.S. Geological Survey Bulletin*, v. 1917, no. 1, p. 1-17.

Currie, P. J., 2003, Cranial anatomy of tyrannosaurid dinosaurs from the Late Cretaceous of Alberta, Canada: *Acta Palaeontologica Polonica*, v. 48, no. 2, p. 191-226.

D'Amore, D. C., and Blumenschine, R. J., 2012, Using striated tooth marks on bone to predict body size in theropod dinosaurs: A model based on feeding observations of *Varanus komodoensis*, the Komodo monitor: *Paleobiology*, v. 38, no. 1, p. 79-100.

DePalma, R. A., Burnham, D. A., Martin, L. D., Larson, P. L., and Bakker, R. T., 2015, The first giant raptor (Theropoda: Dromaeosauridae) from the Hell Creek Formation: *Paleontological Contributions*, v. 14, p. 1-16.

DePalma, R. A., Burnham, D. A., Martin, L. D., Rothschild, B. M., and Larson, P. L., 2013, Physical evidence of predatory behavior in *Tyrannosaurus rex*: *PNAS*, v. 110, no. 31, p. 12560-12564.

Dodson, P., Forester, C. A., and Sampson, S. D., 2004, Ceratopsidae, *in* Weishampel, D.

B., Dodson, P., and Osmólska, H., eds., *The Dinosauria*: Berkeley, California, University of California Press, p. 494-513.

Dominic, S., Rook, L., Benvenuti, M., and Abbazzi, L., 1995, Tapir remains in paralic deposits of Pliocene age in Lower Valdarno (Tuscany, Italy): Facies analysis and taphonomy: Geobios, v. 18, p. 131-135.

Eberth, D. A., Rogers, R. R., and Fiorillo, A. R., 2007a, A practical approach to the study of bonebeds, *in* Eberth, D. A., Rogers, R. R., and Fiorillo, A. R., eds., *Bonebeds: Genesis, Analysis, and Paleobiological Significance*: Chicago, IL, The University of Chicago Press, p. 265-331.

Eberth, D. A., Shannon, M., and Noland, B. G., 2007b, A bonebeds database: Classification, biases, and patterns of occurrence, *in* Rogers, R. R., Eberth, D. A., and Fiorillo, A. R., eds., *Bonebeds: Genesis, Analysis, and Paleobiological Significance*: Chicago, Illinois, The University of Chicago Press, p. 103-219.

Erickson, G. M., and Olson, K. H., 1996, Bite marks attributable to *Tyrannosaurus rex*: Preliminary description and implications: *Journal of Vertebrate Paleontology,* v. 16, no. 1, p. 175-178.

Erickson, G. M., Van Kirk, S. D., Su, J., Levenston, M. E., Caler, W. E., and Carter, D. R., 1996, Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones: *Nature*, v. 382, p. 706-708.

Esperante, R., Brand, L. R., Chadwick, A. V., and Poma, O., 2002, Taphonomy of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, Peru, *Current Topics on Taphonomy and Fossilization*: Valencia, Spain, International Conference Taphos, p. 337-343.

Evans, D. C., Larson, D. W., and Currie, P. J., 2013a, A new dromaeosaurid (Dinosauria: Theropoda) with Asian affinities from the latest Cretaceous of North America: *Naturwissenschaften*, v. 100, no. 11, p. 1041-1049.

Evans, D. C., Schott, R. K., Larson, D. W., Brown, C. M., and Ryan, M. J., 2013b, The oldest North American pachycephalosaurid and the hidden diversity of small-bodied ornithischian dinosaurs: *Nature Communications*, v. 4, no. 1828.

Everhart, M. J., and Ewell, K., 2006, Shark-bitten dinosaur (Hadrosauridae) caudal vertebrae from the Niobrara Chalk (Upper Coniacian) of western Kansas:

Transactions of the Kansas Academy of Science, v. 109, no. 1/2, p. 27-35.

Farlow, J. O., Brinkman, D. L., Abler, W. L., and Currie, P. J., 1991, Size, shape, and serration density of theropod dinosaur lateral teeth: *Modern Geology*, v. 16, p. 161-198.

Fiorillo, A. R., 1984, An introduction to the identification of trample marks: *Current Research in the Pleistocene*, v. 1, p. 47-48.

-, 1987, Trample marks: caution from the Cretaceous: *Current Research in the Pleistocene*, v. 4, p. 73-75.

-, 1989, An experimental study of trampling: implications for the fossil record, *in* Bonnichsen, R., and Sorg, M. H., eds., *Bone Modification*: Orono, ME, Center for the Study of the First Americans, p. 61-71.

-, 1991, Prey bone utilization by predatory dinosaurs: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 88, no. 3-4, p. 157-166.

Fowler, D. W., and Sullivan, R. M., 2006, A ceratopsid pelvis with toothmarks from the Upper Cretaceous Kirtland Formation, New Mexico: Evidence of Late Campanian tyrannosaurid feeding behavior, *in* Lucas, S. G., and Sullivan, R. M., eds., *Late Cretaceous Vertebrates from the Western Interior: New Mexico Museum of Natural History and Science Bulletin*, Volume 35, p. 127-130.

Galloway, W. E., and Hobday, D. K., 1983, Fluvial systems, *Terrigenous Clastic Depositional Systems*: New York, Springer-Verlag, p. 51-79.

Gradstein, F. M., Ogg, J. G., Schmitz, M., and Ogg, G., 2012, *The Geologic Time Scale 2012*, Elsevier.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D., 2001, PAST: Paleontological Statistics software package for education and data analysis: *Paleaeontologia Electronica*, v. 4, no. 1, p. 9.

Happ, J., 2008, An analysis of predator-prey behavior in a head-to-head encounter between *Tyrannosaurus rex* and *Triceratops*, *in* Larson, P., and Carpenter, K., eds., *Tyrannosaurus rex: The Tyrant King*: Bloomington, IN, Indiana University Press, p. 354-368.

Haynes, G., 1980, Evidence of carnivore gnawing on Pleistocene and recent mammalian bones: *Paleobiology*, v. 6, no. 3, p. 341-351.

Heinrich, P. V., 2008, Floating islands as taphonomic agents in the offshore dispersal of vertebrate remains: *Geological Society of America Abstracts with Programs*, v. 40, no. 6, p. 371.

Henderson, D. M., 2002, The eyes have it: The sizes, shapes, and orientations of theropod orbits as indicators of skull strength and bite force: *Journal of Vertebrate Paleontology*, v. 22, no. 4, p. 766-778.

Holtz, T. R., 2001, The phylogeny and taxonomy of the Tyrannosauridae, *in* Tanke, D. H., and Carpenter, K., eds., *Mesozoic Vertebrate Life*: Bloomington, Indiana, Indiana University Press, p. 64-83.

-, 2004, Tyrannosauroidea, *in* Weishampel, D. B., Dodson, P., and Osmólska, H., eds., *The Dinosauria*: Berkeley, CA, University of California Press, p. 111-136.

-, 2008, A critical reappraisal of the obligate scavenging hypothesis for *Tyrannosaurus rex* and other tyrant dinosaurs, *in* Larson, P., and Carpenter, K., eds., *Tyrannosaurus rex: The Tyrant King*: Bloomington, IN, Indiana University Press, p. 370-396.

Holtz, T. R., Brinkman, D. L., and Chandler, C. L., 1998, Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*: *Gaia*, v. 15, p. 159-166.

Holtz, T. R., and Osmólska, H., 2004, Saurischia, *in* D.B. Weishampel, P. D., and H. Osmólska, ed., *The Dinosauria*: Berkeley, CA, University of California Press, p. 21-24.

Hone, D. W. E., and Tanke, D. H., 2015, Pre- and postmortem tyrannosaurid bite marks on the remains of *Daspletosaurus* (Tyrannosaurinae: Theropoda) from Dinosaur Provincial Park, Alberta, Canada: *PeerJ*, v. 3, p. e885.

Hone, D. W. E., and Watabe, M., 2010, New information on scavenging and selective feeding behavior of tyrannosaurids: *Acta Palaeontologica Polonica*, v. 55, no. 4, p. 627-634.

Hutt, S. D., Naish, D., Martill, D. M., Barker, M. J., and Newberry, P., 2001, A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England: *Cretaceous Research*, v. 22, no. 2, p. 227-242.

Jacobsen, A. R., 1998, Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones: *Historical Biology*, v. 13, p. 17-26.

-, 2001, Tooth-marked small theropod bone: An extremely rare trace, *in* Tanke, D. H., and Carpenter, K., eds., *Mesozoic Vertebrate Life*: Bloomington, IN, Indiana University Press, p. 59-63.

Jacobsen, A. R., and Bromley, R. G., 2009, New ichnotaxa based on tooth impressions on dinosaur and whale bones: *Geological Quarterly*, v. 53, no. 4, p. 373-382.

Johnson, K. R., Nichols, D. J., and Hartman, J. H., 2002, Hell Creek Formation: A 2001 synthesis: Geological Society of America Special Papers, v. 361, p. 503-510.

Kidwell, S. M., and Baumiller, T., 1990, Experimental disintegration of regular echinoids: roles of temperature, oxygen, and decay thresholds: Paleobiology, v. 16, no. 3, p. 247-271.

Kidwell, S. M., Fürsich, F. T., and Aigner, T., 1986, Conceptual framework for the analysis and classification of fossil concentrations: Palaios, v. 1, p. 228-238.

Kirkland, J. I., and Bader, K., 2010, Insect trace fossils associated with *Protoceratops* carcasses in the Djadokhta Formation (Upper Cretaceous), Mongolia, *in* Ryan, M. J., Chinnery-Allgeier, B. J., and Eberth, D. A., eds., *New Perspectives on Horned Dinosaurs: The Royal Tyrell Museum Ceratopsian Symposium*: Bloomington, Indiana, Indiana University Press, p. 509-519.

Larson, D. W., and Currie, P. J., 2013, Multivariate analyses of small theropod dinosaur teeth and implications for paleoecological turnover through time: PLoS ONE, v. 8, no. 1, p. e54329.

Larson, P., 2013, The validity of *Nanotyrannus lancensis* (Theropoda, Lancian - Upper Maastrichtian of North America): *Society of Vertebrate Paleontology Abstracts with Programs*, p. 159.

Lee, M. S. Y., 2013, Turtle origins: insights from phylogenetic retrofitting and molecular scaffolding: *Journal of Evolutionary Biology*, v. 26, no. 12, p. 2729-2738.

Lehman, T. M., 1987, Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 189-217.

Leopold, L. B., and Wolman, M. G., 1957, River channel patterns: braided, meandering and straight, *Physiographic and Hydraulic Studies on Rivers*, Volume 282-B, Geological Survey Professional Paper.

Liebig, P. M., Taylor, T.-S. A., and Flessa, K. W., 2003, Bones on the beach: Marine mammal taphonomy of the Colorado Delta, Mexico: Palaios, v. 18, p. 168-175.

Lloyd, E. R., and Hares, C. J., 1915, The Cannonball Marine Member of the Lance Formation of North and South Dakota and its bearing on the Lance-Laramie Problem.: *The Journal of Geology*, v. 23, no. 6, p. 523-547.

Lockley, M. G., Nadon, G., and Currie, P. J., 2004, A diverse dinosaur-bird footprint assemblage from the Lance Formation, Upper Cretaceous, Eastern Wyoming: Implications for Ichnotaxonomy: Ichnos, v. 11, no. 3-4, p. 229-249.

Loeuff, J. L., 2012, Paleobiogeography and biodiversity of Late Maastrichtian dinosaurs: how many dinosaur species went extinct at the Cretaceous-Tertiary boundary?: Bulletin de la Société Géologique de France, v. 183, no. 6, p. 547-559.

Longrich, N. R., Barnes, K., Clark, S., and Miller, L., 2013, Caenagnathidae from the Upper Campanian Aguja Formation of West Texas, and a revision of the Caenagnathinae: *Bulletin of the Peabody Museum of National History*, v. 54, no. 1, p. 23-49.

Longrich, N. R., Horner, J. R., Erickson, G. M., and Currie, P. J., 2010, Cannibalism in *Tyrannosaurus rex*: *PLoS ONE*, v. 5, no. 10, p. e13419.

Manzig, P. C., Kellner, A. W. A., Weinschütz, L. C., Fragoso, C. E., Vega, C. S., Guimarães, G. B., Godoy, L. C., Liccardo, A., Ricetti, J. H. Z., and Moura, C. C. d., 2014, Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles: *PLoS ONE*, v. 9, no. 8, p. e100005.

Meers, M. B., 2002, Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior: *Historical Biology*, v. 16, no. 1, p. 1-12.

Meyer, C. A., 1991, Burial experiments with marine turtle carcasses and their paleoecological significance: Palaios, v. 6, no. 89-96.

Miall, A. D., 1977, A review of the braided river depositional environment: *Earth Science Reviews*, v. 13, p. 1-62.

-, 1978, Lithofacies types and vertical profile models in braided rivers: a summary, *in* Miall, A. D., ed., *Fluvial Sedimentology, Canadian Society of Petroleum Geologists Memoir*, Volume 5, p. 597-604.

-, 1982, Analysis of fluvial depositional systems: *AAPG Education Course Note Series*, v. 20, p. 1-75.

Mikuláš, R., Kadlecová, E., Fejfar, O., and Dvořák, Z., 2006, Three new ichnogenera of biting and gnawing traces on reptilian and mammalian bones: A case study from the Miocene of the Czech Republic: *Ichnos*, v. 13, no. 3, p. 113-127.

Montgomery, S. L., and Robinson, J. W., 1997, Jonah Field, Sublette County, Wyoming: Gas production from overpressured Upper Cretaceous Lance sandstones of the Green River Basin: *American Association of Petroleum Geologists Bulletin*, v. 81, no. 7, p. 1049-1062.

Moore, J. R., 2012, Do terrestrial vertebrate fossil assemblages show consistent taphonomic patterns?: *Palaios*, v. 27, p. 220-234.

Nesbitt, S. J., Turner, A. H., Erickson, G. M., and Norell, M. A., 2006, Prey choice and cannibalistic behaviour in the theropod *Coelophysis*: *Biology Letters*, v. 2, p. 611-614.

Njau, J. K., and Blumenschine, R. J., 2006, A diagnosis of crocodile feeding traces on larger mammal bone, with fossil examples from the Plio-Pleistocene Olduvai Basin, Tanzania: *Journal of Human Evolution*, v. 50, p. 142-162.

Owen, R., 1842, Report on British Fossil Reptiles, Report of the Eleventh Meeting of the British Association for the Advancement of Science.

Padian, K., and Chiappe, L. M., 1998, The origin and early evolution of birds: Cambridge Philosophical Society, v. 73, p. 1-42.

Paik, I. S., Kim, H. J., Lim, J. D., Huh, M., and Lee, H. I., 2011, Diverse tooth marks on an adult sauropod bone from the Early Cretaceous, Korea: Implications in feeding behavior of theropod dinosaurs: *Palaeogeography, Palaeoclimatology, Palaeoecology,* v. 309, p. 342-346.

Palmqvist, P., Renzi, M. D., and Arribas, A., 2002, Taphonomic analysis as a source of paleobiologic information, *in* Renzi, M. D., ed., Current Topics on Taphonomy and Fossilization.

Parsons, K. M., and Brett, C. E., 1991, Taphonomic processes and biases in modern marine environments: an actualistic perspective on fossil assemblage preservation, *in* Donovan, S. K., ed., The Process of Fossilization: New York, New York, Columbia University Press, p. 22-65.

Peterson, J. E., Henderson, M. D., Scherer, R. P., and Vittore, C. P., 2009, Face biting on a juvenile tyrannosaurid and behavioral implications: *Palaios*, v. 24, p. 780-784.

Pirrone, C. A., Buatois, L. A., and Bromley, R. G., 2014, Ichnotaxobases for bioerosion trace fossis in bones: *Journal of Paleontology*, v. 88, no. 1, p. 195-203.

Plotnick, R. E., 1986, Taphonomy of a modern shrimp: implications for the arthropod fossil record: Palaios, v. 1, p. 286-293.

Pobiner, B., 2008, Paleoecological Information in Predator Tooth Marks: *Journal of Taphonomy*, v. 6, no. 3-4, p. 373-397.

Pobiner, B. L., DeSilva, J., Sanders, W. J., and Mitani, J. C., 2007, Taphonomic analysis of skeletal remains from chimpanzee hunts at Ngogo, Kibale National Park, Uganda: *Journal of Human Evolution*, v. 52, p. 614-636.

Polis, G. A., 1981, The evolution and dynamics of intraspecific predation: *annual Review of Ecology and Systematics*, v. 12, p. 225-251.

Rivera-Sylva, H. E., Hone, D. W. E., and Dodson, P., 2012, Bite marks of a large theropod on an hadrosaur limb bone from Coahuila, Mexico: *Boletín de la Sociedad Geológica Mexicana*, v. 64, no. 1, p. 155-159.

Roberts, E. M., Rogers, R. R., and Foreman, B. Z., 2007, Continental insect borings in dinosaur bone: examples from the Late Cretaceous of Madagascar and Utah: *Journal of Paleontology*, v. 81, no. 1, p. 201-208.

Robinson, J. W., Delozier, D. L., and Flinch, R., 1996, Integrated reservoir description and analysis of the Lance Formation at Jonah Field, Sublette County, Wyoming: *American Association of Petroleum Geologists Bulletin*, v. 80, no. 6.

Rogers, R. R., 1990, Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medicine Formation of northwestern Montana: Evidence for drought-related mortality: *Palaios*, v. 5, p. 394-413.

Rogers, R. R., and Kidwell, S. M., 2007, A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations, *in* Rogers, R. R., Eberth, D. A., and Fiorillo, A. R., eds., *Bonbeds: Genesis, Analysis, and Paleobiological Significance*: Chicago, Illinois, The University of Chicago Press, p. 1-63.

Rogers, R. R., Krause, D. W., and Rogers, K. C., 2003, Cannibalism in the Madagascan dinosaur *Majungatholus atopus*: *Nature*, v. 422, no. 6931, p. 515-518.

Rogers, R. R., Krause, D. W., Rogers, K. C., Rasoamiaramanana, A. H., and Rahantarisoa, L., 2007, Paleoenvironment and paleoecology of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar: *Journal of Vertebrate Paleontology*, v. 27, no. Supplement 2, p. 21-31.

Rothschild, B. M., 2015, Unexpected behavior in the Cretaceous: tooth-marked bones attributable to tyrannosaur play: *Ethology Ecology & Evolution*, v. 27, no. 3, p. 325-334.

Rothschild, B. M., and Depalma, R., 2013, Skin pathology in the Cretaceous: Evidence for probable failed predation in a dinosaur: *Cretaceous Research*, v. 42, p. 44-47.

Ryan, M. J., Russell, A. P., Eberth, D. A., and Currie, P. J., 2001, Taphonomy of a *Centrosaurus* (Ornithischia, Ceratopsidae) bone bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with comments on cranial ontogeny: *Palaios*, v. 16, p. 482-506.

Sampson, S. D., Loewen, M. A., Farke, A. A., Roberts, E. M., Forster, C. A., Smith, J. A., and Titus, A. L., 2010, New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism: *PLoS ONE*, v. 5, no. 9, p. e12292.

Schmerge, J. D., and Rothschild, B. M., 2016, Distribution of the dentary groove on theropod dinosaurs: Implications for theropod phylogeny and the validity of the genus *Nanotyrannus* Bakker et al., 1988: *Cretaceous Research*, v. 61, p. 26-33.

Schubert, B. W., and Ungar, P. S., 2005, Wear facets and enamel spalling in tyrannosaurid dinosaurs: *Acta Palaeontologica Polonica*, v. 50, no. 1, p. 93-99.

Seilacher, A., 1953, Studien zur Palichnologie. 1. Über die Methoden der Palichnologie: *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, v. 96, p. 421-452.

Shotwell, J. A., 1955, An approach to the paleoecology of mammals: Ecology, v. 36, p. 327-337.

Shotwell, J. A., 1963, Mammalian fauna of the Drewsey Formation, Bartlett Mountain, Drinkwater, and Otis Basin local faunas: *Transactions of the American Philosophical Society*, v. 53, p. 70-77.

Smith, J. B., Vann, D. R., and Dodson, P., 2005, Dental morphology and variation in theropod dinosaurs: Implications for the taxonomic identification of isolated teeth: *The Anatomical Record Part A*, v. 285, no. 2, p. 699-736.

Smith, R. M. H., 1993, Vertebrate taphonomy of Late Permian floodplain deposits in the southwestern Karoo Basin of South Africa: *Palaios*, v. 8, p. 45-67.

Soares, M. B., 2003, A taphonomic model for the Mesosauridae assemblage of the Irati Formation (Paraná Basin, Brazil): Geologica Acta, v. 1, no. 4, p. 349-361.

Southard, J. B., and Boguchwal, L. A., 1990, Bed configurations in steady unidirectional water flows. Part 2. Synthesis of flume data: *Journal of Sedimentary Petrology*, v. 60, no. 5, p. 658-679.

Sullivan, R. M., 2006, A taxonomic review of the Pachycephalosauridae (Dinosauria: Ornithischia): New Mexico Museum of Natural History and Science Bulletin, v. 35, p. 347-365.

Tanke, D. H., and Currie, P. J., 1998, Head-biting behavior in theropod dinosaurs: Paleopathological evidence: *Gaia*, v. 15, p. 167-184.

Thompson, C. E. L., Ball, S., Thompson, T. J. U., and Gowland, R., 2011, The abrasion of modern and archaeological bones by mobile sediments: the importance of transport modes: *Journal of Archaeological Science*, v. 38, p. 784-793.

Toots, H., 1965, Orientation and distribution of fossils as environmental indicators, Sedimentation of Late Cretaceous and Tertiary Outcrops, Rock Springs Uplift, Annual Field Conference Guidebook, Volume 19, Wyoming Geological Association, p. 219-229.

Torrens, H. S., 2012, Politics and paleontology: Richard Owen and the invention of dinosaurs, *in* Brett-Surman, M. K., Holtz, T. R., and Farlow, J. O., eds., The Complete Dinosaur: Bloomington, Indiana, Indiana University Press.

Varricchio, D. J., 2001, Gut contents from a Cretaceous tyrannosaurid: Implications for theropod dinosaur digestive tracts: *Journal of Paleontology*, v. 75, no. 2, p. 401-406.

Varricchio, D. J., and Horner, J. R., 1993, Hadrosaurid and lambeosaurid bone beds from the Upper Cretaceous Two Medicine Formation of Montana: taphonomic and biologic implications: *Canadian Journal of Earth Sciences*, v. 30, p. 997-1006.

Voorhies, M. R., 1969, Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska: Contributions to Geology, University of Wyoming, v. 1, p. 1-68.

Wang, X., Kellner, A. W. A., Jiang, S., Wang, Q., Ma, Y., Paidoula, Y., Cheng, X., Rodrigues, T., Meng, X., Zhang, J., Li, N., and Zhou, Z., 2014, Sexually dimorphic tridimensionally preserved pterosaurs and their eggs from China: *Current Biology*, v. 24, p. 1-8.

Weeks, S. R., and Chadwick, A. V., 2011, A prominent seismite in the Upper Cretaceous Lance Formation in Northeastern Wyoming as a Stratigraphic Marker: Geological Society of America Abstracts with Programs, v. 43, no. 5, p. 280.

Weeks, S. R., Chadwick, A. V., and Brand, L. R., 2015, Large dinosaur bonebed deposited as debris flow: Lance Formation Niobrara County, Wyoming: *Geological Society of America Abstracts with Programs*, v. 47, no. 7, p. 566.

Weishampel, D. B., 2004, Ornithischia, *in* D.B. Weishampel, P. D., and H. Osmólska, ed., *The Dinosauria*: Berkeley, CA, University of California Press, p. 323-324.

Wells, N. A., Richards, S. S., Peng, S., Keattch, S. E., Hudson, J. A., and Copsey, C. J., 1993, Fluvial processes and recumbently folded crossbeds in the Pennsylvanian Sharon Conglomerate in Summit County, Ohio, U.S.A.: *Sedimentary Geology*, v. 85, p. 63-83.

Wilson, M. V. H., 1988, Paleoscene #9. Taphonomic processes: Information loss and information gain: *Geoscience Canada*, v. 15, no. 2, p. 131-148.

Witmer, L. M., 1995, The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils, *in* Thomason, J., ed., *Functional Morphology in Vertebrate Paleontology*, Cambridge University Press, p. 19-33.

Witton, M. P., and Naish, D., 2008, A reappraisal of azhdarchid pterosaur functional morphology and paleoecology: PLoS ONE, v. 3, no. 5, p. e2271.

Woodruff, D. C., and Varricchio, D. J., 2011, Experimental modeling of a possible *Oryctodromeus cubicularis* (Dinosauria) burrow: *Palaios*, v. 26, p. 140-151.

Xu, X., Zhao, Q., Norell, M., Sullivan, C., Hone, D., Erickson, G., Wang, X., Han, F., and Guo, Y., 2009, A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin: Chinese Science Bulletin, v. 54, no. 3, p. 430-435.

Zanno, L. E., Gillette, D. D., Albright, L. B., and Titus, A. L., 2009, A new North American therizinosaurid and the role of herbivory in 'predatory' dinosaur evolution: *Proceedings of the Royal Society of Biological Sciences*, v. 276, p. 3505-3511.

Zanno, L. E., and Makovicky, P. J., 2010, Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution: Proceedings of the National Academy of Sciences, v. 108, no. 1, p. 232-237.

Zeigler, K. E., Heckert, A. B., and Lucas, S. G., 2005, Taphonomic analysis of a fire-related Upper Triassic vertebrate fossil assemblage from north-central New Mexico: *Geology of the Chama Basin, 56th Field Conference Guidebook, New Mexico Geological Society*, p. 2005.

APPENDIX A

FLUVIAL PROCESSES AND DEPOSITS

The word “fluvial” (from the Latin *fluvius* meaning “to flow”) deals with rivers and streams. Within a river, transported sediment is either considered suspended load or bedload. Fine particles that are carried high in the main flow above the bed make up the suspended load. These particles will remain suspended if their shear velocities exceed their settling velocities (Boggs, 2012). Within the bedload, particles can either be in traction or saltation. In traction, large grains roll, slide, and creep downstream (Boggs, 2012). Saltating grains, however, move downstream in intermittent contact with the bed, bouncing off of the bed and other grains (Boggs, 2012). Saltation can be thought of as an intermediate state between traction and suspension. In addition to these normally occurring processes, sediments can also be transported quickly and catastrophically by mass flows, such as debris flows and mudflows.

There are four principal river types that have been observed in the present: straight, anastomosing, braided, and meandering (Miall, 1977). Straight rivers are rare, and they occur typically as delta distributaries where the slope is very low, such as on the Mississippi delta (Miall, 1982). Very little is known about the deposits made by straight rivers (Miall, 1977).

Anastomosing rivers are characterized by two or more stable channels that exhibit low to high sinuosity in areas with rapid subsidence but low slopes (Miall, 1982). Channel stability in anastomosing rivers is favored by abundant vegetation along the banks (Miall, 1982).

Braided rivers consist of a series of rapidly shifting channels and mid-channel bars, and they are characterized by high width to depth ratios, low sinuosities, and their presence on steep slopes (Miall, 1977). Braided streams can commonly be found at glacial outwash areas, humid fans, and wadis of semiarid regions (Collinson, 1978). Three types of bars are found in braided streams: longitudinal, linguoid/transverse, and compound (point, side, and lateral) (Miall, 1977). Longitudinal bars are elongated parallel to flow direction, diamond or lozenge-shaped in plan view, and are typically gravelly (Miall, 1977). Internally, longitudinal bars are massive or contain crude horizontal beds, but they may also be fining upward and/or have a matrix-filled fabric (Collinson, 1978). Longitudinal bars do not have cross-beds (Miall, 1982). Linguoid and transverse bars are rhombic or lobate in plan view and typically occur in sandy braided streams where they can be found in trains with an out-of-phase relationship with one another (Miall, 1977). Linguoid bars have sinuous crests, whereas transverse bars have straighter crests (Miall, 1977). Compound bars, including point bars, side bars, and lateral bars, form in areas of low fluvial energy and have complex internal structures such as planar-tabular cross-bedding, trough cross-bedding, ripple marks, coarse-grained lag deposits, and fine-grained drapes (Miall, 1977).

Meandering rivers have high suspended load to bedload ratios and are commonly found in areas with low gradient slopes and cohesive banks (Collinson, 1978; Miall, 1982). The channel of a meandering stream occupies only a small part of its alluvial plain at any one time, but over time the bends in the stream meander, which causes the channel to encroach or retreat in various areas of the alluvial plain (Collinson, 1978). Within the curve of a meandering stream, maximum velocities will occur near the outer bank; thus, the outer bank of the curve is eroded while deposition occurs on the inner bank of the curve, often forming a point bar (Collinson, 1978). Levees are ridges that run along the banks of the channel that slope away from the channel. They consist of fine sand, silt, and some clay. Levees are created when the river overflows its banks during a flood, and sediment in the levee is built up higher with each successive flood (Galloway and Hobday, 1983). During a flood, the river may occasionally breach its levee and form a crevasse splay in the shape of fans or tongues on the floodplain. Floodplains are made up of fine sediment deposited during floods, which means that they typically have low sedimentation rates. In a wet climate, swamps may be found on the floodplains of rivers. Sometimes, large bends in a meandering river can be cut off from the main flow either by chute or neck cutoff. In either case, the water left in the cutoff meander results in a body of water called an oxbow lake. Oxbow lakes eventually fill up with fine sediments. Rivers can also change course, in what is called avulsion, abandoning a previous course.

The factors that determine which of the four principal types a river will be are complex and include discharge, sediment load, width, depth, velocity, slope, bed roughness, and vegetation (Miall, 1977). As a result of this complexity, the occurrence of a particular river type does not necessarily lead to any definite conclusions regarding climate or relief (Miall, 1977). A given channel can change from braided to meandering or vice versa in a relatively short distance (Leopold and Wolman, 1957).

Fluvial environments create certain kinds of deposits that are recognizable in the field. Braided stream paleoenvironments will be represented in the rocks by many overlapping channels of coarse material, with the coarsest materials forming a distinct bedload at the base of the channels. Various bars will be visible in the stream consisting of cross-bedded sandstones and conglomerates. Parabolic recumbent folds have been noted in both modern and ancient braided stream deposits (Wells et al., 1993).

Meandering river deposits consist of a trough cross-bedded sandstone channel, or multiple channels, surrounded by mudstone (deposits from the floodplain). Ancient levees of a meandering river would consist of packages of fine sand, silt, and some clay occurring on top of mudstone at the edge of a channel. Such ancient levees can contain fine ripples, climbing ripples, wavy and planar lamination, clay drapes, laminated mud, and root structures (Galloway and Hobday, 1983). Crevasse splays show up in the rock record as fans or tongues of sand, with the thickness of the deposit smaller than the channel and decreasing grain size away from the channel (Collinson, 1978). Paleosols and roots can be associated with crevasse splays (Collinson, 1978; Galloway and Hobday, 1983). Floodplain deposits consist of fine-grained sediment, which is often laminated. However, laminated sediments in a true floodplain can be reworked by burrowing, plant growth, and pedogenic structures. Additionally, desiccation cracks can occur on the floodplain. Coal found in floodplains have been interpreted as evidence for ancient swamps (Galloway and Hobday, 1983).

Point bars typically possess medium to large scale trough cross-beds, but they also can have zones of tabular and planar cross-beds as well as ripple stratification (Galloway and Hobday, 1983). Within a point bar, there is a fining-upward sequence with finer-grained sediments found at the top containing ripples, climbing ripples, mud drapes, and root traces (Galloway and Hobday, 1983). The fining upward sequence is produced by lateral accretion of the point bar (Miall, 1982). Flow within a bend of a meandering river is helical, cutting from the outer bank, and depositing along the inner bank where the point bar forms. As sediment flows across the point bar, it tends to sort by grain size, with the finest particles deposited at the shallowest parts of the point bar (Miall, 1982).

Miall (1978) (cited in Miall (1982)) created 19 lithofacies types that can accurately describe most fluvial deposits. These lithofacies types have been assigned different code letters, and they can be seen in Table 7 along with brief descriptions.

Table 7. Lithofacies codes from Miall (1978) in Miall (1982).

Facies Code	**Lithofacies**	**Sedimentary Structures**	**Interpretation**
Gms	massive, matrix-supported gravel	none	debris flow deposits
Gm	massive or crudely-bedded gravel	horizontal bedding, imbrication	longitudinal bars, lag deposits, sieve deposits
Gt	gravel, stratified	trough cross-beds	minor channel fills
Gp	gravel, stratified	planar cross-beds	linguoid bars or deltaic growths from older bar remnants
St	sand, medium to very coarse, may be pebbly	solitary (theta) or grouped (pi) trough cross-beds	dunes (lower flow regime)
Sp	sand, medium to very coarse, may be pebbly	solitary (alpha) or grouped (omikron) planar cross-beds	linguoid, transverse bars, sand waves (lower flow regime)
Sr	sand, very fine to coarse	ripple marks of all types	ripples (lower flow regime)
Sh	sand, very fine to very coarse	horizontal lamination, parting, or streaming lineation	planar bed flow (lower and upper flow regime)
Sl	sand, fine	low angle (<10°) cross-beds	scour fills, crevasse splays, antidunes
Se	erosional scours with intraclasts	crude cross-bedding	scour fills
Ss	sand, fine to coarse, may be pebbly	broad, shallow scours including eta cross-stratification	scour fills
Sse, She, Spe	sand	analogous to *Ss*, *Sh*, *Sp*	eolian deposits
Fl	sand, silt, mud	fine lamination, very small ripples	overbank or waning flood deposits
Fsc	silt, mud	laminated to massive	backswamp deposits
Fcf	mud	massive with freshwater mollusks	backswamp pond deposits
Fm	mud, silt	massive, desiccation cracks	overbank or drape deposits
Fr	silt, mud	rootlets	seatearth
C	coal, carbonaceous mud	plants, mud films	swamp deposits
P	carbonate	pedogenic features	soil

APPENDIX B

A GUIDE TO TAPHONOMY

Introduction

In the past, paleontologists were only concerned about identification of bones and taxa. Thus, they would extract good fossils while neglecting the surrounding fabric, and they would throw out fragments of bone as useless. This attitude began to change in 1940 with the creation of the field of taphonomy by Efremov to describe “the science of the laws of burial” (Wilson, 1988). Taphonomy utilizes knowledge from paleontology and sedimentology in order to understand everything that happened to an organism from its death to its final exposure as a fossil at the surface by a paleontologist. By studying bone fragments, tooth marks, sedimentologic features, articulation, and association, paleontologists could learn about past environments and past processes.

Identification of Bonebeds, Remains, Taxa, and Individuals

The definition of bonebed varies from author to author. Behrensmeyer (2007) describes it as “a single sedimentary stratum with a bone concentration that is unusually dense (often but not necessarily exceeding 5% bone by volume), relative to adjacent lateral and vertical deposits, and consisting of remains from more than one individual.” Rogers and Kidwell (2007) say a bonebed is “a ‘relative concentration’ of vertebrate hardparts preserved in a localized area or stratigraphically limited sedimentary unit (e.g., bed, horizon, stratum) and derived from more than one individual.” Rogers and Kidwell (2007) in the same volume state that a bonebed is defined as “consisting of the complete or partial remains of more than one vertebrate animal in notable concentration along a bedding plane or erosional surface, or throughout a single bed." This definition, rather than relying on a strict percentage, relies on the thoughts of paleontologists on what is normal or unusual in their experience at a particular site. All of these definitions agree that it is a concentration of vertebrate hardparts derived from more than one individual, which stands out as different or unusual when compared to the surrounding lithologies. Interestingly, the majority of bonebeds published in the literature (according to the ETE Bonebed Database) appear to be found in sandstones, siltstones, or mudstones, and half of the bonebeds occur in fluvial environments (Behrensmeyer, 2007).

Bonebeds can be defined as microfossil bonebeds, macrofossil bonebeds, or mixed bonebeds. A microfossil bonebed contains an assemblage of elements, bone fragments, and bone pebbles where over 75% of the identifiable specimens are smaller than 5 cm along the longest axis (Eberth et al., 2007b). A macrofossil bonebed containing disarticulated and/or articulated elements where over 75% of the elements are larger than 5 cm along the longest axis (Eberth et al., 2007b). A mixed bonebed contains a mixture of more than 25% of each macrofossils and microfossils (Eberth et al., 2007b).

The first paleontological step in studying a vertebrate fossil assemblage is the identification of the bones. The type of bone must be identified as well as the taxon from which it came as precisely as possible. However, simply because a bone cannot be easily identified does not mean that it is of no use. Rather, even bone fragments must be catalogued and kept because they may hold important taphonomic information. As the bones are being identified, it is important to keep track of the number of specimens. The number of each kind of bone and each taxon represented should be tallied. Taxonomic identification of remains should only go as far as possible given the remains present. For instance, several species of ceratopsids are known from the Dinosaur Park Formation in Alberta, Canada including two species of *Chasmosaurus* (*C. belli* and *C. russelli*), *Vagaceratops irvinensis*, *Styracosaurus albertensis* and *Centrosaurus apertus* (Dodson et al., 2004; Sampson et al., 2010), but the postcranial skeletons of ceratopsids are incredibly conservative (Dodson et al., 2004); thus, if an isolated ceratopsid postcranial bone were found, it would probably not be proper to assign it a genus and species designation without further evidence. In contrast, a single mammal tooth may be all that is needed for identification to the taxonomic level of species. Mammals often have highly distinctive teeth from species to species, making identification of taxa from isolated teeth much simpler than in the case of ornithischian dinosaurs, which are much more conservative in morphology (Evans et al., 2013b).

After the number of specimens is known, the number of individuals can be determined. In order to calculate how many individual organisms are present, one can determine the minimum number of individuals (MNI). In order to determine the MNI and NSI (number of specimens per individual), one must know how many of a particular bone each organism would have. It is useful to count diagnostic bones such as skulls, humeri, femorae, etc because there are very few per individual (and, in the case of the humeri and femorae, right and left can be known). The researcher can then pick the most common diagnostic bone and count the number of appearances in the bonebed (Shotwell, 1955). That number is the MNI. The NSI is calculated by dividing the number of specimens of one species present by the MNI of that species in the deposit. It is always important when calculating the NSI to take into consideration that different species have different numbers of identifiable elements (Voorhies, 1969).

It is important to also determine the number of species represented in a bonebed. Assemblages can be described as monotypic or polytypic, as well as monospecific, polyspecific, or paucispecific. A monotypic assemblage contains only species of a single type (e.g., an assemblage consisting only of trilobites) whereas a polytypic assemblage contains multiple types of organisms (e.g., an assemblage containing trilobites, brachiopods, crinoids, and bryozoans). Monospecific describes an assemblage that not only consists of one type, but only one species (e.g., an assemblage consisting only of the trilobite *Flexicalymene meeki*). A polyspecific assemblage, however, consists of multiple species and can thus also be polytypic (e.g., an assemblage consisting of the trilobite *Flexicalymene meeki*, the brachiopod *Zygospira modesta*, the crinoid *Cincinnaticrinus pentagonus*, and the bryozoan *Parvohallopora ramose*) or monotypic (e.g., an assemblage consisting of the trilobites *Flexicalymene meeki* and *Isotelus gigas*). A paucispecific assemblage is one in which the deposit consists of only a few species, and is dominated by one of the species (e.g., an assemblage containing 90% *Parvohallopora ramose*, 10% *Zygospira modesta*) (Kidwell et al., 1986).

An assemblage probably, and almost definitely, does not contain fossils of all the species that were alive in that place or time. Traces of soft-bodied organisms are only rarely ever preserved (Allison, 1986; Parsons and Brett, 1991), and organisms that are rare in life will most likely be rare in the fossil record. As well, rarity in a deposit does not necessarily correspond to rarity in life. An assemblage simply records what was fossilized, not necessarily what lived, what died, or even what was buried in that location.

The description of an assemblage using terms such as monotypic is incredibly important as one seeks to recreate the ancient ecosystem or death profile. If a deposit is monospecific, then that could support the idea of a catastrophic death (such as the drowning of a herd). If a deposit is paucispecific or polyspecific, then it is important to look for differential preservation of species. If one species' remains are better preserved than another species, then that may speak volumes about the taphonomic history of the assemblage. For instance, if the skeletal remains of one species are much better preserved than another, then this might indicate that the poorly preserved specimens were transported farther, scavenged, or decaying sub-aerially for some time before burial.

Catastrophic or Attritional Mortality

One of the most important considerations when observing a bonebed is determining whether the mortality is attritional or catastrophic. This is much easier to determine when dealing with a monospecific assemblage versus a polyspecific assemblage. With a monospecific assemblage, the researcher can determine the ages of the individuals and compare the number of individuals for each age class. Age of tetrapod species can be determined by various factors including 1) stages of dental eruption, 2) body size, 3) fusion of limb epiphyses, 4) fusion of cervical vertebrae, and 5) fusion of vertebral caps (Esperante, personal communication, 2012). After the ages have been determined and compared, the trends can be analyzed. If the deposit is dominated by juveniles and old adults, then it is most likely an attritional mortality. If, instead, the deposit represents the standing population: a large number of juveniles followed by fewer individuals in each successive age class giving a negative exponential curve with respect to age, then it is most likely a catastrophic mortality. However, a lack of juveniles in a bonebed does not mean that a catastrophic mass mortality did not occur, for juveniles are more delicate and could be transported away or preferentially reworked (Soares, 2003). It is important to note that a catastrophic mortality does not necessarily mean the deposit is catastrophic. For instance, if poisonous gases or disease killed off an entire herd of *Einiosaurus*, then that would be a catastrophic mortality. However, unless they were rapidly buried by sediment, the deposit itself is not catastrophic. In order to determine whether a deposit is catastrophic in nature, taphonomic and sedimentologic criteria must be utilized.

Transport

One of the most important determinations that must be made about a fossil assemblage is whether it is autochthonous, parautochthonous, or allochthonous. Autochthonous assemblages are collections of fossils that were buried in place. Parautochthonous assemblages are collections of organisms that were transported, but not out of their environment before burial. Allochthonous assemblages are collections of fossil organisms that have been transported over some distance. Some assemblages can be mixed (i.e., contain both autochthonous and allochthonous elements).

In order to determine whether an assemblage, or a carcass, was physically (as opposed to biologically) transported, one must look at the sedimentology and taphonomy. Sedimentological features such as ripples, cross beds, load casts, flute casts, imbrication, and suspension of cobbles or boulders in finer sediments are all very helpful in determining if transport occurred in the past, and they can also be used as indicators of the direction of past currents (paleocurrents). Taphonomic analysis of a hydraulically transported assemblage focuses on three aspects: amount of abrasion, sorting, and for fluvial assemblages, Voorhies groups (vertebrates only).

Fluvial transport, of disarticulated remains over large distances, should result in abrasion of bones. However, bones deposited from a debris flow may show no such damage, and bones within a fresh carcass should not show abrasion in transport (see C.6 Articulation). Differential abrasion on bones within the same assemblage may be an indicator of a mixed assemblage (Voorhies, 1969).

Sorting of fossils within an assemblage can aid in the determination of whether transport occurred. If disarticulated remains in the assemblage are either normally graded (bigger skeletal elements at the bottom grading up into smaller skeletal elements at the top) or inversely graded (bigger skeletal elements at the top grading down into smaller skeletal elements at the bottom), then this is good evidence that transport has occurred in some sort of debris flow, mud flow, or other mass wasting event. As well, skeletal elements that are not at the same angle as bedding may indicate that transport has occurred, although trampling in soft sediment can also cause bones to orient contrary to bedding (Fiorillo, 1989). In such a case, one would expect to see evidence of sediment disturbance from the trampling.

In general, the smaller and less dense the bone, the farther it can be transported. Shape is also another very important factor. The higher the surface area to volume ratio (SA/V), the easier it is to transport the bone. This and the SI ratio (the ratio of maximum length of a bone to the maximum breadth) are two of the major factors in how likely bones are to be transported. Voorhies (1969), based on a series of observations and experiments carried out on the fluvial transport of vertebrate bones, described a series of bone groups related by their ease of transport. These groups are today called Voorhies groups. Voohies group 1 contains bones that are easily removed by a small current. They typically have a high SA/V index. Group 1 contains the ribs, vertebrae, sacra, and sterna. In an intermediate position between Voorhies groups 1 and 2 are the scapulae, phalanges, and ulnae. Group 2 bones are gradually removed by a current. They have a low SA/V index and an intermediate S/I index. The bones found in Group 2 are the femora, fibulae, humeri, metapodia, pelves, and radii. In an intermediate position between Voorhies groups 2 and 3 is the ramus. Group 3 includes the skull and mandible. These bones are the most difficult to move as they have a low SA/V index and a low S/I index. They can be moved only by strong currents.

Thus, if an assemblage contains only one of the Voorhies groups, then this is good evidence of being hydraulically sorted. If only Voorhies group 3 is present, then this probably indicates a lag deposit. However, if all three Voorhies groups are present, then there may not have been hydraulic transport. It is important to remember that Voorhies groups can only be applied to the fluvial transport of disarticulated bones of vertebrate animals.

However, as mentioned earlier, shape is not the only factor in transport, but also density and size. Thus, small animal bones are more likely to be transported greater distances than are bones of larger animals (Voorhies, 1969). In fact, it seems that in many Neogene deposits, rodents are under-represented compared to larger mammals (Voorhies, 1969). This probably indicates that the rodent bones were either more easily destroyed or more easily transported away from the location of specimen accumulation for the larger mammals.

Shotwell (1955) outlined some criteria for determining which fossils in a mixed assemblage are autochthonous and which are allochthonous. He suggested that mammals from proximal communities would be represented by more specimens per individual in an assemblage than those from far away. He also assumed that if distant communities are represented in an assemblage, then the habitats of those communities must be present in the region contributing specimens to the quarry.

However, Voorhies (1969) correctly noted that these cannot be the only factors in determining the degree of transport for a species represented in a deposit. Shotwell was not taking into consideration animal size. In fact, Voorhies discussed the possibility that the Black Butte fauna mentioned by Shotwell (1963) as an example of species composition reflective of distance from original habitats might actually be a better example of bone size-sorting. One quarry (Quarry 3), interpreted by Shotwell to be a savanna community, contains *Hipparion, Aphelops, Procamelus, Megatylopus*, and *Mammut*, all of which are large mammals. All of the specimens (about 10 specimens per individual) recovered for each genus possessed relatively the same degree of completeness. Another quarry (Quarry 11) about 17 miles away has good representations (about 37 specimens per individual) of *Hypolagus* (a rabbit) and *Eucastor* (a beaver) and poor representations of other species. This, Shotwell called a pond-bank community, and he concluded that the pond-bank was more proximal to the deposit because they are the more abundant animals, and that the distal savanna community must have been transported into the pond-bank community. However, fossils from Quarry 3 (the savanna community) were found in a lens of coarse, cross-bedded sand, whereas fossils from Quarry 11 (the pond-bank community) were obtained from a fine-grained tuffaceous sandstone interbedded with a siltsone.

Thus, Voorhies suggested that the differences between the two quarries may have much more to do with transport than a change in environments. The smaller bones of the beavers and rabbits were transported a greater distance along with the finer particles than the bones of the larger mammals which were deposited with the coarser grains.

Presence of a clearly terrestrial animal in a marine setting or vice versa usually does indicate some form of transport. Typically, the presence of a terrestrial dinosaur carcass in a marine setting is attributed to a “bloat and float” process, in which a dinosaur died and its carcass was washed out to sea where it floated for a time due to built up decay gases before sinking (Buffetaut and Suteethorn, 1989). The presence of the therizinosaurid dinosaur *Nothronychus graffami* in a marine Tropic Shale of Utah (Zanno et al., 2009), indicates that it was somehow carried out to sea. In fact, it has been suggested that it may have been transported on a floating island before the carcass eventually sunk after the floating island disintegrated (Heinrich, 2008). Buffetaut and Suteethorn (1989) commented on a *Bothriospondylus* (a sauropod dinosaur) skeleton found in marine rocks in France in 1934. Associated with this sauropod carcass are a number of theropod teeth, presumably from more than one species. The authors concluded that this could not have been an example of “bloat and float” due to the associated theropod teeth and instead suggested that the carbonate platform must have been elevated above sea level for a short time to allow for the sauropod to die and be scavenged on its surface (Buffetaut and Suteethorn, 1989).

There are other factors than hydraulic sorting or distance from a habitat that can control abundance of specimens in an assemblage. The preferential sorting of skeletal elements by a biological agent such as a scavenger is a possibility (Palmqvist et al., 2002). Evidence for biogenic transport by a scavenger would include tooth marks and preferential sorting of some bones over others. Scavengers seem to prefer some elements over others as teeth, jaws, and foot elements have little to no nutritional value.

Orientation

Orientation of fossils is very much related to transport. Depending on the skeletal element, the orientation must be analyzed differently. Orientations can be planar, convex-up or convex-down, parallel, mechanically unstable, and random (Toots, 1965).

Planar orientation is mainly applicable only to bilaterally symmetrical organisms. It occurs when the long and intermediate axes lie parallel to bedding. Generally, this orientation is mechanically stable and due to a mechanical process, however, this is the life position of some organisms such as oysters (Toots, 1965).

Organisms with one side concave and the other convex will normally face convex up as it is more mechanically stable. Convex-down orientation is very rare and is thought to occur when an organism with only one convex side sinks to the bottom of a body of standing, quiet water. As well, this orientation can occur when shells are settling out of a turbidity current (Toots, 1965).

Parallel orientation defines cases where a fossil shows orientation with respect to the azimuth (i.e., the long axis of an element points toward a compass direction). This kind of orientation is generally mechanical, but it could be due to organisms being fossilized in life position, such as in oyster colonies, in which case there will only be one maximum (as they would all be facing the same direction). Parallel orientation can be formed both longitudinally (parallel) and transversely (perpendicular) in relation to the current direction. If an organism has a long axis (e.g., conispiral gastropods or straight-shelled nautiloids), then the orientation of a given pole will usually show two maxima 180° apart. If these two maxima are significantly unequal, then the only possible explanation for this orientation is a current parallel to the maxima. In this case, the apex of the shell (for shelled organisms) will point upstream. If, however, the two maxima are equal and symmetrical, then this is good evidence of transverse (perpendicular) orientation (Toots, 1965).

If a fossil of an organism is found in a mechanically unstable position, then it could have been altered by post-depositional disturbance or it could represent life position. Diagenetic disturbances of sediment, even though they can result in a mechanically unstable position for an organism, cannot produce a preferred orientation. If a preferred orientation of organisms in a mechanically unstable position is found, then the only explanation is that they were buried and fossilized in life position. If this is the case, then it is good evidence that there has been no mechanical reworking (Toots, 1965).

It used to be thought that random orientation was just the result of normal death and depositional processes, however, it is now known that many processes can cause random orientation of fossils. If organisms were to roll into sediment traps during an episode of hydraulic transport, then that could result in random orientation. As well, if, during some kind of flow such as a turbidity current, movement is stopped before carcasses reach a mechanically stable position, then this can result in random orientation. Furthermore, penecontemporaneous deformation of sediment and reworking of sediment by bioturbators can both result in random orientation (Toots, 1965).

Distribution

Distribution, like orientation, can provide a piece of the puzzle in explaining how an assemblage came to be the way that it is. There are four major distributions of fossils noted by Toots (1965): random scatter, concentration in layers, linear accumulations, and local concentrations.

Random scatter is where fossils are spread vertically and horizontally throughout the outcrop. In this distribution, there does not appear to be any pattern. This can be evidence of a low-energy depositional environment (Toots, 1965).

When fossils are limited to certain bedding planes, their distribution category is called concentration in layers. For example, shell beds commonly occur in deposits with even and clearly-defined bedding. Concentration in layers is a good evidence for high energy depositional environments (Toots, 1965).

Linear accumulations can either be ridges elevated above a bedding plane, or they can be fills of troughs that were cut into the sediment. In cross section, they will appear lenticular. These accumulations can form as ripple-ridges or along lines of extremely rapid energy gradients (Toots, 1965).

The fourth distribution type is the local concentration. In local concentrations, fossils form nearly equidimensional assemblages with a generally small horizontal extent. These are most likely fillings of large depressions such as channels (Toots, 1965).

Articulation

One very important consideration in studying fossil organisms with multi-element skeletons (vertebrates, arthropods, and echinoderms) is their articulation. There are two commonly used scales to measure the amount of disarticulation of fossil organisms within an assemblage. One was developed by Behrensmeyer (1991) and consists of four groups: 1) Articulated: the bones retain their exact anatomical positions relative to one another; 2) Disarticulated but associated: bones are separated from one another but are in close proximity, and they can be determined to be part of a single individual, 3) Associated but dispersed: bones may be scattered over an area much larger than the animals, but can be related to a single individual, and 4) Isolated and dispersed: bones are widely separated from others of the same skeleton. Another methodology that is used widely in vertebrate taphonomy consists of three preservation classes: Class 1) Articulated skeletons with complete articulation and all bones in natural position, Class 2) Partially articulated skeletons with changing degrees of disarticulation from specimen to specimen, and Class 3) Disarticulated bones; this class is split into two subclasses: Class3A) complete disarticulated bones, and Class3B) fragmented disarticulated bones (Soares, 2003).

The state of disarticulation speaks a great deal about the taphonomic history of the assemblage. Skeletons decay and become disarticulated (either through decay, predation, scavenging, or other agents) very quickly as determined by actualistic studies in vertebrates (Meyer, 1991), arthropods (Plotnick, 1986), and echinoderms (Kidwell and Baumiller, 1990). Meyer (1991) noticed that modern marine turtle shells, when buried convex up at a depth of 25 cm in the sands of the intertidal zone of an island of the Seychelles, became completely disarticulated within 10 days after burial. He also placed a marine turtle shell convex down at a depth of 25 cm nearby, and it was partially disarticulated by 15 days.

In the past, it has been suggested that anoxic environments can preserve articulation and/or soft tissues for longer periods of time. However, modern actualistic studies have shown that this is not the case. Kidwell and Baumiller (1990) demonstrated that modern echinoids showed no significant change in decay rate in oxic versus anoxic environments. They suggested that anoxic environments might aid in protecting a carcass from scavengers, but it does not inhibit decay because anaerobic bacteria are still present in carcasses.

It is a common misconception that transport always leads to disarticulation; or rather, that an articulated specimen must not have been transported very far. Several actualistic studies have challenged this hypothesis. Allison (1986) found that modern soft-bodied and lightly skeletized organisms display considerable resistance to disarticulation and damage during transport. In fact, Allison found that “fresh carcasses of polychaetes can tolerate lengthy turbulent transport before fragmenting or disarticulating” (1986). Kidwell and Baumiller (1990) state, “Consequently, state of preservation is not necessarily a good indicator of environmental energy or distance of transport… for proteinaceous and soft-bodied macrofauna.” However, with some decay in soft-bodied or lightly skeletized organisms, disarticulation occurs quickly with very little transport (Allison and Briggs, 1991).

Thus, what can be known about an articulated specimen is that it must have been buried relatively quickly. This could be accomplished by the burial event actually causing the death of the organism, or it could be that the event buried the organism before too much decay or disarticulation occurred. If there are signs of transport, then it must have occurred before the carcass had much time to decay.

Skeletons can be disarticulated by several means. Predators and scavengers disarticulate carcasses, or if they are not actively disarticulating the skeleton, they are catalysts in increasing the rate of decay. Tooth marks should be associated with remains that have been scavenged. Decay alone will lead to disarticulation over time as ligaments and muscles disappear allowing bones to fall out of place. Decay combined with wind or water movement can lead to disarticulation and dispersal.

Abundant completely disarticulated remains, though often a sign of catastrophic deposition, do not represent animals killed by the depositional event (Voorhies, 1969). If there are large bones (a meter long or longer) that show signs of hydraulic transport, then that indicates the current velocities of transport reached 1.8 to 2.7 m/s or more at some point (Voorhies, 1969).

Varying degrees of articulation within the same deposit can be a good indicator of an attritional assemblage (Liebig et al., 2003). However, this is not always the case. For instance, if scavengers were feeding on a carcass, and all were buried in a flashflood, then bones of varying degrees of articulation would most likely be buried together.

According to actualistic studies by Brand et al. (2003), teeth fell out of rodent jaws more readily with increased body size and presence of water in the environment where the rodent was decaying. They concluded that isolated, intact fossil mammal teeth without cracks probably disarticulated in water. Even though Mesozoic mammals are within rodent size limits, they are not eutherians; thus, it is unknown whether they would necessarily lose teeth in a similar fashion, although it is likely.

Breakage

The ratio of broken to unbroken bones in an assemblage can tell paleontologists a great deal about the forces that were applied to specimens before burial. Breakages can be caused by the physical environment or biologic agents in trampling or bone-crushing behaviors in animals such as hyenas. There are five major types of fractures that can occur in vertebrate bones as described by Ryan et al. (2001). The first is the collection fracture, which is a fracture made during collecting or preparing a specimen. Second is the longitudinal fracture. This is a break parallel to the long axis which can be due to desiccation or be a modified compression fracture. Third is the spiral fracture which is also called a green fracture. They are called green fractures because they have to occur prior to fossilization. These fractures are often described as saw-toothed as the breaks occur at an angle that is not perpendicular to the long axis. Even though spiral fractures are called “green”, they may not be fresh and could be somewhat aged. If the fracture surfaces are relatively smooth and the angles are acute or obtuse where the fracture surface intersects the shaft surface then they can be called fresh (Ryan et al., 2001). The fourth kind of fracture is the transverse/compression fracture. This gives the specimen the appearance of being crushed. The pattern can include multiple stepped cracks, but unlike the spiral fracture, all of the steps are parallel to each other or as single or multiple concentric cracks. These are usually attributed to sediment deformation, but they may indicate trampling. Finally, the fifth kind of fracture is the indeterminate fracture. It is necessary to have this category because some fractures are not easily diagnosable, and they should not be forced into any of the above four categories. Fossils preserved in coarse-grained sandstones tend to show little or no evidence of sediment compaction when compared to fossils preserved in finer-grained mudstones or siltstones (Ryan et al., 2001).

Brand et al. (2003) conducted actualistic experiments on rodent teeth and discovered that the teeth would commonly crack in a terrestrial environment. However, if a tooth were submerged from the beginning, then it would never crack. Teeth that were kept in a terrestrial environment for 53 days and then placed underwater would crack.

Abrasion and Weathering

Ryan et al. (2001) designated four stages of abrasion. The stages are roughly equivalent with the rounding descriptors used for grains with Stage 0 equivalent with angular down to Stage 3, which is equivalent to rounded. Stage 0 is when the fossil has a pristine surface and shows no signs of abrasion. Stage 1 describes a fossil with broken edges that are rounded. The fossil might also have a polished surface. The broken and unbroken edges of Stage 2 fossils are well-rounded and the surface well-polished. However, in the Stage 2 fossils it is still possible to discern the original texture. All of the processes on the bones are rounded, but it is still possible to discern the original structure. However, in Stage 3 all edges of the fossil are extremely well-rounded. Processes show up as bumps or protrusions, but they would be unrecognizable if not attached to the bone. The surface is very well-polished (Ryan et al., 2001).

Ryan et al. (2001) also established four categories of weathering on bones. Fossils in the Stage 0 category show no signs of weathering (i.e., no cracking or flaking). Stage 1 fossil surfaces have cracking parallel or near parallel to the internal fibrous structure of the bone. Ends of long bones are probably still in good condition. Stage 2 fossils have parallel or near parallel cracks that are starting to penetrate into the marrow cavities of long bones. Flaking occurs on the surface at these cracks. Ends of the long bones are either deeply eroded or missing. By Stage 3, large chunks of the outer laminated bone have entirely flaked away. Any of the preserved surface remaining is highly cracked and flaking. The long bones no longer possess heads, but if they still do then they are broken (Ryan et al., 2001).

Some bones are more resistant to decay and damage than other bones. Teeth are very dense and strong, and they are often all that is left among small mammals, especially in the Mesozoic. When a skeletal element or skeleton displays differential patterns of weathering within the same specimen, then this is evidence that the specimen may have been exposed for some time while part of it was protected. For instance, if a horse carcass were to be partially buried in a mudflow such that its anterior portion was exposed, then the anterior portion would most likely be scavenged and severely weathered, whereas the posterior portion might be protected. Thus, if the horse became a fossil, then the posterior half would show much better preservation than the anterior half. A lack of differential preservation within a specimen suggests rapid burial (Esperante et al., 2002).

Bioerosion

Bioerosion is damage done to an organism’s hard parts by another organism. It incorporates both bioabrasion (mechanical abrasion from a biological agent such as tooth and claw marks), and biocorrosion (chemical abrasion from a biological agent as occurs in digestion). Molluscs and other marine invertebrates with hard parts are commonly found to have bioerosion marks made by worms, sponges, fungi, or other organisms.

Bioeroders are commonly classified into several categories based on the damage they cause. Microbioeroders (such as bacteria, algae, and fungi) cause bore holes smaller than 100 µm in diameter, and can occur both before and after burial (Esperante, personal communication). Macrobioeroders (such as bivalves, gastropods, arthropods, etc…) bore holes larger than 1 mm in diameter. Other bioeroders include grazers (such as gastropods), scrapers (such as echinoids), swallowers, and biters. If bones or other hard parts are exposed in a subaqueous setting with good oxygen content, then bioerosion will certainly occur. Whale skeletons exposed underwater to bioeroders can be stripped of flesh within a few years at most (Brand et al., 2004). A lack of submarine bioerosion or encrustation on bones in subaqueous settings suggests relatively rapid burial (Dominic et al., 1995).

Among terrestrial vertebrates, the presence of bioerosion marks is very useful in developing taphonomic models. Bioerosion caused by marine organisms on a skeletal element of a terrestrial organism implies that the specimen must have been in the ocean for a period of time. For example, nine hadrosaur caudal vertebrae have been found with bioerosion including shark bite traces and corrosion from digestion (Everhart and Ewell, 2006).

However, bioerosion caused by terrestrial organisms on a carcass indicates that it must have been exposed or only buried in loose sediment for some time before fossilization. An articulated skeleton of *Protoceratops* from the Djadokhta Formation of Mongolia exhibits many insect borings and associated casts of pupae chambers. The insect-induced bioerosion is assumed to have taken place after burial because there is no displacement of bones, and traces of insect digging activity were found in the surrounding sediment (Kirkland and Bader, 2010). Although insect borings are rare in dinosaur skeletons, the majority of dinosaur specimens from the Djadokhta Formation exhibit them (Kirkland and Bader, 2010).

For analysis of tooth traces, Pobiner (2008) suggests some useful methods. First, she defined four types of tooth traces: pits, punctures, scores, and furrows. Pits are roughly circular (sometimes polygonal) traces that are due to direct pressure of a tooth on a bone surface. Pits typically have bowl-shaped cross-sections, but this is not the case for crocodile tooth pits (Pobiner, 2008). Punctures are similar to pits, but they are larger and penetrate the full thickness of compact bone. Punctures will result in a crushing of the cortical bone into the damaged area (Pobiner, 2008). Both pits and punctures have “a long axis no more than three times the length of the short axis” (Pobiner, 2008). Scores and furrows, however, are both linear traces with U-shaped cross-sections and smooth bottoms caused by the dragging of a tooth across the bone’s surface (Pobiner, 2008). Furrows are larger and deeper than scores and penetrate the compact bone layer, whereas scores do not. Interestingly, tooth scores and furrows typically are oriented nearly perpendicular to the long axis of a long bone (Pobiner, 2008). A fifth category could be added for embedded teeth, and a sixth called an edge trace. Edge traces are unique to ziphodont consumers, and are made by “distal carina contact with the edges of processes or elongate elements” (D'Amore and Blumenschine, 2012). Striations are only found on scores, furrows, and edge traces, not on pits or punctures (D'Amore and Blumenschine, 2012).

Second, Pobiner (2008) suggests a method to collecting and reporting data about tooth-traced bones in assemblages. She writes that “tooth trace types (usually pits, punctures, scores and furrows) should be defined, counted, and reported separately, ideally by skeletal element and bone portion (including compact or cancellous bone).” If paleontologists standardize their methods of recording tooth-traces according to Pobiner’s suggestion, then this will aid in discussion and identification of specific tooth trace ichnotaxa, behaviors, and trends.

Tooth traces cannot simply be taken as evidence for terrestrial exposure; rather, the identity of the biter must be established. Theropod dinosaur teeth are ziphodont (possess serrations) and thecodont (fit into sockets). Due to the serrations (denticles) on ziphodont teeth, they can leave striations in a tooth trace. The presence of striated tooth traces indicates a ziphodont consumer, and can also be used to estimate body size of the consumer. The first step in biter identification is a measurement of the striation width. The average striation width per tooth trace is “the distance between the outermost striations at their widest point of convergence divided by the number of striations within the mark” (D'Amore and Blumenschine, 2012), and they can be defined as either regular or irregular based on whether the striations are evenly spaced within a trace. D'Amore and Blumenschine (2012) experimented on a living organism with ziphodont dentition (the Komodo dragon, *Varanus komodoensis*) to see if measurements from its tooth traces were comparable to those from theropods. They discovered that the denticle width typically increases with the size of an organism in a predictable fashion both within and between ziphodont species. However, spinosaurids and troodontids are notable, bizarre exceptions to this rule (D'Amore and Blumenschine, 2012). They also found that the striation width is comparable to denticle width, as expected. However, they discovered that the striation width could underestimate the width of the denticle, which in turn would underestimate the size of the consumer. Ultimately, the maximum striation width can never overestimate the denticle width, so it can be used to give a lower limit of denticle width, and thus, body size (D'Amore and Blumenschine, 2012).

Tooth traces made by theropod dinosaurs can sometimes be identified to the genus or species level (Pobiner, 2008). Measurement of the striation widths, comparison of these with denticle widths of theropod teeth, and knowledge of taxa in an assemblage can lead to a suggestion as to the tooth trace-making consumer. Evidence of dinosaurs biting dinosaurs is known, and this is good evidence for terrestrial exposure of a carcass to carnivores. For example, tooth traces on a bone of the abelisaurid theropod *Majungasaurus* have been attributed to *Majungasaurus* (Rogers et al., 2007) and tooth traces on a ceratopsid pelvis from the Kirtland Formation have been attributed to the tyrannosaurid *Daspletosaurus* (Fowler and Sullivan, 2006). Fowler and Sullivan (2006) noted two kinds of tooth traces on the pelvis: puncture traces and score traces. Score traces are characterized by “an initial indentation, with a subsequent, gradually-shallowing groove scored into the bone surface… Such a groove often shows variable splintering in small bursts around the edges” (Fowler and Sullivan, 2006). The structure and thickness of a bone may play a large role in determining the shape of a tooth trace (Pobiner, 2008).

Even though tooth traces have been found on dinosaur bones, such traces occur on only between 0-4.0% of dinosaur specimens, making them rather rare (Fiorillo, 1991). Ryan et al. (2001) found tooth traces on only 17 bones of the 656 examined specimens, less than 0.02% of their specimens, from bone bed 43 in the Dinosaur Park Formation of Dinosaur Provincial Park in Alberta. Interestingly, the same is not true for mammals as

13.1-37.5% of bones from both modern and fossil mammal assemblages can have tooth traces (Fiorillo, 1991). The vast difference in percentages of tooth-traced bones between dinosaurs and mammals could be due to the fact that dinosaurs shed their teeth continually unlike mammals (Fiorillo, 1991). Some mammals, such as hyenas, crush bones, but this behavior has not been demonstrated in modern or fossil archosaurs (Fiorillo, 1991). Even if scavenging has occurred, tooth traces may not be visible depending on the surface preservation of the bone (Buffetaut and Suteethorn, 1989). As well, bones have been found in the stomach cavities of theropod dinosaurs showing no bite traces (Fiorillo, 1991).

It is unsurprisingly difficult to determine if tooth traces found on a fossil bone are the result of predation or scavenging. Bone regrowth on a tooth-traced injury suggests that an organism survived after it was bitten, perhaps suggesting a failed predation attempt. The absence of bone regrowth at a tooth trace and the presence of long, deep furrows on a sauropod caudal vertebra from South Korea was used as evidence that the present tooth traces were made after the organism was dead (Paik et al., 2011). Paik et al. (2011) also suggested that the lack of tooth traces on any other sauropod bones in the same bonebed is further evidence of scavenging instead of predation. Interestingly, Paik et al. (2011) state, “The distinct preservation of long, deep scours with little physical damage around the trauma of the first group of tooth traces indicates that they were generated when the bone was wet and covered with some flesh.” Another evidence of scavenging is the presence of tooth traces from multiple species on the same bone.

There are features that can be mistaken for tooth traces. For instance, if bones are sitting in a sandy substrate and are trampled by organisms, then thin, shallow, subparallel scratches can appear on the bones. It is thought that these trample marks are caused by the quartz and feldspar sand grains rubbing against the bone as it is pushed into the substrate by a trampler and not by the claws or hooves of the tramplers themselves (Fiorillo, 1989). These features are termed trample marks, and they are typically v-shaped in cross-section. Although it is difficult to distinguish these marks from stone axe cut marks (Behrensmeyer et al., 1986; Fiorillo, 1984), Fiorillo (1989) states that they are easily distinguishable from tooth traces.

As discussed earlier, insects can modify bones, and these modifications can leave traces in bone such as depressions. Notably, the ichnofossil *Cubiculum*, which is thought to have been made by some kind of necrophagous or osteophagous carrion insect fauna (Roberts et al., 2007), has been seen on dinosaur bones in the Lance Formation (Longrich et al., 2010). These traces, however, consist of broad, U-shaped channels often with bioglyphs (Pirrone et al., 2014), and should be readily distinguishable from tooth traces.

APPENDIX C

NEW TOOTH TRACE CRITERIA

Introduction

From our study of the literature and first hand observations of tooth-traced fossil bones, we have developed revised definitions for four different types of tooth traces: pits, punctures, scores, and furrows. Pits and punctures share a similar round or polygonal shape in plan form in contrast to the linear nature of scores and furrows. However, pits and scores are similar in depth in contrast to the deep nature of punctures and furrows (Figure 20). This appendix details the history of tooth traces and our new tooth trace criteria. Much of this content will appear along with experimental data in a future publication.

History of Tooth Trace Definitions and Criteria

Although imprints left by teeth on bones are often referred to as “tooth marks” or “bite marks” in the literature, the appropriate term is actually “tooth trace” or “bite trace”. Seilacher (1953) (in Jacobsen and Bromley, 2009) distinguished between the terms “trace” and “mark”, reserving “trace” for biogenic structures (e.g., root trace, trace fossil, etc.) and “mark” for abiogenic structures (e.g., ripple mark, rill mark, tool mark, etc.). If one can be certain about the origin of a mark, then the appropriate term should be used. If the origin is uncertain, it is probably best to call it a “mark”. Technically, trample marks and cut marks are caused by biological agents, but since the actual object cutting into the

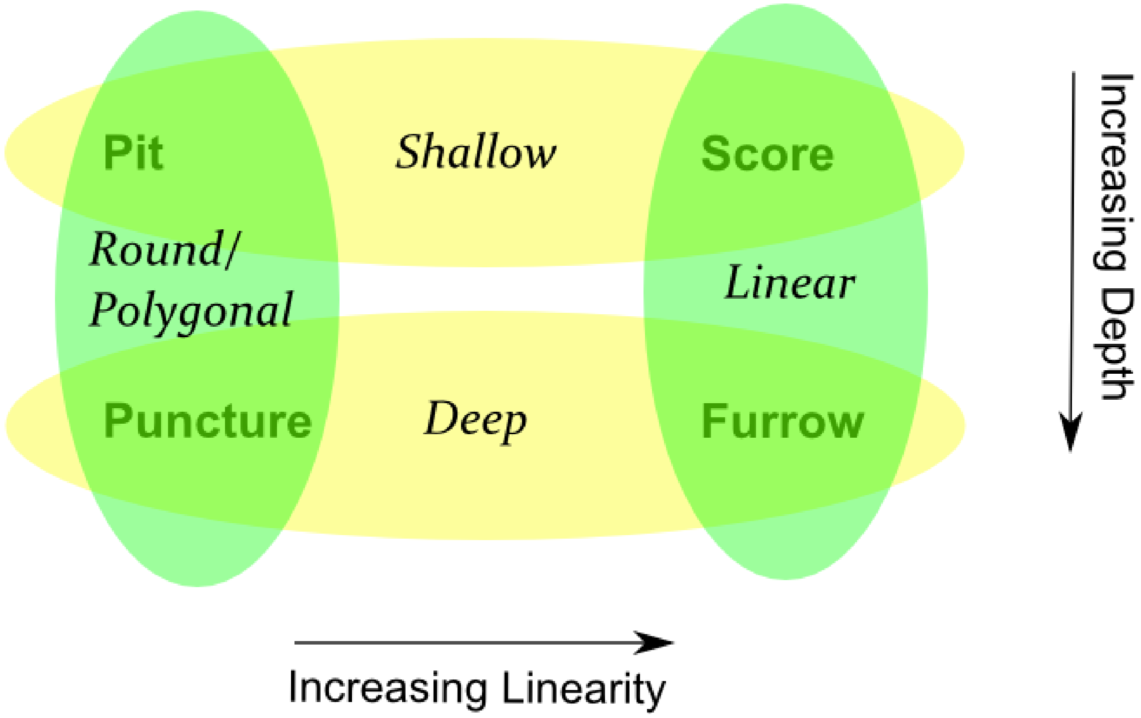

Pit
Shallow
Score
Round/
Polygonal
Linear
Puncture
Deep
Furrow
Increasing Depth
Increasing Linearity

Figure 20. Comparing and contrasting tooth trace types. This diagram compares the four main kinds of tooth traces: pits, scores, punctures, and furrows.

bone is non-living (quartz grains and a tool, respectively), they can still be considered marks. Additionally, the terms “trample mark” and “cut mark” are widely used in the literature, so renaming the terms would only create confusion.

The first author to identify and describe categories of tooth traces was Binford (1981). With bones bitten by mammalian carnivores as his guide, he described four basic types of tooth traces: 1) punctures, 2) pits, 3) scores, and 4) furrows. Although these four types are still in use today, their definitions have changed with the passage of time.

Binford (1981) considered punctures to be “simply where the bone has collapsed under the tooth, frequently leaving a fairly clear imprint of the tooth”. Additionally, he noted that on thin bones the tooth might completely perforate the bone and leave a crenulated edge. Most of the changes to this definition found in the literature focus on the shape of the trace. Njau and Blumenschine (2006) considered punctures to be circular to oval in plan view, a view shared by Pobiner, et al (2007), although Pobiner (2008) added that they could also be polygonal. Concerning the depth of the trace, Njau and Blumenschine (2006) stated that punctures of mammals and crocodilians go through the cortical bone. Pobiner, et al (2007) added that flakes of the outer wall of the bone can be found pressed into the puncture.

Pitting, according to Binford (1981), occurred when the carnivore had reached a dense portion of the bone that its teeth could not puncture. Thus, in Binford’s scheme, a pit is simply a trace without bone collapse or tooth penetration. Njau and Blumenschine (2006) added to the definition that pits are bowl-shaped to irregular in cross-section, and that they can be shallow or deep. Pobiner, et al (2007) and then later Pobiner (2008) added plan view shape to the definition of pits, noting that they are circular, oval, or polygonal in shape. Somewhat following Binford's scheme, these later authors considered pits and punctures to be similar traces, although now the similarity focused more on the shape. Pits and punctures are round to polygonal traces, whereas scores and furrows are linear traces. This difference was quantified by Pobiner (2008) who considered pits and punctures to have a long axis length no more than three times the length of the shorter axis in plan view.

Binford (1981) considered scores to be a result of either the teeth dragging across the bone surface or the bone turning against the teeth. He noted that the traces are linear and resemble cut marks from stone tools. Njau and Blumenschine (2006) agreed that scores were usually linear, but they noted that they can also be curved or angulated in plan. They added that the traces typically have a U-shaped cross-section and have a high breadth to depth ratio. Pobiner, et al (2007) agree with the earlier definitions, but they add that the surface is usually crushed, and that the traces are typically perpendicular to the long axis of the bone. Pobiner (2008), as noted above, quantified the long to short axis ratio of 3:1 to distinguish the long scores and furrows from the round or polygonal pits and punctures.

The definition of furrows is the tooth trace description that has changed the most since its original inception. Binford (1981) adopted the term "furrow" from Haynes (1980) to describe the effect that repeated jaw action with either canines or carnassials produces on relatively cancellous bone. In extreme cases, Binford noted, furrowing will result in "scooping out" where a large hole is left in the bone. This definition precludes use with most animals other than synapsid carnivores as dinosaurs, crocodilians, sharks, and other carnivorous animals lack canines and carnassials. Njau and Blumenschine

(2006), in defining crocodilian and mammalian tooth traces, used a definition of furrow that stressed it is a linear trace which goes completely through the cortical bone. Pobiner, et al (2007) did not include furrows as a category of tooth trace, but Pobiner (2008) defined them as linear traces that vary in length and have U-shaped cross-sections that penetrate through the cortical bone. Pobiner (2008) also noted that they are most often oriented roughly perpendicular or transverse to the long axis of long bones.

Although Binford (1981) described chewing and gnawing, he included the terms in discussions of punctures and furrows. Pobiner, et al (2007) referred to chewing/gnawing as uneven, irregular, jagged edges of long bones in which the epiphyses are destroyed and fraying and peeling back of cortical layers can occur. The same paper described tooth notches as lunate scars or semi-circular to arcuate-shaped indentations on fracture edges corresponding to negative flake scars on medullary surfaces.

As demonstrated, tooth traces have been given various categories and definitions over time. In fact, Mikuláš et al. (2006) designated punch-hole, puncture traces as an ichnotaxon named *Nihilichnus nihilicus*. Jacobsen and Bromley (2009) named two tooth trace ichnotaxa based on dinosaur tooth trace specimens: *Linichnus serratus* and *Knethichnus parallelum*. *Linichnus serratus* is a curved score with a U- or V-shaped geometry in cross-section and a serrated morphology. *Knethichnus parallelum* consists of a series of parallel grooves leading in some cases away from an initial groove, caused by the denticles of a ziphodont tooth dragging along the bone surface. Carnivorans (mammalian carnivores of the order Carnivora), odontocetes, carnivorous non-mammalian synapsids, crocodilians, toothed theropod dinosaurs, sharks, and other organisms are capable of producing *Nihilichnus nihilicus*, but only carnivores with ziphodont teeth, such as theropods, varanids, and sharks are capable of producing *Knethichnus parallelum* and *Linichnus serratus*.

New Tooth Trace Descriptions

In attempting to apply previous tooth trace criteria to the bones from the Hanson Ranch Quarries, we found that the criteria were not built for distinguishing tooth traces from other features on bones such as foramina and tool marks. Through our study of the literature and fossil bones possessing marks of interest, we developed a more rigorous set of tooth trace criteria and definitions including some caveats to tooth trace identification. We retain the four main tooth trace types: pits, punctures, scores, and furrows, although we add some extra criteria to pits and punctures. Through some experiments where we purposely damaged bone fragments with picks, hammers, and air tools (to be included in an upcoming publication), we found that it is typically easy to distinguish tool marks from tooth traces. What follows are our expanded definitions of the four main tooth trace types. We do not include here chewing or shear (bites producing breaks on bones), as we have not been able to find clear examples of such features in our sample bones.

Pits are circular, oval, or polygonal traces that result from direct pressure on bone surfaces. They typically have bowl-shaped cross-sections. They are smaller and shallower than punctures. Unlike punctures, the trace does not penetrate all layers of the cortical bone. The long axis of a pit is no more than three times the length of the short axis. Pits typically do not have a continuous, smooth cortical surface around the lip or extending into the depression, which distinguishes these traces from small foramina. In contrast to foramina, true pits should typically have an irregular or discontinuous cortical surface around and/or extending into the depression.

Punctures are circular, oval, or polygonal traces that result from direct pressure on the bone surface such that the bite was deep enough to penetrate the full thickness of cortical bone whether it is thin cortical bone overlying cancellous bone or thicker cortical bone of limb shafts. These traces are characterized by crushing of the cortical bone into the damage feature, but this impacted exterior surface may have been removed due to physical processes. Like pits, the long axis of a puncture should be no more than three times the length of the short axis. As in pits, the cortical surface of the lip around the puncture should not be continuous and smooth, but rather irregular and/or discontinuous.

Scores are linear traces that result from a tooth dragging along the surface of the bone. They vary in length and often have U-shaped cross-sections. The bottom of these grooves will often be smooth or occasionally with striations (given the right conditions with a ziphodont tooth). The length of the long axis is three or more times the length of the short axis.

Furrows, like scores, are also linear traces (long axis greater than or equal to three times the short axis) resulting from a tooth dragging across the surface of a bone. However, a furrow trace penetrates the full thickness of the cortical bone.

Caveats to Tooth Trace Identification

It is important to note some caveats in tooth trace identification. Firstly, any kind of trace in cancellous (spongy) bone is always questionable. Without the cortical surface present, it is very difficult to have any idea of what happened to cause a hole or groove in cancellous bone. Unless a tooth is found lodged in the trace, all traces in cancellous bone are ambiguous. Secondly, tooth traces found on highly fractured bone will also be questionable. When there are many breaks on a bone, it is difficult to know whether a particular crack or hole is the result of a bite or some other factor. Additionally, true tooth traces may be missed on highly fractured bones as the traces may be obscured by fractures that resulted from or followed the orientation of tooth traces. Thirdly, researchers should always take into account the context of the trace on the bone, namely the location on the bone and the type of bone. Certain bones, such as skull bones or vertebrae, have numerous foramina and grooves that can be easily mistaken for features of taphonomic origin. This is especially true in cases where only a fragment of the bone is preserved. If there is a mark resembling a tooth trace on an ungual or on a difficult to reach surface, then this calls into question the identity of the mark as a tooth trace.

APPENDIX D

ROSE QUARRY THIN SECTION PHOTOS

In the process of studying the sedimentology of the Rose Quarry bonebed, several sandstone and mudstone samples were collected for possible thin sectioning and XRD. Two sandstone samples were thin-sectioned, and what follows are some photographs of those thin sections showing some of the important mineralogical observations I made with the assistance of Dr. Kevin Nick.

The majority of the grains are quartz. Grains are angular and fine (Figure 21). In thin-section, feldspar grains seem to make up around 15-20% of the sample with both plagioclase and K-feldspar grains visible. Micas, possibly biotite, make up < 2% of the grains. Volcanic and metamorphic rock fragments are visible as well as mudstone intraclasts, bone fragments, plant fragments, and rare pyroxene crystals. Red cements suggested the presence of iron oxides, and under reflected light we were able to spot the presence of hematite and goethite (Figure 21). Occasional opaque crystals were noted in the thin-sections (Figure 22), which we suspect represent pyrite or oxidized siderite, both of which have been observed in the field site.

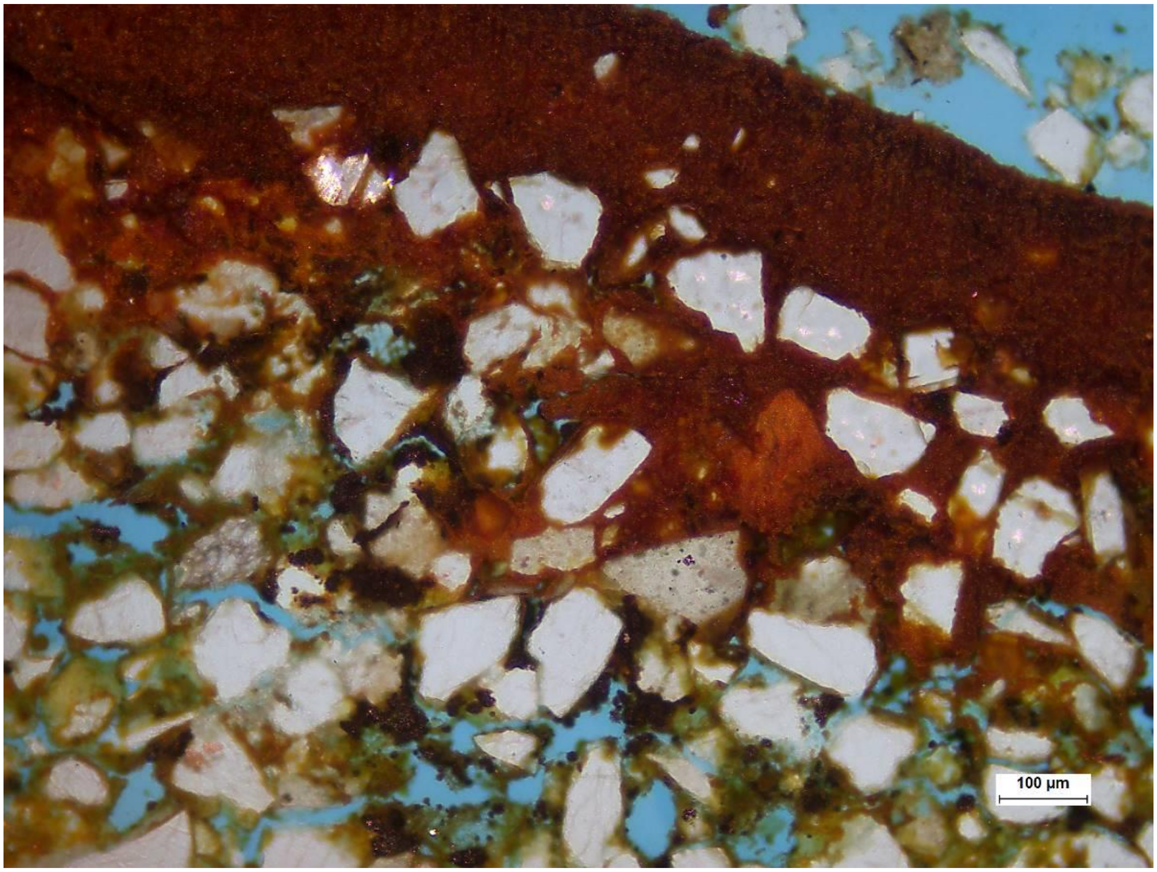

100 µm

Figure 21. Thin-section showing grain angularity and iron minerals. This thin-section of a rock sample (RQ1A-06-23-13) from Rose Quarry at 100x magnification is shown under reflected light. The angular nature of the sand grains is obvious. The reflected light brings out the red of the hematite cement, the yellow in what is probably goethite, and the metallic shimmer of what were only black, opaque crystals under plane-polarized light, which are probably pyrite crystals. The very fine sediment cemented by hematite in the upper right corner of the picture is a part of a small mudstone clast.

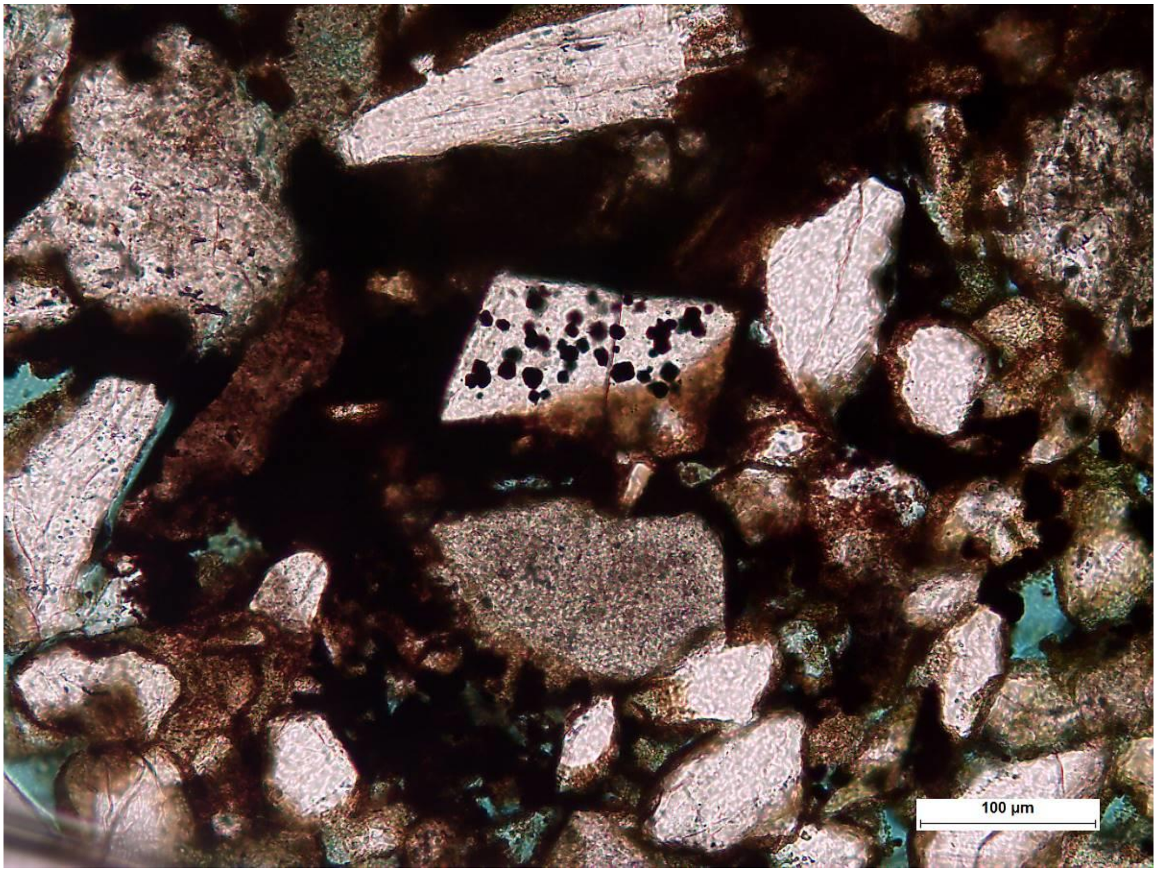

100 µm

Figure 22. Thin-section showing possible pyrite crystals. This thin-section photo of a rock sample (HRS199781A) from Rose Quarry at 200x magnification is shown under plane-polarized light, showing abundant small opaque crystals on an angular grain at the center of the photo. We suspect that these grains are probably pyrite.

APPENDIX E

XRD OF ROSE QUARRY ROCKS

Introduction and Methods

In order to better understand the chemical composition of the Rose Quarry bonebed, I analyzed collected rock samples through X-ray diffraction (XRD) on an X-ray diffractometer at Loma Linda University. Results were analyzed via the software Jade. I also included rock samples from two nearby sandstone bonebeds: Ivarrest and Gar Ridge. The analyzed samples are listed in Table 8.

Results and Discussion

All of the samples had similar compositions. Quartz dominates all of the samples, representing abundances from 45.9% to 64.2%. The next most abundant minerals are usually feldspars, which took three main forms: microcline, albite, and orthoclase. All of the samples appear to possess albite, and all but the Gar sample possess microcline. Only the samples from Rose and Gar possess orthoclase, which is absent from the two Ivarrest samples. Chlorite is also a major constituent of most of the samples. RQ1C-06-12-14 has a peak representing 12.9% of the sample that Jade did not immediately identify. We determined that the best match was the feldspathoid nepheline. We were unable to observe definite nepheline grains in thin section to confirm this assignment. It is possible that the samples containing nepheline included lithic fragments, which we have observed in thin-section. Other accessory minerals includes gypsum, calcite, and dolomite – none of which were surprises given observations in the field.

Table 8. Minerals present in rock samples according to XRD analysis.

Quarry	Sample Number	Quartz	Microcline	Albite	Orthoclase	Chlorite	Other
Rose	HRS19979A	64.2%	13.5%	12.2%	10.1%	-	-
Rose	RQ1C-06-12-14	45.9%	6.7%	10.7%	5.4%	16.2%	Nepheline - 12.9% Muscovite - 2.1%
Ivarrest	IV4-06-23-13	52.0%	21.0%	16.3%	-	8.5%	Nepheline - 2.1%
Ivarrest	IV5-06-23-13	47.3%	9.5%	9.1%	-	13.1%	Chabazite - 3.7% Gypsum - 1.2%
Gar	Gar3-06-23-13	49.5%	-	11.2%	17.9%	9.0%	Calcite - 1.9% Dolomite - 4.1% Illite-montmorillonite - 6.4%

Muscovite has been observed in thin-section, and it is surprising that it did not turn up in more of the XRD results. Illite-montmorillonite and other clays occur throughout the bonebed, but we did not attempt to get clay signatures in every sample. In the Ivarrest sample IV5-06-23-13, we discovered a peak that seemed to match with a calcium-rich variety of the zeolite mineral chabazite. This is not impossible, but we have no other evidence from thin sections or field observations that this is the case.

Overall, these results agree well with observations in the field and in thin-section. The Rose Quarry bonebed sandstone is predominately quartz with associated feldspars, muscovite, and chlorite. Although carbonate minerals do not show up in the Rose Quarry XRD samples, we have observed the presence of carbonates in the field in and around Rose Quarry.