UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

PALEOECOLOGY OF MEDIAL CRETACEOUS DINOSAURS FROM WESTERN NORTH AMERICA

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

Degree of

DOCTOR OF PHILOSOPHY

By

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Norman, Oklahoma
2018

PALEOECOLOGY OF MEDIAL CRETACEOUS DINOSAURS FROM WESTERN NORTH AMERICA

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BIOLOGY

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Acknowledgements

Finishing my doctorate has been the most rewarding experience of my life. The growth I’ve made as a scientist and a teacher during this time has prepared me for my dream career as a vertebrate paleontologist. I thank the Biology Department at the University of Oklahoma and the Sam Noble Oklahoma Museum of Natural History for the opportunities provided to me over the last five years.

Above all, I thank my advisor Dr. Richard Cifelli for making all of this possible. Not only for collecting and giving me access to all of the specimens used in these chapters, but also for your mentorship during an instrumental time in my career and life. From our multi-hour car ride conversations to pass the time in the field, to your steadfast but pragmatic views on science eloquently written in red pen across a draft of one of my manuscripts, I will cherish everything I’ve learned from you. In a similar sense, I’d like to thank my doctoral committee (Drs. Czaplewski, Engel, Kelly, and Siler) for their efforts, suggestions, and stimulating conversations to the benefit of this work and to improve me as a scientist. In addition, Dr. Michael Engel deserves extra recognition for providing all of the equipment, material, and effort to perform the isotope analyses in these studies. I’ve learned a great deal from all of you and cannot stress enough how thankful I am for all you’ve done.

Fundamentally, I thank my wife, Dr. Janessa Doucette, for her constant support while pursuing my passion. Without her love and belief in me I’d never have the courage to get two graduate degrees, move across the country three times, adopt all our fur-babies, or create such a perfect home. This home, however, would not be what it is without the addition of our roommate, friend, and little sister Jordan, whose late night food runs and help watching the pets has given me the time and peace of mind needed to complete much of this research.

This work was not performed in a vacuum and required the direct and indirect contributions of countless individuals. Specifically, I thank Jen Larsen and Kyle Davies for being the best museum professionals a student in a vertebrate paleontology department could ask for. Further, I thank the collaborators and colleagues, specifically Dr. Andrew Bentley, Dr. Alyson Brink, Dr. Joshua Cohen, Dr. Brian Davis, Tyler Hunt, Scott Schaefer, Dr. Brent Tweedy, and Greg Wilbert, who helped create a culture of camaraderie that has allowed me to do far more than I could ever have dreamed of alone. I also thank my previous paleontological mentors, including Drs. Thomas Carr, Margaret Fraiser, Stephen Dornbos, and Allison Tumarkin-Deratzian for their continual support and friendship as I progressed through my formative years in the field.

Finally I thank my friends and family, who always encouraged me to follow my dreams and pursue a career that I find fulfilling. Thank you to my father Kurt Frederickson for instilling a love of science in me and for drawing dinosaurs with me (to the best of his ability) at a very early age. To my sister Kelsey, thank you for being my best friend and for watching *Jurassic Park* with me so many times as a kid. I thank my grandmother, Geri Mascari, and my aunt and uncle, Marilyn and Tim St. Martin, for spending an untold fortune on my dinosaur fascination as a child. Last, I thank my friends for providing emotional support throughout my life, especially during graduate school. Each of you have contributed in some way to this work beyond your realization.

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Abstract

This dissertation is broken into four chapters. In chapter I, I cover background literature and set the framework for the following chapters by describing the relationship between dinosaur ecology and ontogeny. In chapters 2 through 4 I cover different aspects of dinosaur paleoecology from the middle Cretaceous of North America.

In chapter II, the hypothetical ecologies are explored for multiple theropods derived from the Upper Cretaceous Mussentuchit Member of the Cedar Mountain Formation of Utah. The samples for this study come from six microsites, ranging in depositional setting from distal floodplain to channel lags. In total 866 teeth were analyzed, of which 309 were found to represent four unique tooth morphotypes: a large theropod, a medium-sized dromaeosaurid, a small dromaeosaurid, and a tooth-morph similar to the genus *Richardoestesia*. The four morphotypes vary significantly in mean size, from 15.1 mm in the large theropod (5.2–34.7 mm) to 3.7 mm in *Richardoestesia* (2.1–7.6 mm). Further, tooth representation from two of the best-sampled microsites show differing patterns. The large theropod teeth are about twice as common in the floodplain environment (V695, 15.6% of 135 teeth) as compared to the splay/channel (V794, 7.7% of 104 teeth); while medium-sized dromaeosaurid teeth are more than three times as common in the floodplain (12.5 to 41.5%). Small dromaeosaurid teeth show little difference between the sites (30.8 to 38.45%), but *Richardoestesia* teeth increase more than three-fold in abundance from the floodplain to the splay/channel (12.8 to 41.3%). Preliminary sedimentological and taphonomic data suggest that sorting bias is not responsible for the observed faunal differences. Stable isotope analysis

($\delta^{13}C_{VPDB\text{-}LSVEC}$; $\delta^{18}O_{VSMOW\text{-}SLAP}$) of tooth carbonate from the theropod morphotypes, goniopholidids (crocodylians), and matrix from V695 and V794 were also analyzed. Statistical differences between the matrix and theropod teeth for both $\delta^{13}C$ and $\delta^{18}O$ in V695 and for $\delta^{18}O$ in V794, indicate that the samples have not been completely homogenized by diagenesis. The theropods show only small differences in $\delta^{13}C$ values between each other, with morph 4 being the most depleted and most similar to goniopholidids in V695, as compared to the other theropods. In the sample fromV794 morph 2, which is the relatively most-enriched morphotype in V695, is the most-depleted morphotype in V794. In V695, morphs 1, 3, and 4 all show modest enrichment in $\delta^{13}C$ indicating a level of dietary of plasticity not observed between the two different environmental samples for morph 2. Taken as a whole, we hypothesize that these data indicate that the Mussentuchit theropods had different habitat preferences, and presumably different niches within the predator guild. Most notably, morph 2, the medium-sized dromaeosaurid shows little difference in diet between sites indicating a stricter reliance on a single food source, presumably one not found near the channel. *Richardoestesia* (morph 4) conversely shows a wide-ranging diet depending on environment, but is more-often isotopically lighter than the other morphs. Given its small size, tooth shape, isotopic signature, and abundance near the channels, we interpret this animal as having an analogous diet to a modern wading bird. Finally, the large theropod (morph 1) and small dromaeosaurid (morph 3) appears to have had cosmopolitan tastes and wide-distribution. These lines of evidence all suggest plausible means by which ecospace was divided among the predatory dinosaurs of the Mussentuchit local fauna.

Chapter III focusses on the diet and ontogeny of the large herbivorous dinosaur, *Tenontosaurus tilletti*. *T. tilletti* was one of the most common herbivorous dinosaurs in North America during the Aptian-Albian stages of the Early Cretaceous. With a fossil record composed of hundreds of specimens, including multiple nearly complete individuals, its superior fossil record has made *T. tilletti* one of the best known ornithischian dinosaurs. Here, I investigate the consistency of multiple proxies for growth in this dinosaur, in order to determine the relative maturity of individual specimens of *T. tilletti* using a cladistic methodology. In total, 32 post-cranial characters were coded for eight of the most complete specimens. The resulting tree was highly consistent (CI=0.97) arranging the specimens into seven growth stages. In general, growth follows a pattern from gracile to more robust, with the largest changes appearing to track the transition to greater quadrupedality in the largest individuals. The arrangement of specimens is strongly correlated with size, histological, and bone textural changes. These data were then used to test the least and most mature specimens for dietary differences using stable isotope analysis. This follows the general line of reasoning that some herbivores tend to be more carnivorous when young to increase nutritional uptake during rapid stages of growth. Analysis of OMNH 10144 (least mature) and OMNH 10132 (most mature) show no statistical difference in either $\delta^{13}C$ or $\delta^{18}O$, nor do they differ in tooth wear angle significantly, implying that by the time they reach the size of OMNH 10144, the diet of juveniles is not substantially different from that of adults.

Finally, chapter IV looks at one the most well-known examples of speculative dinosaur behavior. The image of the highly intelligent, pack-hunting raptor has become

engrained in the scientific literature and popular works. First proposed to explain the relatively common co-occurrence of the large-bodied iguanodontian *Tenontosaurus tilletti* and the wolf-sized *Deinonychus antirrhopus* from the Early Cretaceous of North America; a canid-like social hunting structure has become the standard depiction of dromaeosaurs in popular works over the last three decades. This reconstruction, however, is problematic, largely due to the fact that highly coordinated hunting strategies are rarely observed in modern archosaurs. This debate has led to the alternative hypothesis that *Deinonychus* was more analogous to agonistic reptilian carnivores, like the Komodo dragon (*Varanus komodoensis,* Squamata, Varanidae). Among the many differences between these two analogs is how social and asocial organisms rear their young, producing a diagnostic pattern based on the presence or absence of ontogenetic dietary changes. In order to test for dietary changes through growth, stable carbon isotope ($\delta^{13}C$, VPDB-LSVEC) analysis was performed on tooth carbonate from small (<4.5 mm crown height) and large (>9 mm crown height) *Deinonychus* specimens from two microsites from the Early Cretaceous Cloverly and Antlers formations (in Montana and Oklahoma, respectively). Further, goniopholidid crocodylian teeth varying in size from the Cloverly Formation were also tested as a control. The results show that the Cloverly goniopholidids, like their modern counterparts, went through a distinct transition in diet as they grew, where the smallest teeth were the relatively most enriched (avg. -9.32‰; n=5), the medium-sized teeth were the most-depleted (avg. -10.56‰; n=5) , and the largest teeth were in-between (avg. -10.12‰; n=6); characteristic of the dietary shifts seen in modern asocial reptiles. *Deinonychus* showed this same pattern in both formations, with small teeth being the more enriched (avg. -8.99‰; n=10) and the large teeth being more depleted (avg. -10.38‰; n=10). These differences indicate that juvenile and adult *Deinonychus* from both formations likely consumed different prey. Hypothetical food sources, such as *Tenontosaurus tilletti*, are close to the ^{13}C isotopic signal of adult *Deinonychus*, consistent with the hypothesized trophic relationship between these two species. Juvenile *Deinonychus* had a more enriched-diet, likely composed of smaller, but trophically-higher species. Taken together, these data add to the growing evidence that *Deinonychus* was not a complex social hunter, at least by modern mammalian standards.

CHAPTER I: ONTOGENETIC DIETARY CHANGES AS A PROXY FOR SOCIAL BEHAVIOR IN DINOSAURS

Joseph A. Frederickson

INTRODUCTION

The diet of growing organisms can vary significantly from that of the skeletally-mature individual. In some animals where distinct life stages are achieved through growth, as in the metamorphosis of frogs and salamanders, diet will change between two different sources, such as a mostly aquatic to a largely terrestrial diet. More dramatically, some animals even switch their diet entirely from carnivorous or insectivorous adolescents to herbivorous adults (as in the Spiny-tailed Iguana *Ctenosaura similis* [Gray, 1831; Durtsche, 2000]), though the reversed scenario is rarely seen. The most commonly encountered ontogenetic dietary changes are likely related to food size and masticatory processes. Indeed, most organisms lacking complex hunting strategies or food processing abilities are limited to a diet of food items that can fit in their mouth. This is the case in many (if not most) fish, where diet changes with the size of the individual based on their ability to capture and engulf differently-sized prey (e.g., Olson, 1996). Though these dramatic dietary changes can be produced for a variety of reasons, including nutritional advantage through growth, evolutionary history, size-limitations to feeding, and niche separation from adults, they all represent an important aspect of an animal's life history and ecology.

The importance of these changes is often unappreciated in the fossil record, where juvenile or subadult ecologies are often disregarded when discussing the lifestyles of an extinct organism. In some extinct animals, like in predatory sharks such as the 20+ meter long *Carcharocles megalodon* (Agassiz, 1843) (Dooley et al., 2004), these dietary changes would certainly be present and significant just as they are in living relatives, like the white shark, *Carcharodon carcharias* (Linnaeus, 1758) (Estrada et al., 2006). Even in organisms without living relatives, morphological and size differences between different growth stages would make ontogenetic dietary differences the rule rather than the exception. An example of this is sauropod dinosaurs, some of which would have been capable of reaching vegetation at the very top of the canopy, while the juveniles would have been limited to plants in the understory. Even so, exceptions to ontogenetic dietary niche changes in modern animals do occur and are usually associated with aspects of an animal's lifestyle, such as social behavior and parental care. The presence of these two examples in particular are commonly debated by dinosaur paleontologists (see below). Given that the presence of one (e.g., ontogenetic niche partitioning) is normally tied to the presence of the other (e.g., social behavior), this provides a rare opportunity to test indirectly for behavior that normally does not fossilize.

Here, I briefly summarize the wealth of evidence for archosaurian ontogeny, diet, and social behavior in order to introduce the following chapters of this dissertation. In doing so, I do not attempt to answer, refute, or clarify any of the previous literature's questions or arguments; these will be expanded upon in the forthcoming chapters.

ECOLOGY AND LIFE HISTORY

Mating behavior and parental care in archosaurs

Discussion of dinosaur ontogeny begins with mating behavior and physiology, which are often important factors that determine an animal's appearance and life history. Though parental care comes in a spectrum of forms, reptile-grade tetrapods, as a whole, are considered relatively primitive in pre- and post-hatching behavior. In general, these animals are socially diverse, but with only a few examples of social sophistication, all of which is well below that of derived birds or mammals (Wilson, 2000). Only 1-3% of squamate species practice egg-guarding, with the most prevalent behavior found in larger or venomous snake species; likely a result of effective defense strategies in these animals (Neill, 1964; Shine, 1988; Clutton-Brock, 1991). One exception to this pattern in reptiles does occur in the crocodilians, in which all 21 species practice some degree of nest guarding (Greer, 1971). Most parental care in crocodilians is done by the female only; however, in at least eight species, biparental care is known to exist and likely evolved from female only care two to three times (Greer 1971; Shine 1988; Aggarwal et al., 1994). Male-only care, exhibited in some birds (discussed below), is not known in any squamate or crocodilian species (Reynolds et al., 2002). The most primitive reproductive behavior in living neosuchians is hole nesting, seen predominately in the gharials (*Gavialis gangeticus*, Gmelin, 1789), where eggs are deposited into pitcher-shaped holes along sandy banks of water bodies. Other species exhibit more advanced nest-building behavior, creating mound nests using sticks and leaves. Besides nest defense, mothers will assist freeing young from the nest upon hatching, while few others will lead their progeny to water and protect them for some period after (Wilson, 2000). Juveniles are born fully mobile, capable of swimming, and procuring their own prey. It is important to note that parental feeding is never observed during the guarding period and that parental abandonment occurs relatively rapidly after hatching (Grigg and Kirshner, 2015). At this time, juveniles become increasingly timid around larger individuals, as cannibalism is commonplace in most species, making up as much as 50% of hatchling mortality (Rootes and Chabreck, 1993).

Unlike in reptiles, parental care is nearly ubiquitous in avians. The only birds not known to care for their eggs or young are brood parasites and the megapodes, the latter abandon their eggs in large mounds and the young emerge fully independent. All other species exhibit some degree of nest and brood defense, but vary widely in parental feeding (Lack, 1968; Clutton-Brock, 1991). In no doubt, this diversity can be attributed to differing degrees of post-hatching development between precocial (the basal condition for neornithines, McKitrick, 1992; Sillén-Tullberg and Temrin, 1994; Varricchio and Jackson, 2016) and altricial (a highly-derived condition requiring substantial parental investment) young. Though there has been plentiful debate on the ancestral parental condition in birds, recent paleontological and neontological studies have shown that biparental care (found in 81% of avian species; Cockburn, 2006) is a derived condition, likely evolving in congruence with the development of altricial young and widespread monogamy. Male-only care is found in ~1% of species (Cockburn, 2006), including many of the most primitive living birds, the palaeognaths (Burley and Johnson, 2002; Varricchio and Jackson, 2016). These birds are usually typified by self-feeding, precocial young, and likely represent the basal neornithine condition (McKitrick, 1992; Sillén-Tullberg and Temrin, 1994).

Unraveling non-avian dinosaur reproductive strategies is understandably difficult. Egg clutches purportedly from dinosaurs come in a variety of assemblages, ranging from isolated or disorganized collections to highly-organized nests. In all cases, however, eggs are laid within rounded depressions and were at least partially buried

(Erben et al., 1979; Seymour, 1979; Seymour and Ackerman, 1980; Mikhailov et al., 1994; Faccio et al., 1994; Norell et al., 1995; Varricchio et al., 1997; Horner, 2000). Although hypothesized to occur, to date no dinosaur nests are known to contain sticks and leaves as seen in modern crocodilians (Horner, 2000). The most advanced dinosaur nests were those described from the maniraptoran *Troodon*. These nests were constructed in a circular arrangement with high rims and partially buried eggs, allowing for the brooding parent to sit at the center (see Horner, 2000 for a summary). Varricchio et al. (2008) hypothesized that based on the body mass to clutch volume ratio, maniraptoran nests were likely created by paternal parental care, a hypothesis corroborated by the lack of medullary bone in known brooding individuals of *Troodon formosus* and *Citipati osmolskae*. The degree of neonatal self-sufficiency is still a matter of debate in Dinosauria. Based on the degree of epiphyseal development, Horner and Weishampel (1988; 1996) argued that the hadrosaur *Maisaura* had semi-altricial young, an observation extended to other hadrosaur species based on histological results (Horner et al., 2000; see Geist and Jones, 1996 for an alternative interpretation). The discovery of trampled egg shells in the nesting site was used to argue that young would remain in the nest for a prolonged period after hatching. Altricial young have also been hypothesized in prosauropods (Reisz et al., 2010), ceratopsians (Meng et al., 2004), and hypsilophodons (Winkler and Murry, 1989). Conversely, these same authors argue for precocial young in the theropod *Troodon*. Following these revelations and studies of living archosaurs, Varricchio and Jackson (2016) put forth a hypothetical evolutionary progression of reproductive traits in derived Theropoda. In this scheme, pre-maniraptoran theropods (and dinosaurs in general) are hypothesized to have practiced egg-burying behavior and produced either self-sufficient precocial or semi-altricial young. Maniraptoran theropods modified their eggs and produced tightly-fitted and organized clutches varying between gently buried (as in oviraptorans) to partially exposed (as in troodontids) allowing for some degree of paternal incubation, and produced young that were likely fully self-feeding and precocial.

Growth in dinosaurs

Like dinosaur reproductive strategies, growth has a long and interesting history of study in paleontology. I encourage the reader to delve into the literature starting with Chinsamy-Turan (2005 and citations therein) for a more thorough treatment on the subject. Modern understanding of dinosaur growth patterns was revolutionized with the utilization of histological methods in the field. Over the course of multiple studies, Erickson et al. (2001) showed that dinosaur growth fits a sigmoidal curve, with a prolonged adolescent period followed by a rapid growth period (between 1 and 6 years), where somatic maturity is reached between 3 and 13 years. Erickson (2005) also hypotheses that old individual dinosaurs are relatively rare, in part due to the fact that dinosaurs only spent about 30% of their life at full skeletal maturity. Lee and Werning (2008) also showed that ornithoscelidians (ornithischians and theropods) do not fit a reptilian growth model, with extended growth over long generation times; however, they do note that reproductive maturity occurs in a similar way to reptiles, in that reproductive age occurs while growth is still highly active. These authors note how this reproductive strategy is also reminiscent of growth in large bodied mammals, but strikingly different from those of small mammals or birds.

One of the most fascinating aspects of dinosaur ontogeny is how these animals changed in appearance throughout growth. One of the more shocking realizations is that many dinosaurs went through a “showy teenage” phase. First explicitly described by Carr (1999), he noted in his landmark study of tyrannosaur growth that subadult individuals of *Albertosaurus sarcophagus* developed cornual horns, which change to low rounded masses in adult individuals. A similar pattern was also noticed in the ontogenetic smoothing of facial texture in *Daspletosaurus horneri* and *Tyrannosaurus rex* (Carr and Williamson, 2004; Carr et al., 2017). Dramatic ontogenetic facial ornamentation reduction is not limited to Tyrannosaurs, however. Horner and Goodwin (2009) outlined the dramatic growth changes of pachycephalosaurus, synonymizing the well-adorned *Stygimoloch* as a lower ontogenetic stage of the more conservative *Pachycephalosaurus wyomingensis*. Likewise, Sampson et al. (1997) noted a resorption of supraorbital ornamentation in Late Cretaceous centrosaurine dinosaurs. This was corroborated and elaborated by Frederickson and Tumarkin-Deratzian (2014) in *Centrosaurus apertus*. This animal goes through an impressive transition from a subadult with tall, straight nasal and supraorbital horns to an adult with a relatively smaller procurved nasal horn and resorbed supraorbital horns. Chasmosaurines, the other branch of the neoceratopsian family tree, also went through substantial changes in horn shape and ornamentation reduction through ontogeny (Horner and Goodwin, 2006; Scannella and Horner, 2010). The reason for these changes is still unknown, but likely reflects the role of these structures as either interspecific or sexual indicators (see Padian and Horner, 2011 for more on this debate).

Social behavior in archosaurs

Gregariousness in animals ranges through a spectrum, from antagonistic solitary lifestyles to eusocial hierarchical societies. Living archosaurs can exhibit much of this range. The most primitive members, the crocodilians, show a generally high-degree of social tolerance; with large congregations of these animals occupying the same habitat during more than just a single breeding season. These groupings normally follow a strict hierarchy, with a dominant male occupying the most favorable localities and feeding first on available food sources. Females will also occasionally show territorial behaviors, but this is normally only for the purposes of nest guarding, and will often tolerate one another as they freely move between different male-dominated congregations (Garrick and Lang, 1977). Generally seen as agonistic towards one another, crocodilians have been known to injure or kill one another during breeding-season competition or in acts of apparent cannibalism (Rootes and Chabreck, 1993). Even so, these animals can show an impressive array of cooperative behaviors for animals generally associated with more reptilian characteristics. For example, two species, the Nile crocodile *Crocodylus niloticus* of Sub-Saharan Africa and Yacare caiman *Caiman yacare* of central South America, have been observed cooperatively hunting fish by coordinated placement of feeding individuals as to block the flow of rivers and streams (Pooley and Ross, 1989; Ross, 1989). Even more impressive, Nile crocodiles are notorious for their behavior of holding large prey in the water while other members break off digestible pieces (Pooley, 1982; 1989). In all cases, these actions can be classified as commensalistic behaviors which increase the efficiency of the capture of fish and the use of large carcasses to the benefit of all participating members (Pooley and Ross, 1989; Ross, 1998; Roach and Brinkman, 2007).

Birds, conversely, show more variation than crocodilians in their social structure. The least social being solitary species, which either only pair to mate (such as hummingbirds or woodpeckers) or, as often the case, will form long-term monogamous bonds with a single mate (such as roadrunners), but will otherwise avoid other members of the same species. More social still are flocking birds which will gather together for protection or increased foraging efficiency. These congregations are usually hierarchical with dominant animals in the most highly-valued spots and subordinate individuals at the periphery. Flocks, however, come in a variety of forms and can even be composed of mixed species working together (e.g., Morse, 1970), though caution should be taken when using this behavior as an example of social structure as undoubtedly most cases of flocking are not done for altruistic reasons and may only represent a minor improvement upon the social behavior observed in crocodilians. The most advanced form of social interaction is cooperative hunting. In the most well-studied examples, such as the Aplomado falcons *Falco femoralis* and Harris' hawk *Parabuteo unicinctus*, closely related individuals or breeding pairs will work together to flush out and catch small prey items (Bednarz, 1995; Keddy-Hector, 2000). Habitual cooperative hunting to catch prey too large to be subdued by a single individual is currently only known in the Golden eagle *Aquila chrysaetos*, with documented attacks on ungulates, large birds, and carnivorans (see Roach and Brinkman, 2007); however, anecdotal occurrences of cooperative hunting of large prey by corvids have also been reported (Bowman, 2003; Yosef and Yosef, 2010). Though they are generally more socially advanced than crocodilians, antagonistic behavior is widespread in birds. Many species, including the previously aforementioned cooperative hunting species like the Golden eagle, can be extremely territorial (Bergo, 1987). Cannibalism is also noted in a variety of species, including hawks, owls, gulls, and vultures (Stanback and Koenig, 1992).

Bailey et al., (2013) modified from Boesch and Boesch (1989), classifies group hunting into five categories: passive, similarity, synchrony, coordination, and collaboration. Of these, crocodilians mostly show passive hunting strategies, grouping together to hunt the same prey but taking no actions to compensate for the movements of the other predators. However, rare cases of higher cooperation are documented (see above) and can be interpreted anywhere from synchrony to coordination depending on the perspectives held by the researcher (Dinets, 2015). Avian cooperation is generally more complex and is likely classified as coordination at its most advanced. However, no known avian species has yet shown the cooperative hunting abilities of mammalian packs, which can be extremely advanced and require high degrees of organization between members (such as the hunting strategies of African Wild Dogs [Sheldon, 2013; Creel and Creel, 2002] and novel hunting tactics [such as wave-washing by Orca whales; Smith et al., 1981; Visser et al., 2008]). This type of advanced cooperation falls into the collaboration category and requires a separation of roles which do not change based on the prey's reactions.

Social hunting groups in mammals usually form from closely-related individuals. For example, the normally solitary Lynx (*Lynx canadensis*) will occasionally hunt in small groups, either composed of mother and her young, or the young individuals hunting together (Saunders Jr, 1963). More social species, such as hyenas, lions, and various canids, create social units formed of extended family members and fewer unrelated migrants. Rarer still, brother cheetahs and lions will on occasion form lifelong hunting coalitions, a behavior generally unknown in other felids (Bailey et al., 2013 and citations therein).

Group member relatedness and the burdens of prolonged child care likely play into the development of social hunting groups. Organisms with minimal parental care, such as crocodilians, show very rudimentary forms of social interactions during prey acquisition. The same can be said for predatory lizards and snakes, where parental care is minimal post-hatching and cooperative hunting has only been recently and sporadically reported (Dinets, 2017). Predatory birds will at least seasonally work together to rear young and occasionally work together to hunt large prey (see examples above). Modern birds grow at an accelerated rate as compared to mammals, meaning adult size and presumably an adult diet, is reached relatively more quickly. Many large-bodied mammals require multi-year parental care before separation. In some solitary predatory species (like in the above example of *Lynx*), "pack hunting" may only occur near this separation point, when young individuals are learning to hunt. Though the technical definition of this type of educational group hunting strategies may fall outside true cooperative hunting, since novice hunters are likely hindering more than assisting.

Social behavior in dinosaurs has been thoroughly discussed in the primary literature (e.g., Ostrom, 1986). Monodominant bonebeds are known for every major group of dinosaur, including assemblages that are predominantly composed of juveniles or subadult (Jerzykiewicz et al., 1993; Varricchio and Horner, 1993; Lehman, 2006; Garrison et al., 2007; Myers and Storrs, 2007; Varricchio et al., 2008)). Varricchio et al.

(2008) hypothesized that these juvenile groups are a byproduct of multiyear maturation period. Some dinosaur bonebeds, can be staggering in size, preserving the remains of thousands of individuals. Bonebeds of this size are understandably rare, but are known for theropods (Currie and Eberth, 2010) and a variety of centrosaurine ceratopsians (Sampson et al., 1997). Ichnological evidence of sociality also exists, including juvenile-only group trackways. Both lines of evidence unambiguously demonstrate that dinosaurs, at least periodically, formed groups, some of which were distributed by age class (Myers and Fiorillo, 2009).

Social behavior in Dinosauria may not be disputed; however, cooperative hunting remains a relatively controversial idea. First proposed by Ostrom (1969; 1986) to explain the occurrence of multiple *Deinonychus antirrhopus* alongside remains of the larger *Tenontosaurus tilletti*, this hypothesis was thoroughly challenged by Roach and Brinkman (2007), who preferred the interpretation that these groupings represent crocodilian-style mass feeding events. These authors argued that cooperative hunting behavior is notably rare in living archosaurs and intraspecific aggression is generally high (see above). Indeed, theropod material from multiple localities show strong evidence that intraspecific competition and cannibalism were present throughout the clade (Rogers et al., 2003; Currie et al., 2005; Longrich et al., 2010). Currie and Eberth (2010) challenged these reinterpretations based on multiple lines of evidence including the widespread presence of monodominant theropod bonebeds that cannot as easily be explained through coincidental or taphonomic aggregation. Besides bonebeds, trackway evidence shows multiple examples of theropods traveling in the same direction in close association, which is most-parsimoniously interpreted as social behavior (Li et al., 2008). Even so, the evidence of social hunting in predatory dinosaurs is not absolute, and lacking more complete fossil evidence, a new technique is needed to investigate this problem.

Niche transitions in ontogeny

Ontogenetic changes in diet are largely driven by the size differences between juveniles and adults. In some species, body size can increase up to four orders of magnitude (Werner and Gilliam, 1984), which often exceeds the size differences of other competing species. Importantly, niche dietary changes are strictly limited to those without long-term parental care. In species with parental care, the parent(s) will provide food, either directly or through lactation, which in both cases can be derived from a diet similar to that of the adults. In animals without parental care, the young are required to procure their own food, and thus limited by what they can catch and swallow. In fish, for example, ontogenetic changes in diet are nearly universal (Werner and Gilliam, 1984 and citations therein). Piscivorous species, especially, will go through as many as four shifts in diet correlating with increased prey size. Other species, like the pinfish *Lagodon rhomboides*, will progress from carnivore to herbivore through approximately five growth stages (Werner and Gilliam, 1984). Similarly, in many reptiles, dietary shifts occur. For example, water snakes such as *Nerodia erythogaster*, will transfer diet from aquatic to semi-aquatic prey at about 50 cm in length. Even more dramatic, turtles will often switch from carnivorous diets as juveniles to largely herbivorous diets as adults (Werner and Gilliam, 1984). Like in crocodilians, these groups are typified by little parental care (beyond maybe nest protection) and high degrees of cannibalism. In these animals, dietary proxies, such as stable isotopes, should be noticeably different between juveniles and adults due to their non-overlapping diets.

Conversely, many animals with long-term parental care show few dietary differences. Ontogenetic studies of communal cetaceans show a consistent isotopic pattern to diet where the suckling young tend to be relatively enriched as compared to the adult diet and less widely distributed, but overall there is no shift (Knoff et al., 2008). Occasionally, however, transient individuals (like young males) may leave the group and can show modest dietary shifts (Newsome et al., 2009). Similarly, social canids do not show such diversity in diet through ontogeny. In these animals, such as the Grey Wolf *Canis lupus*, the protection of the pack allows all members to feed upon similarly sized prey items, though juveniles may get the optimal fare (Bryan et al., 2006). More work is needed to test for isotopic differences between these individuals, but observations of feeding do not necessarily point to much variance in diet. Further, birds (and presumably dinosaurs) would not have a lactation period, and thus young would not have the obligatory isotopically-enriched diet during the early part of their lives as seen in mammals.

Though parental care and gregariousness are not necessarily equivalent, it does generally follow that social mammals and birds tend to have more prolonged and involved parental care than asocial individuals. Further, most modern birds differ from dinosaurs in that they grow relatively rapidly, an adaptation associated with a volant lifestyle, so any parental care is often concluded within the first year of life (see Ashmole and Tovar, 1968 for an overview and a notable exception). Dinosaurs, however, show longer growth periods, where many animals are not near full somatic growth at the end of the first year. Multi-year parental care, in association with annual reproduction, would lead to the creation of groupings composed of multiple growth stage.

Niche partitioning in dinosaurs (especially amongst precocial young)

Taken as a whole, we can make a well-reasoned hypothesis for the basic life history traits of many types of dinosaurs. In the large-bodied species, skeletal maturation was a multi-year or multi-decade long process, where individuals would transition between a generalized (non-specialized) juvenile morphology, to a showy young adult phase, before ultimately reaching a more bland-looking full-sized adult. Sexual maturity would occur sometime during this middle transition, before the individual reached full adult size. Reproductive styles would likely vary but it does seem as if most maniraptorans had parental care, with paternal nest occupation. Evidence from ornithischians shows that nests were not abandoned immediately after hatching, as in many reptiles, and the juveniles often are found alongside the adults (e.g. Forster, 1990). Further, theropod bonebeds containing both juvenile and adult individuals are also common and would signify that, even if the hatchlings left the nest and went on their own, they would return before full somatic maturity to occupy similar environments as the adults. What is missing in our knowledge of dinosaurian behavior is whether long-term parental care was practiced, and whether this can explain the apparent social structures of many dinosaurian groups.

Here, I hypothesize that dietary ontogenetic changes can answer this question. By looking at modern analogs we see an existent pattern where long-term parental care is linked to the absence of dramatic dietary niche transitions. Since dinosaurs were more mammalian in growth dynamics than they are to modern birds, it is likely that the demands of this lifestyle would translate into a comparable ecology. To more fully illustrate the hypothesis, I will use arguably the most famous dinosaur, *Tyrannosaurus rex* (Osborn, 1905) as an example. *T. rex* is a large-bodied coelurosaurian theropod, reaching lengths over 12 m and weights estimated to 9000 kg (Hutchinson et al., 2011). Neonatal material, and thus a complete growth record, is not known, but growth curves produced from individuals ranging from 2 to 28 years of age (correlated from 29.9 to 5,654 kg in body size) indicate that these animals could achieve a maximum growth rate of 767 kg/yr . The highest growth rates were achieved during a transition to exponential growth at around 10 years of age, and highest for approximately 4 years prior to reaching somatic maturity at roughly 18.5 years of age (Erickson et al., 2004). Social structure in *T. rex* is disputable with multiple cases of monodominant bonebeds reported (and common in less derived tyrannosaurs; Currie, 1998); however, antagonistic behavior was also common with evidence for habitual face-biting and cannibalism preserved in multiple specimens (Longrich et al., 2010). Testing *T. rex* specimens for niche changes through ontogeny could produce multiple hypothetical patterns, but in essence only two would be relevant. If dietary analysis showed juveniles had vastly different diets than the adults we can assume that their niche is different. Alternatively, juveniles that fall into the range of adult diet indicate that these animals would be in competition for the same food. Since adult animals of 10 m in length would not likely feed on small-bodied fare, we are left to assume that the juveniles would be eating larger-bodied animals like the adults. If juveniles and adults are found in the same environment, this would be an extremely dangerous lifestyle considering that scavenging adult kills could result in death, further catching these large animals by themselves would similarly be difficult. Like non-social modern animals, we would assume that young *T. rex* would simply have a diet composed of smaller organisms before reaching sizes where catching and dispatching larger prey would be more convenient. Thus, we are left with the most parsimonious explanation that this dietary signal is derived from cooperative behavior, where the juveniles and adults eat the same food but are not in competition with one another. It is this theme of niche competition and ontogeny which I will focus on for the rest of this dissertation.

OUTLINE AND CONCLUSIONS

In the next chapter (chapter II), I attempt to establish the ecological diversity of theropod dinosaurs from a single, middle Cretaceous formation. This study challenges previous assumptions about dinosaur trophic ecology and begins to paint a picture of Cretaceous ecosystems with substantially more complex predator guild structure. Using taphonomic, biological, and geochemical techniques, I identify the theropod diversity of the Mussentuchit Member of the Cedar Mountain Formation in order to determine how these organisms coexisted within their ecosystem.

Chapter III pivots and investigates the relative trophic abilities, through morphological and isotopic data, of a middle Cretaceous herbivore, *Tenontosaurus tilletti*. The abundance of material allows for individual assessment of different ontogenetic stages. Here, I attempt to reconstruct progressive stages of skeletal maturity and investigate the consistency of this record with osteohistological, size, and periosteal aging methods. In doing so, I establish a tentative growth series for the species allowing for direct dietary comparison of the least and most mature specimens investigated.

Last, in chapter IV, I investigate one of the most-longstanding debates in theropod ecology, the cooperative hunting hypothesis in *Deinonychus antirrhopus*. I use stable isotopes to test whether this dinosaur shows ontogenetic dietary changes. The results form the basis for the new hypothesis on the social behavior of this animal.

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CHAPTER II: THEROPOD ECOLOGY OF THE MEDIAL CRETACEOUS: DIET AND HABITAT PREFERENCE IN SMALL TO MEDIUM-SIZE PREDATORS FROM THE UPPERMOST CEDAR MOUNTAIN FORMATION (UTAH, U.S.A.).

Joseph A. Frederickson, Michael H. Engel, and Richard L. Cifelli

INTRODUCTION

Niche partitioning is an ecological phenomenon, where multiple competing organisms are able to coexist in the same environment by maximizing their occupation of non-overlapping lifestyles. Although generally well-documented in modern species, demonstrating niche partitioning in Mesozoic ecosystems has been challenging. Much of this difficulty has been alleviated through decades of research showing that dinosaurs were highly derived animals with complex ecological relationships (e.g., Fricke and Pearson, 2008). In no group has this realization been more apparent than in non-avian theropods, which possess many morphological specializations associated with unique lifestyles, such as pachyostotic bones and dorsally-placed nostrils in aquatic spinosaurids (Ibrahim et al., 2014), digging-style claws in alvarezsaurids (Chiappe et al., 2002), and edentulous beaks in multiple herbivorous clades (Zanno and Makovicky, 2010); all of which likely evolved to exploit food sources unavailable to other theropods. In addition, there is evidence that some members of this group were capable of complex behaviors, such as pack hunting (Maxwell and Ostrom, 1995), which would further differentiate their predatory trophic abilities. Even so, our general understanding of theropod ecology and interrelationships between sympatric species is sorely lacking. This is due, in part, to the fact that most theropods (besides those mentioned above) do not possess obvious adaptations associated with particular diets. Without further lines of evidence, determining the precise trophic ecology of these dinosaurs is problematic beyond characterization as "generalist predator", a label that could reasonably be attributed to any sharp-toothed species.

In many Late Cretaceous environments, multiple small- to medium-sized predatory theropods coexisted together (Larson and Currie, 2013). These dromaeosaurs, troodontids, and small (or juvenile) tyrannosaurs show clear adaptations for predatory lifestyles, such as sharp, recurved teeth and long sickle-shaped claws with enlarged basal tubercles (for attachment of flexor tendons), meaning that they would be in direct competition if they preyed upon the same species. This high diversity of competitors contradicts the Competitive Exclusion Principal (Hardin, 1960), which states that species occupying the same niche cannot exist indefinitely in the same environment. In order to maintain such high diversity, these predatory species would have had to minimize competition amongst themselves through behavioral or spatial dietary segregation. Modern animals provide good examples of how niche partitioning can be manifested, primarily by specializing in different prey items (e.g., Magnusson et al., 1987), feeding at different times of day (e.g., Albrecht and Gotelli, 2001), or occupying different subenvironments (e.g.,Leal and Fleishman, 2002). By adopting one (or more) of these strategies, similar organisms can coexist without directly competing for resources. Thus, it stands to reason that, in diverse theropod communities, we would expect to see some level of niche partitioning following the strategies observed in modern fauna.

Determining behavior from the fossil record is a difficult, sometimes impossible, task. It can be assumed that animals are adapted to a specific lifestyle, allowing for broad generalizations about the animal's ecology based on morphology alone. For example, the sharp, recurved teeth and long legs of dromaeosaurids leave little doubt that these animals were cursorial predators; however, what they were eating cannot be precisely determined. In the best-case scenario, animals are preserved in the act of feeding or with stomach contents still in place. Famous examples such as the fighting dinosaurs, a *Velociraptor mongoliensis* and *Protoceratops andrewsi* preserved in an eternal predator-prey struggle (Carpenter, 1998), unambiguously show that this trophic relationship occurred at least once. Even further, trackway evidence occasionally show evidence of presumed hunting or packing behavior (Ostrom, 1972). Fossils of this ecological caliber are rare, leaving paleoecologists to rely on more indirect proxies for ancient behavior; namely, through geochemical or taphonomic evidence. To date, few of these ecological studies have focused on theropods, and when performed most focus on the large or enigmatic species (e.g., Horner et al., 2011;, Amiot et al., 2011). Unsurprisingly, it is mainly in these large species that strong evidence for niche partitioning has been presented (Henderson, 1998).

In this study, we investigate the realized dietary niche of theropods from relatively well-sampled microbonebeds, derived from the Late Cretaceous Mussentuchit Member (herein referred to as MM) of the Cedar Mountain Formation of Utah. Through morphological, taphonomic, and geochemical techniques we investigated the dietary and habitat preferences of superficially similar species, in order to more fully understand the Mussentuchit ecosystem, as well as the ecology of many of these poorly-known theropod species.

Geologic Setting

The MM is the uppermost unit of the Cedar Mountain Formation exposed on the western side of the San Rafael Swell anticline in Emery County, Utah (Fig. 1). This unit is composed of terrestrial sediments, varying between sandstones, mudstones, and altered volcanic ash layers; the latter of which comprise much of the grey, smectite-rich badlands characteristic of the unit (Kirkland et al., 1999;, Suarez et al., 2012). The MM formed as shed sediments deposited in the foreland basin during the Pavast thrust event, dated from 98.3 ±0.1 Ma (Cifelli et al., 1997) to 96.7 ±0.5 Ma (Garrison et al., 2007), placing the member in the Cenomanian stage of the Late Cretaceous. The unit is generally highly fossiliferous, with a diverse fauna composed of freshwater fishes, lissamphibians, lepidosaurs, crocodilians, dinosaurs, and mammals (Cifelli and Madsen, 1998), (Kirkland, 1998;, Cifelli et al., 1999;, Fiorillo, 1999;, Nydam, 2003; Garrison et al., 2007; Zanno and Makovicky, 2013; Frederickson and Cifelli, 2017; Frederickson et al., 2017).

MATERIALS AND METHODS

The samples analyzed here come from six microbonebeds collected by crews from the Sam Noble Museum in the Mussentuchit Wash and Short Canyon areas of Emery County, Utah (Cifelli et al., 1999; Goldberg, 2000; Suarez et al., 2012). Stratigraphically, localities V235, V694, and V794 are located near the same level, above a marker ash bed, 15 m from the base of the overlying Naturita Formation, while V695 and V868 are found immediately below this same layer. V239 is found near the contact of the MM with the Naturita Formation. Though they differed in depositional setting (see Table 1), Goldberg (2000) showed that faunal composition between the sites was not dramatically affected by differences in taphonomic history. Further, specimens between sites tend to show a similar minor degree of wear attributable to transportation, indicating that hydraulic transport and reworking was minimal. Most importantly for our purposes, previous isotopic analyses from this same sample demonstrates the expected variation for modern fauna, implying that biogenic signals were not lost due to diagenetic alteration (Suarez et al., 2012; Suarez et al., 2014).

The first step of this analysis was to identify visually distinct tooth morphotypes from the bonebeds. Once morphs were determined, specimens were identified and grouped, to the best of the authors' abilities, using a Nikon SMZ-10A dissecting microscope. Incomplete specimens were not included in the analysis unless they could be assigned to one of the morphotypes with a high degree of confidence. Specimens were then measured, using hand calipers, for crown height, fore-aft basal length, basal width, and denticles per one mm (rounded to the nearest whole denticle) at the curve on both the posterior and anterior carinae. In order to assess the validity of the provisional morphological groupings, measurements (with length, width, and height data Log-transformed to control for size) were analyzed with a discriminant analysis using PAST3 (Hammer et al., 2008).

Next, to determine trophic ecology, we used a multi-tiered approach. First, tooth size was contrasted using a Kruskal-Wallis Test of tooth crown height for all complete specimens, to determine whether statistically significant size differences exist between the morphs. Next, we ran a χ^2-test to compare the distribution of morphotype between sites and to determine if any showed preference for a particular depositional setting (following Lyson and Longrich, 2011). In order to test for taphonomic sorting bias, specimens for the most abundant tooth type (morph 3) and goniopholidid crocodilians were compared between two sites using the a Two-sample T-Test and Mann—Whitney

Test for Equal Medians of tooth crown height. Finally, we determined the stable isotope composition of carbonate associated with tooth enamel and/or dentine ($\delta^{13}C$ and $\delta^{18}O$) to approximate the diet and habitat for each morph. Specimens for geochemical analysis were taken from incomplete, but morphologically distinguishable specimens for each morphotype, as well as small (<10 mm tall) goniopholidid teeth and matrix samples for comparison. Ideally, samples would be taken only from enamel (see Fricke, 2007); however, many of the teeth were too small or had insufficient amounts of enamel for analysis alone. Dentin has more pore space then enamel and is more susceptible to groundwater alteration; however, given that these samples come from the same microsites (and thus the same diagenetic history) we assume that we are increasing type II error. By including this material, we acknowledge that the values obtained are the coarsest approximation for diet and habitat obtainable for our sample. Isotope samples were treated following a modified technique of Koch et al. (1997). Powdered specimens were first treated for one day using a 2% solution of NaOCl, washed five times with distilled water and then allowed to dry overnight, followed by a three-day treatment using 0.1 M acetic acid solution. Next, the samples were washed 10 times with distilled water and allowed to dry for three days.

The carbonate samples analyzed for their stable carbon and oxygen isotope compositions as follows. Approximately 200-300 μg of each carbonate was loaded into a 12 ml borosilicate exetainer vial (Labco 938 W) which were sealed with butyl rubber septa caps. The vials were then placed in a thermostated sample tray heated at 50° C and flushed with ultra-high purity He (99.999%) using a ThermoGas Bench II equipped with a PAL auto sampler flushing needle for 360 seconds to remove the air. Then 0.4 ml of 100% phosphoric acid was manually injected into the vials with a syringe and the reaction was allowed to proceed at 50° C for 2 hours. The vials were then sampled with the PAL measurement needle and the headspace CO_2 was analyzed for $\delta^{13}C$ and $\delta^{18}O$ using a Thermo Delta V Plus isotope ratio mass spectrometer. The carbon and oxygen isotopic compositions are expressed as (Coplen, 2011):

$$\delta^{13}C_{VPDB} = [\, R(^{13}C/^{12}C)_P \,/\, R(^{13}C/^{12}C)_{VPDB} \,] - 1$$

and

$$\delta^{18}O_{VPDB} = [\, R(^{18}O/^{16}O)_P \,/\, R(^{18}O/^{16}O)_{VPDB} \,] - 1$$

where $R(^{13}C/^{12}C)_P = N(^{13}C)_P / N(^{12}C)_P$ which is the ratio of the number of ^{13}C and ^{12}C atoms in sample P and equivalent parameters apply for VPDB and where $R(^{18}O/^{16}O)_P = N(^{18}O)_P / N(^{16}O)_P$ which is the ratio of the number of ^{18}O and ^{16}O atoms in sample P and equivalent parameters apply for VPDB.

The $\delta^{13}C$ values of the calcite samples are reported relative to VPDB on a scale normalized such that the $\delta^{13}C$ of NBS18 is -5.01‰ (Kim et al., 2015). The $\delta^{18}O_{VPDB}$ values of the calcite samples are reported on a scale normalized such that the $\delta^{18}O$ of SLAP is -55.5‰ relative to VSMOW. On this $\delta^{18}O_{VPDB}$ scale , the values of NBS 18 and NBS 19 are -23.01‰ and -2.2‰, respectively (Brand et al., 2014). The oxygen isotope acid fractionation factor for calcite used for 50° C is 1.00934 (Kim et al., 2015). The calcite $\delta^{18}O_{VSMOW\text{-}SLAP}$ values were converted from the $\delta^{18}O_{VPDB}$ values by using the IUPAC-recommended relation Kim et al., 2015):

$$\delta^{18}O_{VSMOW\text{-}SLAP} = 1.03092\ \delta^{18}O_{VPDB} + 30.92‰.$$

The isotopic data were finally compared using the Mann-Whitney Pairwise test.

DESCRIPTIONS

Tooth morphotypes

In total, 866 small- to medium-sized theropod teeth from the MM were analyzed and found to represent at least seven different morphotypes, many of which have been identified elsewhere (Cifelli et al., 1999; Fiorillo, 1999; Garrison et al., 2007). Here we recognize the following morphotypes in our sample sites:

Morphotype 1: These teeth are the tallest of the morphotypes analyzed, with the largest being approximately 35 mm (Fig. 2A$_{1-3}$). These teeth are not as laterally compressed as other morphotypes and possess denticles on both carinae. The denticles on the anterior carina are proximodistally short, apicodistally wide, and oval in cross-section; the denticles on the posterior carina are proximodistally long and chisel-shaped. These teeth are likely the same as “Theropod A” of Fiorillo (1999). The teeth are of uncertain origin, showing similarities with tyrannosaurs (previously reported from the unit by Cifelli et al. (1999), but lack the basally-deflected blood groove diagnostic of this group (Currie et al., 1990). These teeth are similar in size and appearance to those described as morphotype 1 by Krumenacker et al. (2016) from the contemporaneous Wayan Formation of Idaho. Lacking more complete material, these authors tentatively refer to these teeth as belonging to a moderately-sized tyrannosauroid or basal tetanuran. The only large-bodied theropod currently known from the MM is *Siats meekerorum* (Zanno and Makovicky, 2013); unfortunately, the holotype (and only definitively known material) contains no teeth. Regardless, among the huge number of theropod teeth recovered from the MM, none is large enough to belong to an adult *S. meekerorum*.

Morphotype 2: Reaching heights up to 15.69 mm tall, these teeth are generally shorter than morphotype 1, but taller than the other morphotypes (Fig. $2B_{1-3}$). The lingual side is often flattened, while the labial side is more inflated, forming a slight D in cross section. The anterior carina rarely possesses denticles, and curves lingually as it travels towards the base, a feature seen most prominently in lateral teeth of *Dromaeosaurus*, as well as anterior teeth of other dromaeosaurids (Longrich, 2008). The posterior denticles are relatively elongate and rounded on the ends. These teeth match the description for Dromaeosaurinae teeth by Fiorillo (1999), and those figured by Garrison et al. (2007; though misidentified in the figure caption). In addition, a large dromaeosaurid scapula (380 mm in length) is known from V865; given its large size, it is tentatively attributed to this same species.

Morphotype 3: Morphotype 3 is composed of teeth that are generally small and relatively recurved as compared to morphotypes 1 and 2 (Fig. $2C_{1-3}$). These teeth possess denticles on both carinae, with the anterior denticles being wide, low, and rounded; while the posterior denticles are taller, and point slightly apically. Unlike morphotype 2, the anterior carina never curves lingually. The large, upturned posterior denticles with subequally-sized anterior denticles identify these teeth as belonging to a small species of dromaeosaurid (Larson and Currie, 2013). Morphologically similar, but relatively larger teeth are also known from the contemporaneous Wayan Formation of Idaho (Morphotype 4 of Krumenacker et al., 2016).

Morphotype 4: Small, tall, and relatively rounded, these teeth are only moderately recurved (Fig. $2D_{1–3}$). In most specimens denticles are absent from both carinae; when present, they are relatively small and low and usually only found on the posterior end. In the largest specimens, there are 9–10 denticles per mm; however, most lack them completely. Some of these specimens show a slight lingual curvature on the anterior carina, indicating that these may be anteriorly-located teeth. These teeth are nearly identical to those identified as tall variations of cf. *Richardoestesia isosceles* from the Santonian Milk River Formation of Canada (Larson, 2008; fig 3G). Due in part to substantial variation known for *Richardoestesia* teeth (Currie et al., 1990), we cannot confidently assign these teeth beyond the generic-level.

Morphotype 5: Triangular teeth with relatively small denticles on both carinae (9–10 per mm) were first identified in the MM by Cifelli et al. (1999) and subsequently described by Garrison et al. (2007) (Fig. $2E_{1–3}$). These teeth match most closely to those described as cf. *Richardoestesia* sp., though their small, rounded denticles and isosceles-triangular shape in lateral view are unquestionably similar to those of the enigmatic, and possibly non-theropodan (Company et al., 2005), *Richardoestesia isosceles* from the Late Cretaceous Aguja Formation of Texas (Sankey, 2001). Similar triangular teeth are known from the contemporaneous Woodbine formation of Texas, which have also been attributed to *Richardoestesia* (Lee, 1997). It is possible that morphs 4 and 5 represent teeth from a single species, but without any associated material this is simply conjecture.

Morphotype 6: These relatively large teeth with one flattened side and longitudinal grooves are similar to *Paronychodon* specimens described from other Late Cretaceous formations (Fig. $2F_{1–3}$). Conversely, the *Paronychodon* specimens from the MM typically have large, rounded denticles on the posterior carina, while those in geologically younger formations often lack denticles entirely (Larson and Currie, 2013). Currie et al. (1990) hypothesized that these teeth do not belong to a unique taxon, but instead represent malformed dromaeosaur teeth. Without more complete material it is difficult for us to contribute to this discussion; however, the general scarcity of morph 6 to other theropod teeth supports the assertion that these teeth are pathological.

Morphotype 7: Slightly recurved teeth, lacking denticles on the anterior carina and possessing apically-upturned denticles on the posterior carina (Fig. $2F_{1–3}$) are most similar to those identified from the MM as Velociraptorinae by Fiorillo (1999). These teeth are often very short (less than 5 mm long), with the smallest containing as few as seven large denticles. These diminutive specimens superficially appear most similar to *Troodon* teeth and were originally identified as such by Cifelli et al., (1999) and Goldberg (2000); however, morphologically similar, but larger, teeth retain the same amount of denticles per mm (5–6), implying that they belong to the same species differing only in ontogenetic status or alveolar position. These larger teeth have relatively smaller denticles than those of most Late Cretaceous troodontids (e.g., fig. 2H of Larson and Currie, 2013); though more associated material is needed to unequivocally dismiss this identification. Some specimens appear to bear longitudinal grooves, similar to those of Morph 6*,* but to a lesser degree. These individuals may also belong to the same species as Morph 6, which in themselves may belong to one of the other morphotypes.

Though the MM theropods are a seemingly diverse assemblage, it is most likely that multiple morphotypes belong to single species. For the remainder of this study we focused on four of the most common and morphologically discrete morphotypes (morphs 1–4; 309 specimens of the subsample) to maximize the likelihood that we analyzed distinct species. The taxonomic identifications are tentative, based on the lack of more complete material from the MM. Regardless, these identifications are peripheral to our main concern, the relative differences in distribution and diet.

RESULTS AND DISCUSSION

Ordination

A discriminant function analysis of the four morphotypes conducted on 77 complete teeth found that 83.12% of all teeth were correctly identified. In this analysis, axes 1 and 2 account for 61.5% and 32.22% of the maximum discrimination, respectively; and the biplot shows the strongest contributions from the anterior and posterior denticle counts largely in the direction of axis 2 (Fig. 3). Morph 4 was the most consistently identified morph, with 93.3% of specimens correctly placed and only one specimen misidentified as belonging to morph 2. Morph 3 was identified correctly 90.9% of the time, with two out of the 22 specimens misidentified as belonging to morph 1. Morph 2 was identified 80.8% of the time correctly, with morph 4 being the most commonly mistaken morph (11.5%) and morphs 3 and 1 each predicted once (3.8%). Morph 1 was the most poorly-predicted with only a 64.3% success rate, where the other five out of the 14 specimens are identified as morph 2. Following Larson and Currie (2013), hit ratios between 75–100% can be considered quantitatively distinct morphs, as opposed to Hammer and Harper (2006), who limit this threshold to 90% and above. Using either guideline, morphs 3 and 4 can be differentiated based on these measurements alone, while morph 2 can only be recognized based on the more liberal categorization. In neither case is the analysis sufficient to identify morph 1 using measurements alone. However, based on its inflated widths, denticle shape, and lack of a lingually-curved posterior carinae, it is sufficiently likely that morph 1 can be recognized based on qualitative characteristics. We tentatively accept the overall hit-ratio as indicative that indeed all four morphs are sufficiently different qualitatively to consider them separate taxonomic entities.

Size and inferred diet

The four morphotypes vary significantly in mean size, from 15.1 mm in morph 1 (5.2–34.7 mm) to 3.7 mm in morph 4 (2.1–7.6 mm), arranged into multiple size classes (Fig. 4). The results of a Kruskal-Wallis test shows that each of the four morphs have unequal medians, indicating that regardless of overlap between the smallest and largest teeth of any two morphs there is a distinct difference in size among the four species. This size diversity, would presumably, translate into differential trophic abilities for each morph.

The largest teeth from morph 1 are comparable in size to those of a small *Allosaurus fragilis,* an 8.5 m long Jurassic apex predator (Foster, 2007). Hypothetically, this morph would have been capable of feeding on varying sized prey, from large-bodied dinosaurs as well as the other, smaller morphotypes. Morph 2 has the next largest teeth, with crown heights (up to 15.7 mm tall) often exceeding those of *Deinonychus antirrhopus*, a 3 m long dromaeosaurid from the Aptian/Albian of North America (Brinkman et al., 1998), which possesses teeth rarely surpassing 12 mm in height (Smith et al., 2005). Strong evidence exists that *Deinonychus antirrhopus* habitually fed upon the large iguanodontian *Tenontosaurus tilletti* (Ostrom, 1969; Maxwell and Ostrom, 1995). This trophic relationship led to the widely touted hypothesis that, like modern canids, *Deinonychus* could have used pack hunting strategies to catch and dispatch large prey (Ostrom, 1986); although this hypothesis has recently been challenged (see Roach and Brinkman, 2007 for further discussion). Morph 2's superior size, as well as the possibility of pack hunting behavior, indicates that this species would have been a relatively uninhibited predator, though like *Deinonychus* it may have specialized in large ornithopod dinosaurs. Morph 3, unlike morph 1 or 2, would have faced more dietary limitations due to its small size. These small dromaeosaurids have teeth ranging from 1.7 to 7.6 mm tall, roughly equivalent to teeth from the 1 to 2 m long Late Cretaceous *Bambiraptor feinbergi* (Burnham et al., 2000). This small size likely limited this species to feeding upon smaller prey, such as baby dinosaurs, mammals, reptiles, amphibians, and fish. Even smaller still is morph 4, which was tentatively assigned to the genus *Richardoestesia.* This genus was originally named for lower jaws and numerous isolated teeth discovered in Campanian-age sediments of what is now considered the Dinosaur Park Formation of Western Canada (Currie et al., 1990). *Richardoestesia* teeth are thought to belong to a piscivorous species based on its elongate dentary, high tooth count, and straight crowns with reduced curvature and minute denticles (Currie et al., 1990; Longrich, 2008). Further, apical wear patterns on *Richardoestesia* teeth from the latest Cretaceous are consistent with a fish-eating diet (Longrich, 2008). Given what is known about this genus, it is possible that morph 4 had a diet similar to modern wading birds, consisting of fish as well as opportunistically feeding upon small mammals, reptiles, amphibians, and invertebrates (Kushlan, 1978; Bryan et al., 2012).

Taphonomy

Among the four depositional environments represented across the six microsites, there is a distinct difference in the relative abundances of the morphotypes. Unfortunately, small sample sizes at many of the microsites prevent a robust characterization of their respective assemblages. To address this limitation, sites were grouped and analyzed based on their inferred depositional setting (Table 1; Fig 5A). In the grouped data sets, specimens belonging to morph 1 are found in lower abundances than the other three morphotypes, making up approximately 14.3% (channel and floodplain) of the teeth across the environment, and never accounting for more than 16% from any single microsite. Conversely, teeth assigned to morph 3 are the most consistently abundant, composing between 31.9% (floodplain) to 58.8% (splay/floodplain) of the observed population. Unlike the previous two examples, fossils belonging to morph 2 are unequally distributed, and show a general trend of increasing in relative abundance moving distally from the channel. This morph only makes up 23.8% of channel deposit abundance, while composing 40.8% of the floodplain census. In direct contrast, morph 4 shows an increased relative abundance moving from the floodplain (12.9%) to the channel (28.6%), with the largest abundance in the splay/channel environment (35.4%). When constrained to only microsites with substantial sample sizes (Fig. 5B, C), morph 1 is about twice as common in the floodplain environment (V695; 15.6%) compared to the splay/channel (V794; 7.7%); while morph 2 teeth are more than three times as common in the floodplain (12.5% to 41.5% respectively). Morph 3 show little difference between the two sites (30.4% to 38.5%), and Morph 4 increase more than three-fold from the floodplain to the splay/channel (12.6% to 41.3%). These differences are significantly non-random ($\chi^2 = 40.57$, d.f. = 3, $P < 0.01$). Morph 1 and morph 3 are not skewed toward either depositional environment ($\chi^2 = 2.93$, d.f. = 1, $p > 0.05$; $\chi^2 = 0.89$, d.f. = 1, $p > 0.10$), while morph 2 are statistically more abundant in the floodplain (V695; $\chi^2 = 25.88$, d.f. = 1, $p < 0.01$) than morph 4, which are more abundant in the splay/channel (V794; $\chi^2 = 22.05$, d.f. = 1, $p < 0.01$).

Initial comparisons between the two microsites (V794 and V695) would seemingly indicate a bias based on size, possibly due to hydrologic sorting. To test this possibility, we looked at the distribution of teeth for the much more abundant goniopholidid crocodilians from both sites. In general, V695 (n=222) has the largest teeth (range from 0.85 to 30.43 mm, mean=6.16, median 4.36), while V794 (n=184) has the smallest (0.65 to 22.45 mm, mean=6.08, median=5.45). However, both sites show a strong bias toward the smallest teeth and neither site was found to be significantly different using either a Two-sample T-test for unequal variance (t=0.1753, p>0.10) or a two-tailed Mann-Whitney U-test (U=18600, z=-1.55, p>0.10). In contrast, the theropod data when pooled show a significant difference in size, where V695 (n=68) contains significantly taller teeth than V794 (n=53) (t=4.33; p<0.01) (U=869; z=-4.87; p=<0.01). This result, however, is unsurprising given the higher abundance of large (morph 1) theropod teeth at V695 relative to V794. To test for size differences within groups, we performed the same analysis for specimens of the most equally abundant theropod, morph 3 (n=25 for both sites). As in the goniopholidids, morph 3 shows a higher mean tooth height in V695 (4.50 mm) compared to V794 (4.07 mm); however, neither the T-test (t=1.15; p>0.10) nor the Mann Whitney U-test showed significant differences between these populations (U=244.5; z=-1.31; p>0.10). Although taphonomic sorting by size cannot be conclusively ruled-out as a cause of this distribution, these data and those by other authors (e.g., Goldberg, 2000) seemingly point to a more-complicated explanation than taphonomic bias alone for the observed distribution between sites.

An alternative hypothesis is that the distribution of theropods in these sites is controlled by stratigraphy, not by the environments in which these sites formed. Although all four morphotypes are found in the stratigraphically lowest (V868 and V695) and highest (V239) sites, the distribution may not be consistent. Indeed, relative abundance of V868 is more similar to V695, a site at the stratigraphically similar position, than it is to V794, a site reflecting the same depositional environment. Conversely, the stratigraphically equivalent V694, V235, and V794 vary in depositional setting, and show few similarities in their respective morphotype abundances; in particular with respect to morph 2 and morph 4. Given the small sample sizes from these sites (excluding V794 and V695) and their limited stratigraphic separation, it is difficult to explain the observed distribution based on the stratigraphy alone. Instead, we hypothesize that, at least in part, the distribution of the MM theropod morphotypes is a result of behavior by the organisms causing preferential burial in certain environments. This behavior is consistent with the morphology of each tooth type; such as an affinity for the channel in the hypothetically piscivorous *Richardoestesia* teeth (morph 4) and a penchant for floodplain settings in the proto-typical theropod teeth of the medium dromaeosaurid (morph 2). These findings also generally agree with modern ecological trends; such as the scarcity of large predators (morph 1) when compared with smaller species (such as morph 3).

Geochemical analysis

Stable isotope analyses of tooth-associated carbonate ($\delta^{13}C$ and $\delta^{18}O$) were conducted on all four morphotypes for both V695 and V794, as well as samples of small goniopholidid crocodilian teeth and rock matrix. The $\delta^{18}O$ values showed no statistical difference between morphotypes, but did differ between the matrix and all morphotypes at V794 ($P<0.05$) (Table 2). However, differences in $\delta^{13}C$ values between morphotypes are somewhat more significant (Table 3). Between the morphotypes in V695, morph 4 ($n=6$, mean $\delta^{13}C=-4.38‰$, $SD=1.15‰$) and morph 2 ($n=12$, mean $\delta^{13}C=-3.18‰$, $SD=1.07‰$) contrasted the most substantially (significantly different at $P<0.10$). Goniopholidids in V695 had mean values slightly more depleted than morph 4 ($n=10$, mean $\delta^{13}C$=-4.39‰, SD=1.09‰), followed by morph 3 (n=10, mean $\delta^{13}C$=-3.75‰, SD=1.41‰) and morph 1 (n=11, mean $\delta^{13}C$=-3.61, SD=1.29‰) respectively. In V794, goniopholids retain a relatively low mean average (n=10, mean $\delta^{13}C$=4.48‰, SD=0.66‰) that is significantly lower than all of the theropod morphotypes ($P<0.05$). Unlike in V695, however, morph 2 (n=8) has the lowest mean average (n=8, mean $\delta^{13}C$=-3.07‰, SD=1.52‰), followed by morph 4 (n=13, mean $\delta^{13}C$=-2.72‰, SD=1.66‰), morph 3 (n=10, mean $\delta^{13}C$=-2.38‰, SD=1.74‰), and morph 1 (n=7, mean $\delta^{13}C$=-1.93‰, SD=1.80‰), respectively. In all morphotypes, except morph 3, variance increased between the V695 and V794 analysis.

Although many factors could explain the high variability observed between analyses, we reject the hypothesis that the results are entirely a result of diagenesis. Mineral alteration has undoubtedly taken place to some extent, but we acknowledge that dietary, behavioral, ecological, and environmental factors can have likewise substantial effects on the isotopic signature of a given sample (see Fricke, 2007). For example, significant differences between the $\delta^{13}C$ and $\delta^{18}O$ of the matrix and the teeth, as well as the $\delta^{13}C$ of goniopholidid teeth and theropods in V794 show that the entire sample has not been isotopically homogenized by ground water replacement. In addition, the carnivorous theropods in this study have similar high $\delta^{13}C$ values as seen in previous studies of dinosaurs from the Late Cretaceous (Fricke and Pearson, 2008). Finally, comparisons with Suarez et al.'s (2012) phosphate isotope data set on the same microsite material (goniopholidid teeth from V794) show an offset of approximately +4.5‰ between the phosphate and carbonate phase $\delta^{18}O$, lower than the approximately +7‰ mean average difference obtained by Thomas and Carlson (2004) in hadrosaur tooth enamel from the Late Cretaceous, but nonetheless promising, given variation between sample and preparation in the two studies.

For herbivores, differences in $\delta^{13}C$ values are commonly derived from the base of the food chain, reflecting contemporarily by differences in photosynthetic pathways between plant types (C3 vs C4 carbon fixation). The Mussentuchit ecosystem likely lacked appreciable C4 producers and thus the majority of $\delta^{13}C$ differentiation at the base of the food chain would be caused by variation in the uptake and retention of CO_2. In this system, the differences between microsites may represent varying degrees of canopy cover. Closed canopy forests, in general, tend to exhibit lower carbon isotope ratios due to the effects of plant respiration and decomposition near the forest floor (van der Merwe and Medina, 1991). Carbon in tooth carbonate is derived from ingested organics and modified through fractionation based on the consumer's metabolic processes (Fricke and Pearson, 2008). These differences are further exaggerated with each step up the food chain, as predators will often increase by approximately one per mil in relation to their prey (DeNiro and Epstein, 1978). $\delta^{18}O$ in tooth carbonate is derived from ingested water and is variable based on the source of the water and the body temperature of the organism (Fricke and Pearson, 2008).

These data indicate that the theropods as a whole did not differ substantially in bulk diet or ingested water, though given their significant difference in size and shape, subtle isotopic variation between morphotypes are still worthy of discussion. $\delta^{18}O$ showed no noticeable trend, indicating that all organisms (here theropods and goniopholidids) used similar water sources. This is a relatively surprising result, since Suarez et al. (2012) found that theropods (mean $\delta^{18}O = 18.3 \pm 1.0‰$) in V794 had a relatively depleted phosphate $\delta^{18}O$ compared to goniopholidids (mean $\delta^{18}O$ =16.3 ±1.0‰) (Fig. 6). Differences in the relative stability of the phosphate mineral and the size classes sampled (only presumed immature crocodilians were sampled here) may explain the differences between studies. $\delta^{13}C$ had more interesting results, where goniopholidids were on average isotopically the most depleted. In modern environments $\delta^{13}C$ is reflective of relative environmental cover and trophic-level, meaning these small crocodilians were likely eating trophically-low organisms and/or organisms living in a well-vegetated environment. Modern young crocodilians all transition through a similar ontogenetic dietary progression, with the youngest individuals consuming a high degree of invertebrates, which is gradually replaced by a diet of fish (e.g., Wallace and Leslie, 2008), followed by (depending on the species and environment) an additional switch to a diet including mammalian and reptilian components (Blomberg, 1976). Isotopically, this is reflected in the tissues, as demonstrated by Radloff et al. (2012) in *Crocodylus niloticus*. Scute samples from individuals showed at least two transitions in $\delta^{13}C$ correlated with the length of the individual (SVL – length from tip of the snout to the end of the first scale row after the cloaca). The smallest animals hypothetically ate primarily invertebrates and showed a wide-ranging isotopic signature with a mean of approximately -21‰. This $\delta^{13}C$ trend decreased linearly as the animal grew to an average of -25‰ at approximately 130 cm in SVL, likely reflecting an increasing level of fish in the diet of these individuals. Finally, at 240 cm SVL, the $\delta^{13}C$ values dramatically increase to approximately -16‰, resulting from an increased diet of C4 consuming mammals with the onset of larger sizes.

If young goniopholidids were ecologically similar to living crocodilians, then we can assume that these depleted isotopic signals represent animals feeding on small, trophically-low, and possibly aquatic fauna (e.g., small fish and crustaceans). In V695, morph 4 has a similar mean and range $\delta^{13}C$ as the goniopholidid, implying a similar dietary type for both animals. In V794, morph 4 is more enriched than the goniopholidids, but still remains more depleted on average than morph 3 and morph 1, and further contains the most-depleted sample analyzed for any morphs (-6.4‰). Morph 2 shows the largest relative change between sites (from most enriched on average to least). Between the sites, the absolute differences are roughly equal for the goniopholidids (± 0.10‰) and morph 2 (±0.11), but more substantial for morphs 3 (±1.37‰), 4 (± 1.66‰), and 1 (±1.68‰). Ecologically, these differences can be explained by a shifting toward higher trophic foods for each of these morphs, a possible result of longer food chains in more aquatic environments. More interesting, however, is the observation that morph 2 is relatively depleted in environments in which it is poorly represented, possibly indicating a lack of dietary plasticity in this species and a reliance upon food sources more common in the floodplain setting. Though tantalizing as it may be to speculate on a behavioral basis for this disparity, caution will be taken here as not to over-interpret the isotopic results. Taken as a whole and given the high variability observed in these analyses, we interpret these results as suggestive, rather than indicative, of dietary niche partitioning between these theropods.

CONCLUSIONS

Piscivory is hypothesized to have been relatively common form of dietary partitioning in theropod dinosaurs. Many species of theropods have morphological features consistent with modern, fish-eating species; some to an absurd degree, such as the procumbent front teeth in the noasaurid *Masiakasaurus knopfleri* (Sampson et al., 2001). Evidence beyond morphological grounds is tentative, but supported for many of these species. For example, at least one specimen of the four-winged dromaeosaurid *Microraptor gui* preserves fish remains within its gut-region (Xing et al., 2013); however, other specimens preserve the remains of a mammal and a bird (Larsson et al., 2010; O'Connor et al., 2011), indicating that this species was a more generalist predator and not primarily feeding-upon fish. Spinosaurid theropods show the morphological adaptations and geochemical signal of an aquatic predator (Amiot et al., 2010). Indeed, gut contacts from the spinosaurid *Baryonx walkeri* preserve acid-etched fish scales, but like the previous example of *Microraptor*, *B. walkeri* also preserves the remains of a juvenile iguanodontian (Charig and Milner, 1997). Further, an embedded spinosaur tooth in a pterosaur vertebra indicates that this group would often feed on other prey items besides fish (Buffetaut et al., 2004).

Like these examples, the species investigated here do not show obligate dietary or behavioral patterns for a single prey item or environment. Instead we see subtle, but nonetheless diagnostic patterns associated with differing lifestyles. *Richardoestesia* teeth (morph 4) are by far the most distinct, with a preference for channel environments, and a variable isotopic signature consistent with an ^{13}C-depleted diet. In contrast, the medium dromaeosaur (morph 2) is found more often in floodplain settings, but only varies slightly isotopically depending on the environment in which it is found. Morph 1, the large theropod, shows low abundance in both environments and has a geochemical signal consistent with an animal high on the food chain. Last is morph 3, a small dromaeosaur, which is found in high abundances in all environments and maintains relatively diverse $\delta^{13}C$ values, typical of a small-bodied opportunistic predator.

Larger bodied species (such as morphs 1 and 2) have the lowest abundances near channel deposits. Although it is almost certain that these species would frequent any available water source at least temporarily, the data seemingly indicate that this was not a place of substantial tooth loss. One possible explanation for this distribution is that these large theropods were competitively excluded from the near-water settings by large-bodied gnathosuchian crocodilians. Some of these species potentially reached sizes over 5 m (Frederickson et al., 2017), and were some of the most commonly encountered vertebrate fossils found in the MM (Garrison et al., 2007). Alternative hypotheses ranging from poor pedal traction near water to overgrown hunting terrain could also be viable explanations for this distribution.

In summary, we have shown here that it is possible to recover an ecological signal in theropod fossils without the need for direct evidence from preserved stomach content or feeding events. Through morphological, taphonomic, and geochemical proxies, we recognize that at least one species of MM theropod (morph 4 - *Richardoestesia* sp.) habitually lived and fed in aquatic environments, presumably specialized for a diet of small vertebrates (Fig. 7). Previous hypotheses for piscivory in this species are tentatively supported, though an obligate diet of fish or aquatic organisms can likely be dismissed. Individually, these results may be inconclusive, but taken together the consistency of the three lines of evidence presents a strong case for niche partitioning in the MM theropod community.

ACKNOWLEDGEMENTS

The authors thank Steve Westrop and Roger Burkhalter for photographic assistance and Brent Tweedy for his help prepping samples for isotopic analysis. Partial funding for this project was provided by the Jurassic Foundation. Specimens were collected under the auspices of grants from the National Geographic Society (4761-91 and 5021-92) and National Science Foundation (BSR-8906992, DEB-9401094, DEB-9870173) to RLC.

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Table 1. Depositional environments used in this study. C = channel, C/S = channel/splay, S/F = splay/floodplain, F = floodplain. Data from Goldberg (2000) and Suarez et al. (2012).

Microsite	***868***	***794***	***695***	***694***	***239***	***235***
Dep. Env.	C/S	C/S	F	F	C	S/F
m below Dakota SS	8	15	19	15	4	15

Table 2. $\delta^{18}O$ data for all morphotypes, goniopholidid teeth, and matrix from both V695 and V794.

Morphotypes	*Microsites*	$N_{samples}$	*Min‰*	*Max‰*	*Avg‰ ±1σ*
1	V695	11	16.35	21.94	20.23 ± 1.56
	V794	7	19.84	21.42	20.83 ± 0.59
2	V695	12	19.12	21.35	20.46 ± 0.66
	V794	8	18.75	21.73	20.32 ± 0.89
3	V695	10	18.84	22.66	20.50 ± 0.99
	V794	10	19.29	23.13	21.02 ± 1.13
4	V695	6	19.61	21.29	20.16 ± 0.58
	V794	13	19.6	21.06	20.55 ± 0.50
Goniopholidid	V695	10	19.70	21.04	20.53 ± 0.44
	V794	10	19.99	22.54	20.82 ± 0.75
Matrix	V695	12	18.78	25.31	21.36 ± 2.11
	V794	6	16.6	20.23	17.81 ± 1.28

Table 3. $\delta^{13}C$ data for all morphotypes, goniopholidid teeth, and matrix from both V695 and V794.

Morphotypes	*Microsites*	$N_{samples}$	*Min‰*	*Max‰*	*Avg‰ ±1σ*
1	V695	11	-5.49	-1.65	-3.62 ± 1.29
	V794	7	-4.38	0.76	-1.93 ± 1.80
2	V695	12	-4.42	-1.24	-3.18 ± 1.07
	V794	8	-5.79	-1.38	-3.03 ± 1.52
3	V695	10	-6.30	-1.89	-3.75 ± 1.41
	V794	10	-4.47	-0.50	-2.38 ± 1.32
4	V695	6	-5.74	-2.69	-4.38 ± 1.15
	V794	13	-6.44	-0.20	-2.72 ± 1.66
Goniopholidid	V695	10	-5.99	-2.55	-4.31 ± 1.09
	V794	10	-5.33	-3.44	-4.55 ± 0.67
Matrix	V695	12	-12.24	-0.42	-6.05 ± 3.09
	V794	6	-18.76	-5.82	-15.95 ± 4.98

FIGURE LEGENDS

Figure 1. Map of the western interior during the Cenomanian (grey is highlands, green is lowlands, and blue is water) and a pullout of Emery County, Utah with the Mussentuchit Member exposure and microsites analyzed in this study. Based on maps and data from Cifelli et al. (1999) and Suarez et al. (2012).

Figure 2. Tooth morphotypes from the Mussentuchit Member. (A1-3) Morph 1, large theropod; (B1-3) morph 2, medium-sized dromaeosaurid; (C1-3) morph 3, small dromaeosaurid; (D1-3) morph 4, Richardoestesia indet.; (E1-3) morph 5, cf. Richardoestesia isosceles; (F1-3) Morph 6, Paronychodon indet.; (G1-3) morph 7, ?troodontid. Scale is 5 mm.

Figure 3. Discriminant function analysis (DFA) for the four most distinct, best-sampled morphotypes (morph 1 is blue, morph 2 is green, morph 3 is yellow, and morph 4 is red). Axis 1 and 2 account for 93.72% of the maximum discrimination. CH is crown height, BL is basal length, PD is posterior denticle count, and AD is anterior denticle count.

Figure 4. Size (in mm) of crown height for each tooth morphotype. Color scheme follows Fig. 3.

Figure 5. (A) percent composition for each morphotype in deposits identified as channel (n= 21, V239), splay/channel (n=124, V794 and V868), splay/floodplain (n=17, V235), and floodplain (n=147, V694 and V695); (B) pie chart showing the tooth composition of V695 (n=135; floodplain); (C) pie chart showing the tooth composition of V794 (n=104; splay/channel). Color scheme follows Fig. 3.

Figure 6. $\delta^{13}C$ max, min, and mean for four theropod morphotypes (1 through 4) and goniopholidids (G) in (A) V695 and (B) V794. Morphs 1, 3, and 4 show a significant increase in $\delta^{13}C$ between V695 and V794, while morph 2 and goniopholidids show no variation. Color scheme follows Fig. 3.

Figure 7. An artist's reconstruction of V794. Image by Maija Karala.

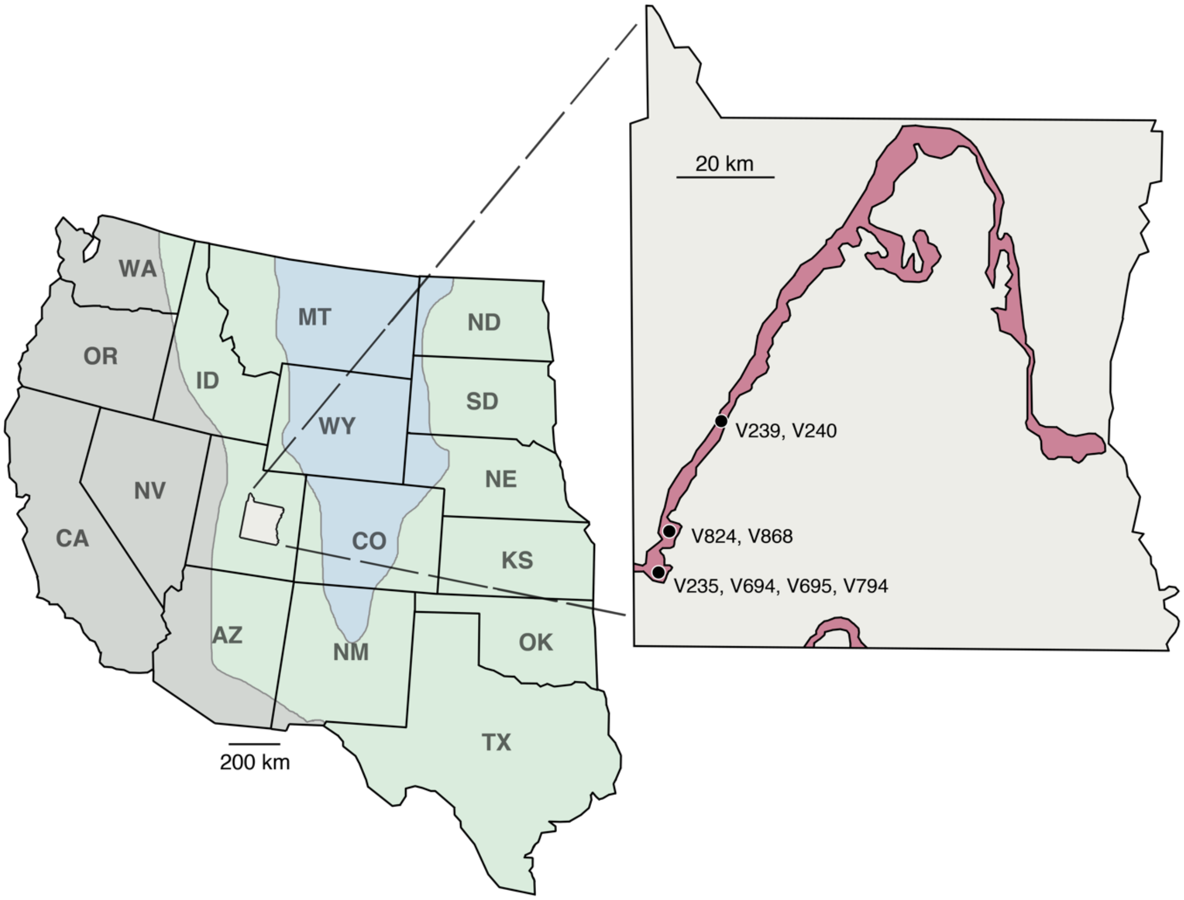

Figure 1. Map of the western interior during the Cenomanian.

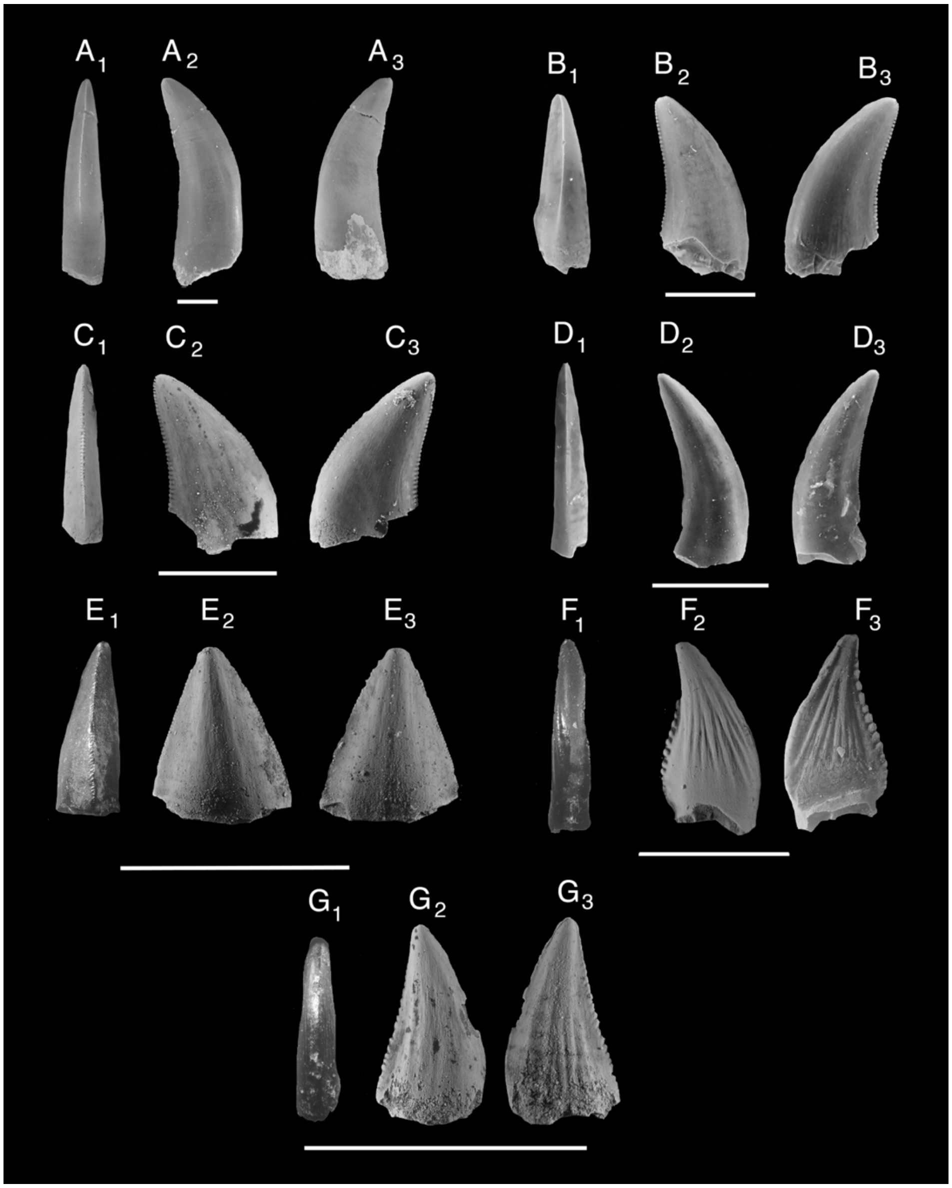

Figure 2. Tooth morphotypes from the Mussentuchit Member.

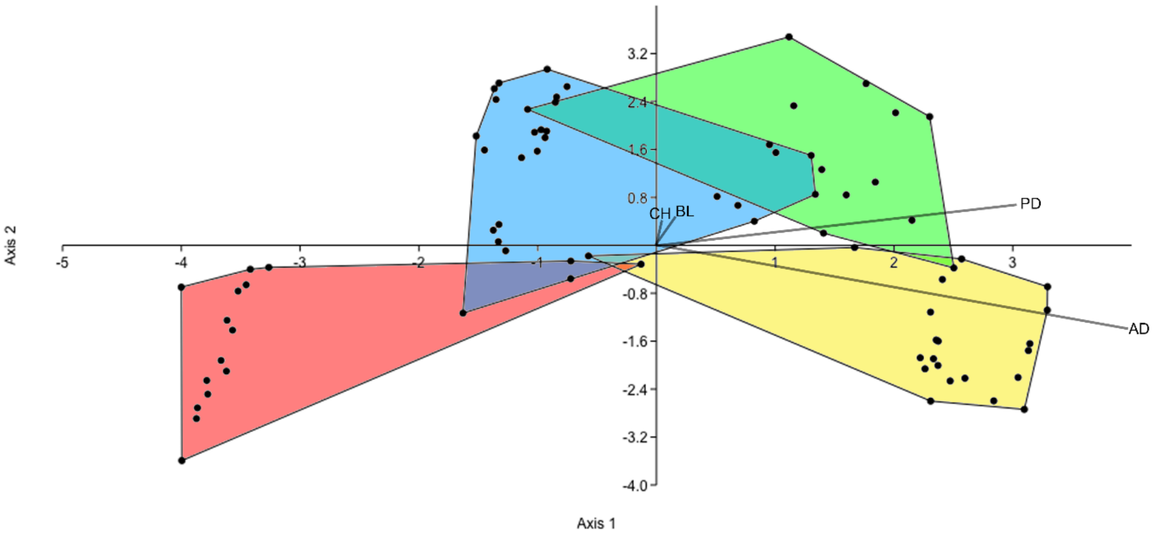

Figure 3. Discriminant function analysis (DFA) for the four morphotypes.

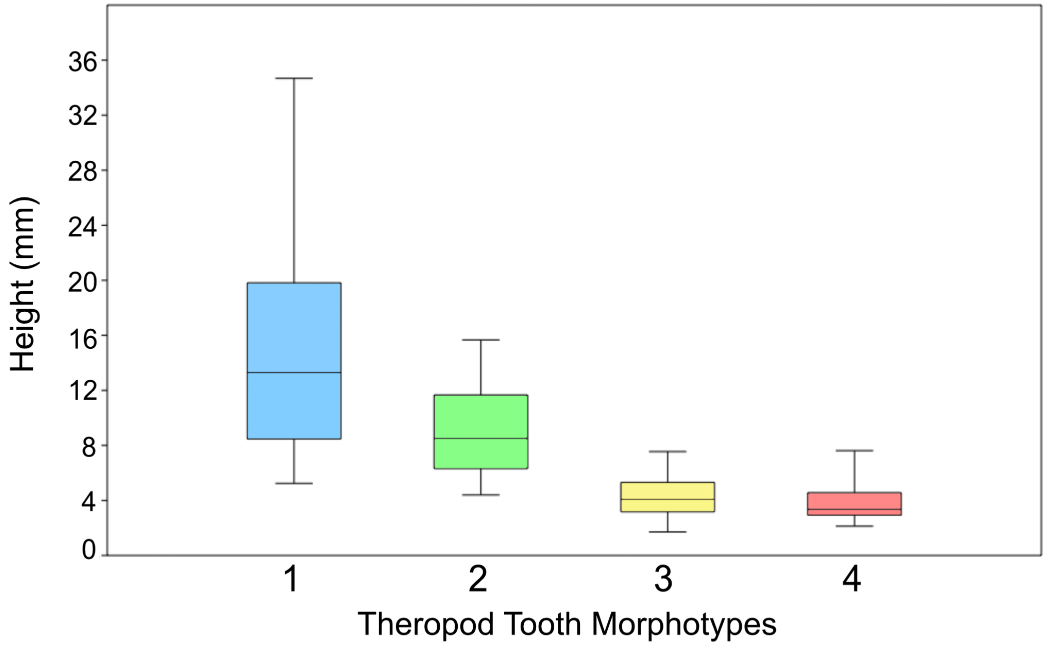

Figure 4. Size (in mm) of crown height for each tooth morphotype. Color scheme follows Fig. 3.

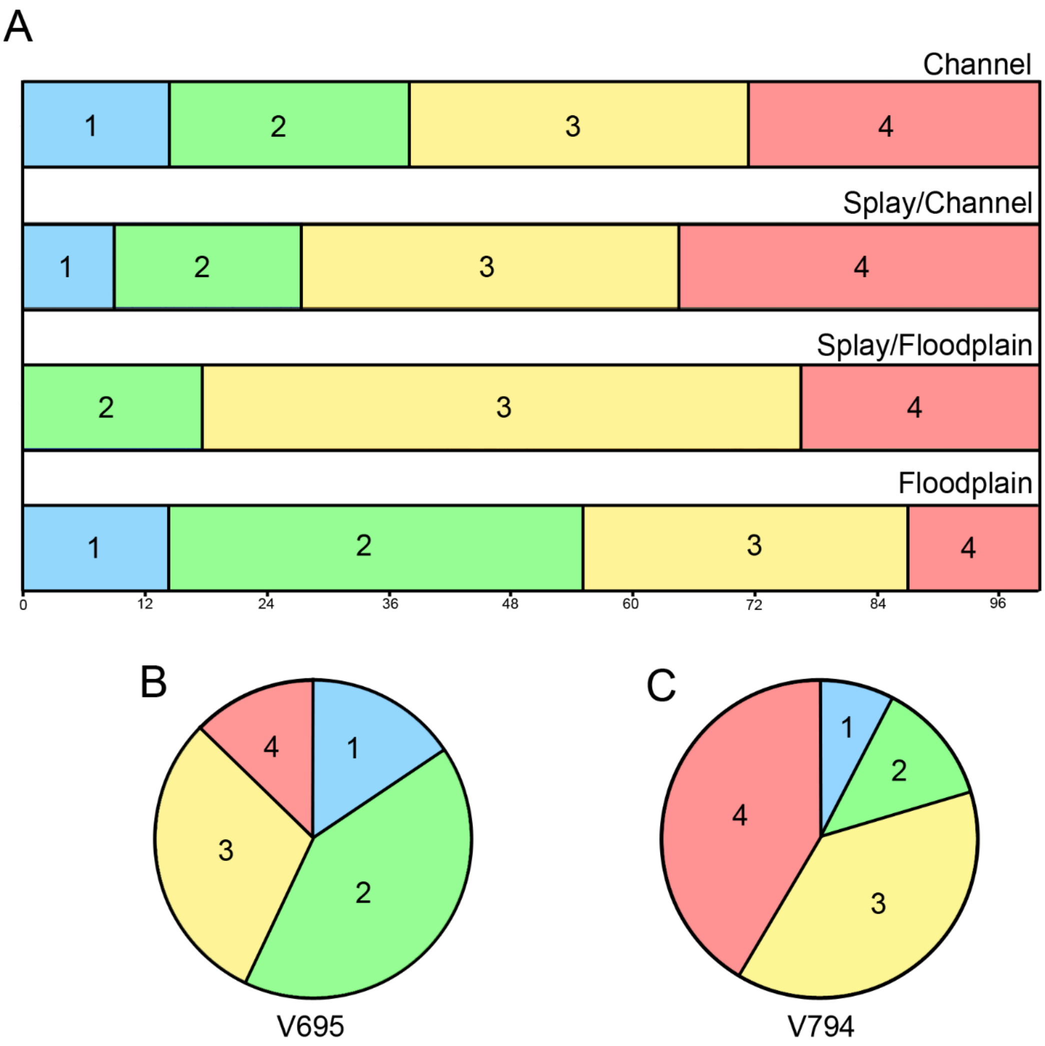

Figure 5. Taphonomic data from the MM microsites.

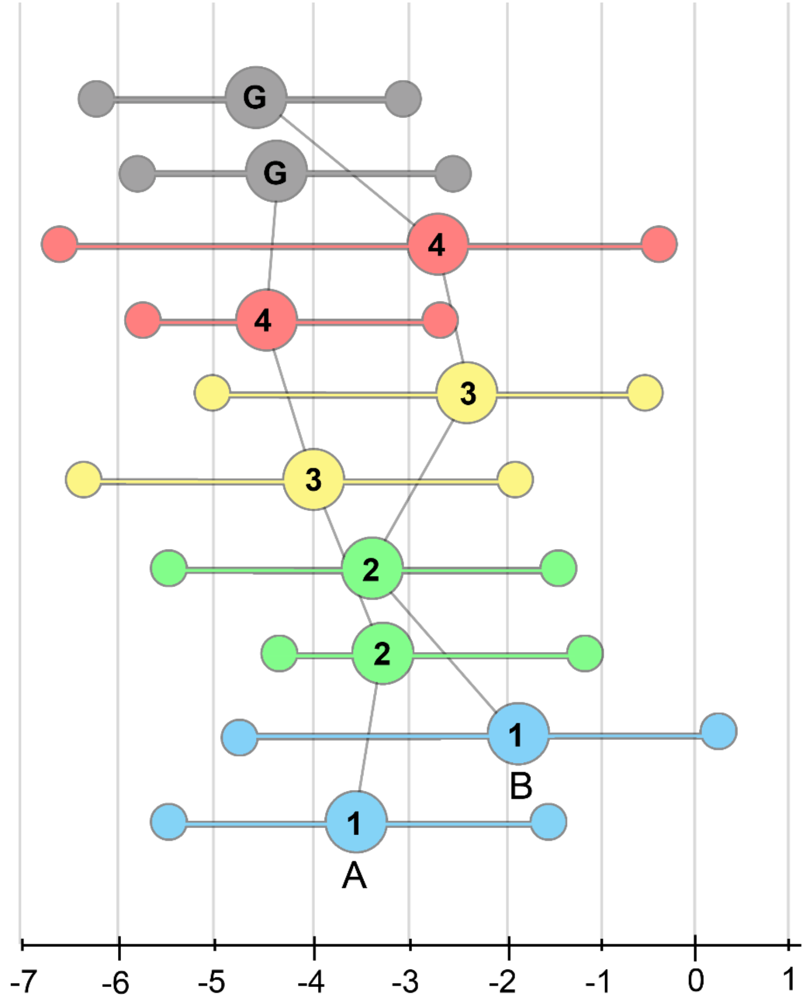

Figure 6. $\delta^{13}C$ max, min, and mean for four theropod morphotypes (1 through 4) and goniopholidids (G) in (A) V695 and (B) V794. Morphs 1, 3, and 4 show a significant increase in $\delta^{13}C$ between V695 and V794, while morph 2 and goniopholidids show no variation. Color scheme follows Fig. 3.

Figure 7. An artist’s reconstruction of V794. Image by Maija Karala.

CHAPTER III: GROWTH AND ECOLOGY IN *TENONTOSAURUS TILLETTI* OSTROM, 1970

Joseph A. Frederickson

INTRODUCTION

Tenontosaurus tilletti (Ostrom, 1970) was a dominant member of the Early Cretaceous ecosystem of North America. By far one of the most common large-bodied dinosaurs encountered in the Aptian-Albian aged rocks of the Antlers and Cloverly formations, *T. tilletti* has a fossil record represented by hundreds of specimens and over 30 partial to complete skeletons (Werning, 2012). These individuals come from both skeletally immature and adult individuals, with the smallest likely hatchling or yearling at the time of death (Forster, 1990a; Werning, 2012). The osteology of this species is well-known, with original descriptions by Ostrom (1970), and later supplemental descriptions of the braincase, post-crania, and skull (Galton, 1989; Forster, 1990b; Thomas, 2015).

The genus *Tenontosaurus* is represented by two species, the aforementioned *T. tilletti* and *T. dossi* from the sub-contemporaneous Twin Mountains Formation of Texas (Winkler et al., 1997). In the original description of the genus, Ostrom (1970) assigned *T. tilletti* to the family Iguanodontidae. This position has fluctuated, ranging from referrals to Hypsilophodontidae (Dodson, 1980; Weishampel, 1984; Norman, 1986) to the sister taxon to Iguanodontia (Butler et al., 2008; McDonald et al., 2010). Thomas (2015) recently reanalyzed the genus, upholding the two known species, and supporting the phylogenetic position as a basal iguanodontian.

Biologically, *Tenontosaurus* was a medium-sized herbivore reaching lengths over 6.5 m (Ostrom, 1970; Maxwell and Ostrom, 1995). Full-grown individuals are relatively rare, with the majority of the record composed of juveniles, subadults, and young adults (Werning, 2012; this study; Figure 1). The relative commonality of specimens and range of ontogenetic classes make *T. tilletti* a model organism for testing a hypothesis related to growth and ecology in herbivorous dinosaurs.

Since the difference in hatchling to adult size likely exceeds 2 orders of magnitude, it begs the question, how did these organisms manage such a dramatic transition? One such hypothesis has been proposed by a variety of authors and relates growth to diet in fast-growing dinosaurs. Nestling herbivorous birds and young herbivorous reptiles often supplement their diet with insects or small vertebrates (Ricklefs, 1983; Carpenter, 1999). The increased protein received from eating animal tissue helps speed growth in these young individuals, allowing them to reach the safety of large sizes faster than if their diet relied solely on plant material. For this same reason it can be hypothesized that herbivorous dinosaurs with fast growth rates, such as *Tenontosaurus* (Werning, 2012), may have also had more omnivorous diets as juveniles.

Before such a hypothesis can be tested, however, a consensus on the relative maturity of specimens must be established. In the first major description of the post-crania of the species, Forster (1990b) defined multiple characters that were ontogenetically variable across the entire skeleton. More recently, osteohistological approaches were performed on this species by (Horner et al., 2009) and Werning (2012). Unfortunately, overlap between these studies was minimal, meaning matching the histology to the skeletal changes was still not known. Here, I combine these data into a single hypothesis on the relative skeletal maturity of *Tenontosaurus* and use this arrangement to sample the most skeletally immature and mature specimens for dietary analysis.

Ontogeny background

The ontogeny of non-avian dinosaurs is of widespread interest to paleontologists because the life history of an organism can provide intimate details of an animal's biology. Unlike neontological studies, however, growth in fossils cannot be directly observed and thus must be inferred. To this end, paleontologists have often relied upon proxies such as the degree of fusion of skull bones and vertebrae, absolute size, bone surface texture, or the development of secondary display structures (such as frills or crests) to differentiate between immature and mature individuals. More recently, destructive histological sampling has become the standard technique employed to determine the age and relative maturity of dinosaurs. Although each of these techniques has benefits, all fail to unequivocally characterize growth through every stage of life, especially in an incomplete fossil record.

Major skeletal size changes are probably the most basic and easy to interpret ontogenetic indicators used in fossils. Working under the basic assumption that older individuals tend to be larger than smaller ones, size has been shown to be a reliable indicator in at least one dinosaur clade (Centrosaurinae; Ryan et al., 2001; Frederickson and Tumarkin-Deratzian, 2014). Bone fusion, the coalescing of two or more individual bones, has also historically been a prominent relative aging technique in fossil vertebrates. In dinosaurs specifically, many authors have used fusion of different parts of the skeleton, including the skull, pelvic girdle, and neural arches of the vertebrae to determine the relative maturity between specimens (Hone et al., 2016). An additional growth proxy is bone textural analysis applied to both the cranial bones and the long bones in dinosaurs (Brown et al., 2009; Tumarkin-Deratzian, 2009; Tumarkin-Deratzian et al., 2010; Frederickson and Tumarkin-Deratzian, 2014). this technique has also been used to estimate ontogenetic status in basal synapsids (Brinkman, 1988), pterosaurs (Bennett, 1993; Cohen et al., 2018), marine reptiles (Johnson, 1977), and modern archosaurs (Tumarkin-Deratzian et al., 2006; Watanabe and Matsuoka, 2013). This technique is essentially an external application of histology, a growing field in itself in dinosaur paleontology. Histology, analysis of the microstructure of bone, gives important information on the speed and duration of growth for animals (Chinsamy-Turan, 2005). Last, the presence of secondary display structures is commonly used as an indicator of adult status, as these features likely evolved for either species or sexual-display purposes (Padian and Horner, 2011).

Hypothetically all of these proxies could be used to judge growth, however, none of these individually work for the entirety of the vertebrate ontogenetic record. Size growth slows with age; bone fusion may reach a point where all synchondroses are completely obliterated or fusion may occur only late in life; bone surface texture is limited by the number of texture classes used; display structures only develop after the onset of maturity and may remain relatively stable through late life; and histology can be affected by significant resorption and variability between elements (see Hone et al., 2016 for a fascinating discussion on the shortcomings of these proxies). For this reason, individual ontogenetic proxies may be, at best, a coarse approximation of growth and at worst completely useless. More often than not, the estimates based on two proxies are roughly consistent, allowing development of an extended growth hypothesis. Even so, individual variation can complicate comparisons, making it difficult to distinguish a growth series without quantitative means.

In order to make sense of these multiple independent measurements of growth, a new technique was developed that used a cladistic methodology in order to arrange these growth changes into a single parsimonious hypothesis called an ontogram (derived from cladogram by Frederickson and Tumarkin-Deratzian, 2014) supported by synontomorphies (derived from synapomorphies by Frederickson and Tumarkin-Deratzian, 2014). Brochu (1996 and citations therein) first used this technique to order neurocentral fusion events in modern crocodilians. Since then this approach has been applied to variety of modern and extinct archosaurian taxa (Carr and Williamson, 2004; Tumarkin-Deratzian et al., 2006; Carr, 2010; Longrich and Field, 2012; Frederickson and Tumarkin-Deratzian, 2014). Since hypotheses on the *Tenontosaurus* growth record cover the gambit of body size, bone fusion, and histological data, a cladistic ontogenetic approach is highly appropriate for this species.

Stable isotope background

Dinosaur teeth, like those of other vertebrates, are composed of a matrix of organic molecules (such as collagen) surrounded by crystals made of bioapatite [$Ca_5(PO_4, CO_3)_3(OH, CO_3)$] and adsorbed inclusions (e.g., Pb, Sr, etc.). Most of the chemical constituents of teeth derive from an organism's diet, thus preserving an ideal record of an animal's ecology. Further, unlike bone and dentine, enamel tends to have large crystals, low porosity, and little organic matter making it resistant (though not immune) to diagenetic alteration (Koch, 2007). Far and away the most commonly analyzed components of dinosaur teeth are carbon and oxygen isotopes, usually derived from carbonate or phosphate in the enamel (e.g., Fricke, 2007; Fricke and Pearson, 2008; Suarez et al., 2010; Suarez et al., 2012). Carbonate (CO_3) is fairly abundant in teeth, readily substituting for the phosphate and hydroxyl in the bioapatite matrix. The carbon in the carbonate is derived largely from an animal's diet, which can vary isotopically based on the animal's lifestyle. Carbon isotope differences in diet begin at the base of the food chain with kinetic fractionation causing large negative shifts in the $\delta^{13}C$ in organic tissues (characteristic of most biological processes). Plants using different photosynthetic pathways (C3 vs. C4) transform CO_2 into organic molecules (such as carbohydrates) at with chemical weights. Fractionation in plant tissue occurs based on the efficiency of the plant at capturing and recycling atmospheric CO_2 and during the reduction of this CO_2 into organic molecules via enzymatic reactions. The dominant vegetation during the Cretaceous was C3 plants, which tend to vary in $\delta^{13}C$ between -32 and -21‰ compared to Vienna Pee Dee Belemnite (VPDB). This variability is a reflection of environmental conditions, where plants living in more arid, saline, or open landscapes tend to have more positive $\delta^{13}C$ values, because they must close their stomata more often to preserve water, thus trapping atmospheric CO_2 and forcing more of the heavy isotope to be used in the photosynthetic reactions (Fricke et al., 2007). At each step in the food chain, the $^{13}C/^{12}C$ ratio becomes more fractionated (usually enriching in the heavy isotope), the degree of which is based on the physiology of the digester. The largest offset in modern mammals occurs in ruminant herbivores. Although there has yet to be a sufficient explanation for why the metabolic processes of animals tend to enrich the tissue $\delta^{13}C$ relative to the dietary $\delta^{13}C$, some of the light isotope loss may be due to the production of CH_4 in the gut, which unlike CO_2, is preferentially enriched in the light isotope and is largely released from the body (Koch, 2007). Multiple studies on Late Cretaceous hadrosaur tooth $\delta^{13}C$ found that these organisms tend to have greater isotopic offset than modern herbivorous mammals (~18‰ in Fricke et al., 2008). These data may imply that these large-bodied ornithischians used a form of gut fermentation to digest low-quality plant material.

Oxygen isotopes in bioapatite are derived from ingested and atmospheric H_2O (Koch, 2007). Unlike carbon, oxygen isotopes reveal more about environmental preference than diet. Oxygen isotope ratios are controlled by both kinetic and equilibrium reactions, with the water source, climate, and geography dictating the ultimate $^{18}O/^{16}O$ ratio. Because terrestrial animals derive most of the oxygen in their tissues from ingested water, the factors controlling the abundance of ^{18}O in local water sources are of primary importance. Evaporation enriches bodies of standing water in the heavy isotope through the preferential vaporization of $H_2{}^{16}O$. This is a result of higher vapor pressure in the light isotope caused by the reduced mass of the water molecule. This fractionation is important, because animals drinking from sources prone to intense evaporation will be ingesting water that is isotopically heavy. Condensation and precipitation have the opposite effect. As atmospheric water cools, condensation occurs, preferentially forming liquid water with more of the heavy isotope. As the precipitation source moves further inland, to higher elevations, or to more northern latitudes, the atmospheric water will become more depleted in ^{18}O (Ufnar et al., 2002), because molecules containing the heavy isotope precipitate out faster than those that contain only the light isotope. This means that animals drinking from coastal ponds will have heavier values of $\delta^{18}O$ than animals drinking montane meltwater (which is depleted in the heavy isotope). One caveat to this pattern is that there is additional fractionation of oxygen within the animal, which is largely dictated by the physiology (namely the gut temperature) of the organism (Fricke, 2007). This means that in the present study, differences in $\delta^{18}O$ between young and adult tenontosaurs could either represent physiological or ecological differences between the ontogenetic classes.

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, NY; BB, Buffalo Bill Center of the West, Cody, WY; MOR, Museum of the Rockies, Bozeman, MT; OMNH, Sam Noble Oklahoma Museum of Natural History, Norman, OK.

METHODS

Reconstructing relative maturity

In order to determine relative maturity between specimens, I used a cladistic methodology first described by Brochu (1996; and citations therein) and later modified by Carr and Williamson (2004) and Frederickson and Tumarkin-Deratzian (2014). Due to the high prevalence of disassociation between cranial and postcranial material in the available sample, growth characters were limited to just those of the postcrania in order to better associate this data set with previous work by other authors. In total 58 growth characters were identified either through direct comparison or by the primary literature (Dodson, 1980; Forster, 1990b). Of these 58 characters only 32 could be coded for more than two individuals or multiple states could be recognized. These characters represent multiple different types, including fusion events, gross bone textural changes, and changes in bone shape. Character states were largely taken directly from the literature, but some were modified slightly to better fit dichotomy in the data set.

All specimens investigated were compiled in a data matrix using MacClade v. 3.0 (Maddison and Maddison, 2008), where the juvenile or nascent (primitive) state is scored 0 and the more mature (derived) state is scored 1 or higher. The juvenile state was determined using the smallest known individual (OMNH 10144) which becomes the *de facto* least mature individual. Given the drastic size difference between this and the largest individuals (which always show the opposite mature state) this coding is reasonable. For multiple characters that are not preserved in the smallest individuals, coding followed a basic set of generalities. First, bone fusion follows from unfused to completely fused. Though this pattern has been shown to be reversed in the skull of American alligators (*Alligator mississippiensis*) (Bailleul et al., 2016), this is likely an adaption to a macropredatory lifestyle and is almost unique among vertebrates. Other unobserved characters in the smallest specimens were coded based on a logical progression from more gracile to more robust (as seen in other bones). Though it is possible these characters could be miscoded, they would likely be been detectable in the final tree as character reversals. In addition, an artificial embryo and adult were added to polarize the characters following the procedure of Carr and Williamson (2004). The artificial embryo acts to fill in gaps missing from the actual specimens and to give the program a starting point of 0s for every character state. The artificial adult determines the axis of maturity by identifying which of the two most mature specimens is closer to this hypothetical individual.

Redundantly coded specimens were then removed from the analysis. This largely included specimens that were fragmented or lacking proper description, resulting in less than 30% of characters being coded. Since this unnecessarily adds to the length of the tree, these specimens were excised from the matrix. In total, 44 specimens were analyzed either firsthand or from the primary literature. Of these, 8 specimens were retained. These remaining specimens were the most complete, ranging from 34.4 to 93.8% of characters coded. Finally the analysis was executed in Phylogenetic Analysis Using Parsimony v. 4.0b (PAUP; Swofford, 1999) using an exhaustive search under both ACCTRAN and DELTRAN optimization with all characters unordered and equally weighted.

Additional ontogenetic maturity indicators

In addition to the aforementioned analysis, I made four *a posteriori* comparisons for the cladistic hypothesis of growth. The first used size estimates to test for correlation with increasing maturity. Here, femur length was used as a proxy for total size. I used two spearman-rank correlations to test against maturity. First, the femoral length was used for only specimens with at least one complete femur preserved. For the second, I used a ratio of femur vs. tibia or humerus (in cases with both humerus and tibia available, the number was averaged) to reconstruct missing data.

Histological changes were compared qualitatively to the maturity record using data from Horner et al. (2009) and Werning (2012). In this section, specimens were examined individually to assess how broad tissue changes relate to their placement on the ontogram. Next, tooth wear angle was measured in OMNH 10144 and 10132, the two specimens sampled for isotopic analysis. Tooth angles were taken using a small protractor to best approximate the angle between the wear facet and the tooth body on either side of the central cusp. Last, bone textural analysis was performed on a representative sample of *Tenontosaurus* bones from the OMNH collections following the procedure of Tumarkin-Deratzian (2009). In order to recognize textural types, photographs were captured at both the mid-diaphysis and lateral epiphyses using an Olympus Tg-4 camera with the microscope-mode and ring-light. Texture type was determined based on the best approximation of definitions by Tumarkin-Deratzian (2009). These specimens were compared with the length of the element using a Spearman Rank Correlation.

Stable Isotopes

To test for carbon and oxygen isotopes, two specimens (OMNH 10144 and 10132) were sampled for two teeth each. These teeth were cut using a mini Dremel saw with a serrated metal blade to separate into approximately equal occlusal and basal halves, and then sanded to remove as much dentin as possible without losing appreciable enamel. Ideally, samples would be 100% enamel; however, the enamel was extremely thin and inevitably dentin was also included with the samples (see previous chapters for justification). Thus I acknowledge that these data are the coarsest approximation for diet obtainable. Isotope samples were treated following a modified technique of Koch et al. (1997). Powdered specimens were first treated for one day using a 2% solution of NaOCl, washed five times with distilled water and then allowed to dry overnight, followed by a three-day treatment using 0.1 M acetic acid solution, rinsed 10 times with distilled water and allowed to dry for 3 days. The carbonate samples were analyzed for their stable carbon and oxygen isotope following the same procedure as described in chapter II. The resulting data were compared using an ANOVA with a Tukey's Pairwise Post-hoc test.

RESULTS AND DISCUSSION

A single most parsimonious tree (MPT) was recovered of 35 steps and CI of 0.97. The following growth stages were recovered from this ontogram and defined by 26 synontomorphies; 11 of which show no variation based on character optimization (Figure 2). Given that missing data can alter the placement of these characters, I erect seven growth stages based on these 11 characters, but present all 26 (in both ACCTRAN and DELTRAN optimization figurations) as supporting this tree topology (Table 1).

Growth Stages

<u>*Growth Stage 1*</u> – OMNH 10144.

In this stage, all characters are coded for the juvenile or nascent state. These individuals are characterized by having elongate (relative to the more mature individuals) lower legs, with tibiae and metatarsals being relatively longer than in later growth stages. In addition, the femur is more curved and the humerus has a relatively shorter deltopectoral crest. The exemplar for the stage is OMNH

10144, one of the smallest specimens of *Tenontosaurus tilletti* known. This specimen is actually composed of at least four individuals that were found together in association with the much larger OMNH 10132 (see below) from the OMNH’s V184 bonebed in the Cloverly Formation of Big Horn County, Montana (Forster, 1990a). Given the similarity in size and inability to differentiate the four individuals, I follow the convention of others (Forster, 1990b; Werning, 2012) and treat this juvenile group as a single specimen and discuss them as if they were a single individual.

Multiple other specimens, including AMNH 3022, OMNH 34785, and OMNH 53781 also fell into this stage (all zeros coding) but were removed for redundancy. Interestingly, these specimens range in size with OMNH 34785 and AMNH 3022, both from the Cloverly Formation, varying from 1.11 to 1.32x larger in femoral length than OMNH 10144; while OMNH 53781, from the Antlers Formation, is 1.75x larger. No specimens close to the size of OMNH 10144 are yet known from the Antlers Formation, a possible indication that nesting didn’t take place there.

<u>Growth Stage 2</u> – OMNH 63525

Stage 2 is the first to be supported by growth characters. At this stage, the scapula body begins to straighten, the humerus develops a noticeable and robust head, and the metatarsal shortens in respect to the femur (0.43% or less). The exemplar is OMNH 63525, a medium-sized individual from V706 Antlers Formation of Oklahoma. Based on femur length, this stage contains animals over 50% the size of the largest individuals. OMNH 63525 is relatively complete with 78% of characters coded and all of the major limb elements preserved. Only the sacral vertebrae and odontoid are missing or are too obscured to code with confidence.

Growth Stage 3 – BB1

Stage 3 is typified by an ulna with an obtuse angle between the cranial and lateral coronoid process. The growth stage is represented by BB1, a skeleton partially described by Forster (1990b) which is only slightly larger than OMNH 63525 (stage 2). This specimen preserves much of the animal, including parts of the skull, vertebral column, shoulder girdle, arm, hand, hip, and parts of the leg. In total, 53% of the specimen was coded in this analysis.

Growth Stage 4 – OMNH 34191 and MOR 682

At Stage 4, the caudal ilium border thickens, the ischium thickens distally and becomes longitudinally bowed, and the obturator process of the ilium becomes crescentic in shape. Two specimens OMNH 34191 and MOR 682 represent the stage. Individually under both optimization types, these specimens represent consecutively mature specimens with OMNH 34191 being the less mature of the two. However, the characters that defined the separation of MOR 682 are variable depending on the type of optimization. Since this is a result of missing data and not a reflection of character changes, I chose to collapse these two into a single stage. Based on femur length OMNH 34191 is only 88% the size of

MOR 682 leaving open the possibility that these stages could be split once more complete specimens are added to this matrix. Interestingly, OMNH 34191 is from V821 in the Antlers Formation of Oklahoma, while MOR 682 is from the Cloverly Formation. The discrepancy in size and maturity-level may reflect regional ontogenetic variation based on climate or nutritional differences between populations, if they were actually separated. More likely, however, this difference can be attributed to different degrees of preservation, as OMNH 34191 is only coded for 34% of characters, while MOR 682 has 81% coded.

Growth Stage 5 – OMNH 58340

Stage five continues the trend of modifying the forelimbs. At this stage the ulnar and radial condyles of the humerus become rugose and the radius distal condyle becomes square-shaped. The exemplar, OMNH 58340 is an immaculately preserved specimen from V821, first described in part by Thomas (2015). This specimen preserves an impressive, undistorted skull; the entire cervical, dorsal, and sacral regions; all arms, legs, manus, and pes; and part of the tail; allowing coding for 93% of characters in this study.

Growth Stage 6 – AMNH 3040

At this stage the Ilium develops a discrete supracetabular shelf. This stage is exemplified by AMNH 3040, the genotype specimen of *T. tilletti*. This specimen is relatively large, with a reconstructed femur length of ~54 cm or around 81%

the largest measured individual. Unfortunately, due to the composition only 38% of characters could be coded.

<u>*Growth Stage 7*</u> – OMNH 10132

This is the final growth stage, though more mature individuals likely exist but are only represented by scant material. At this stage the fourth trochanter of the femur becomes thickened. The exemplar, OMNH 10132, is a very large individual but still only represents 86% the femur length of the largest individual observed. However, at this point growth characters are hard to distinguish. OMNH 2526, an isolated femur with a length of 66.3 cm is the largest specimen identified. Other specimens redundantly coded with OMNH 10132 were MOR 2558, OMNH 62290 and OMNH 16563.

Ontogenetic trends

Based on the recovered ontogram, multiple growth trends can be reconstructed. As noted by Forster (1990b) the scapula in the least mature individuals has a concave dorsal border of the body and a caudal end that is straight and angled caudodorsally. By growth stage 2, this dorsal border straightens, while the caudal border doesn't become rounded or convex until sometime between the 3rd or 4th growth stage. Further, during the 6th to 7th growth stage, the scapula develops a well-defined rugose texture on the glenoid and caudal surfaces, as well as on the coracoid rostral edge. Finally, at this same time a large muscle scar for the m. biceps develops. A similar pattern can be seen in the development of the humerus, which grows a noticeable head at stage 2, rugose distal condyles at stage 5, and a relatively long (+50% length) deltopectoral crest with a deep medial groove at stage 6 or 7 (Figure 3). In the forearm, an increased angle between the cranial and lateral coronoid process develops at stage 3. At stage 5 the distal head of the radius becomes more square-shaped.

Like in the arm and pectoral girdle, the leg and pelvic girdle goes through multiple changes. At stage 2 or 3 the ischium becomes rugose and scarred distally; at stages 3 or 4 a dorsal bump develops on the ilium and a ventral kink develops on the pubis; the preacetabular process also begins to point ventrally at this stage. Next at stage 3, the Ilium border thickens, the ischium thickens distally and bows longitudinally on the distal end, and the obturator process extends out to take a crescentic shape. At stage 3 or 4, the sacral neural spines thicken and become rugose. Finally, at stage 6 the ilium develops a noticeable supracetabular shelf. In the leg, the first growth changes occur at stage 2 when the femur lengthens relative to the metatarsal. Next between stage 3 and 6 the femur lengthens relative to the tibia, exchanging as the longest element of the leg. At stage 5 the femur straightens and between stages 5 and 6 the greater and less trochanters begin to fuse. Finally, at stage 7 the fourth trochanter thickens.

Both the arm and leg show a general growth pattern that recapitulates the transition from small, fleet-footed basal ornithopods to larger quadrupedal iguanodontians. Basal ornithopods, like *Hypsilophodon*, share multiple characteristics with immature *Tenontosaurus*. In many taxa, the scapula is strap-like with an expanded distal and proximal end giving the element a curved appearance. Further the caudal end is often flattened and not circular, exemplified by *Hypsilophodon foxii* (Hulke, 1882). Even further, as in small *Tenontosaursus*, the deltopectoral crest composes 40% of the humerus length in many basal ornithopods, including *Heterodontosaurus tucki* and *Hypsilophodon foxii* (Norman et al., 2004). Similarities exist in the legs as well. The femur is slightly bowed in lateral view and the tibia exceeds the length of the femur in all basal ornithopods. The ilium is low primitively, and lacks the bump seen on the dorsal margin in *Tenontosaurus* (Norman et al., 2004).

These changes taken as a whole demonstrate a transition from a biped to quadruped. The changes of the pectoral girdle all seemingly point to an increase in muscle attachment area (muscle scar and rugose texture expansion) with maturity. In the forearm, shape changes in the radius and ulna likely relate to increasing the degree of rotation, and the expansion of the deltopectoral crest would accommodate added muscle for adduction of the forearms. Large deltopectoral crests are similarly present in other large quadrupedal dinosaurs such as ceratopsids and hadrosaurs. The general pattern of the hips and legs show an increase in robusticity and growth of the proximal elements relative to the distal ones. This implies an increase in muscle attachment and reduction of cursoriality.

Correlations with size

Size data for femur length for six of the individuals for five of the growth stages was compared using a Spearman Rank Correlation. The results show an R of 0.986 and a two-tailed value of $P<0.01$. Using reconstructed length from the relationship between humerus/femur and femur/tibia length, a Spearman Rank Correlation for all eight individuals and seven growth stages show an R of 0.994 and a two-tailed value of $P<0.01$. By any standard both of these results are statistically significant. At least based on this small data set, the postcranial changes are consistent with increases in body size as calculated by femur length (Figure 4).

Correlations with histology

Horner et al. (2009) and Werning (2012) investigated the osteohistology of *Tenontosaurus tilletti*. Fortunately, much of the material sectioned overlaps with the specimens included in this analysis, allowing for a moderate comparison of skeletal maturity to histological growth. OMNH 10144 (growth stage 1) was sectioned by Werning and deemed to be unequivocally a juvenile. Histological examination showed extensive bacterial invasion, obscuring much of the original tissues. No lines of arrested growth (LAGs) could be seen and where original tissue is present woven bone texture with simple vascular canals are visible; consistent with the small size of this material as a young juvenile.

Next, a tibia of OMNH 63525 (growth stage 2) was also sampled by Werning (2012). Largely the cortex is composed of woven bone with only a few instances of secondary osteons in the endosteal region. In total, five LAGS are observed with two of them being doubled. Given the limited remodeling and presence of juvenile tissues, it is likely that this animal osteohistologically represents a young subadult.

Growth stage 3 represented by BB1 has not been histologically sectioned. Growth stage 4 is represented though. Horner et al. (2009) sectioned a partial femur from MOR 682 and found possibly two dimly-lit lines of arrested growth (LAGs). In addition, they did not see any evidence for growth cessation (i.e., no external fundamental system was present) but secondary remodeling was locally extensive, indicating that this individual was a late sub-adult. Werning (2012) reanalyzed this sample and provided some additional information. The medullary cavity of this specimen is infilled with calcite, obscuring much of this cavity, however broken pieces of trabecular bone around these crystals are woven with simple canals, similar to those observed in perinatal and juvenile individuals. The other individual in this growth stage, OMNH 34191, was also sampled by Werning (2012). The ulna of this individual showed extensive secondary remodeling within the inner cortex and three LAGS, with the outer being a double LAG.

Growth stage 5, represented by OMNH 58340, was sectioned by Werning (2012). The tibia of this individual shows more advanced bone texture implying that this specimen represents an old subadult or young adult. The bone of the outer cortex shows greater organization, transitioning to lamellar bone near the outside. In addition, secondary remodeling in this individual extends into the mid-cortex and even into the outer cortex in some areas. Eight to nine LAGs are preserved, though more were likely present before being lost to the expansion of the inner cortex.

Werning (2012) sectioned only two specimens considered to be osteohistologically adult. These specimens, FMNH PR 2261 and OMNH 62990, were not kept in the present analysis because they were redundantly coded with OMNH 10132. FMNH PR2261 preserves nine LAGs in the humerus and seven in the ulna, though more may have been lost to tissue remodeling. OMNH 62990 preserves five to six LAGs in the ulna. More importantly, OMNH 62990 has an external fundamental system in the outer-cortex, indicating a dramatic slowing of growth associated with full skeletal maturity. These individuals also show a general pattern towards greater lamellar bone deposition in the outer-cortex and a general decrease in vascularity. OMNH 62990 is approximately the same size as OMNH 10132 (growth stage 7) based on ulna and humerus size. Given its large size and advanced skeletal maturity, it is probably safe to assume that OMNH 10132 would also show histological evidence of old age.

Bone Texture

The bone texture of four limb elements (humerus, ulna, femur, and tibia) was investigated for multiple individuals. Growth classes follow Tumarkin-Deratzian (2009) and can be seen in Figure 5. All bones show a strong correlation between periosteal stage and size (Table 2). No individuals completely reach stage 5 of periosteal maturity and stage 4 was not witnessed in the ulna of any specimen. This ontogenetic pattern precisely follows the hypothesis of skeletal maturity shown above. The least mature individual, OMNH 10144 (growth stage 1) has relatively smooth midshafts with pores present throughout and long-grained texture dominant on the epiphyses (n=3, mean stage=1). The next most mature individual, OMNH 63525 (growth stage 2) shows dimpled and porous texture on the mid-shaft and long-grained as well as fibrous tissue on the epiphyses (n=4, mean stage=2). The next specimen investigated was OMNH 58340 (growth stage 5) shows a combination of smooth, dimpled, and porous texture on the midshaft and dominant fibrous texture on the epiphyses (n=4, mean=3). Interestingly, this specimen seems to show the most intraskeletal variation, with the humerus characterized as texture stage 4, the ulna and femur coded as having texture stage 3, and the tibia as having texture stage 2. This variation was driven by the presence of long-grained bone on the epiphyses and the dominance of dimpled vs smooth texture in the midshaft. Finally, OMNH 10132 (growth stage 7) showed advanced periosteal textures, largely composed of smooth bone on the midshaft and fibrous or smooth bone on the epiphysis (n=4, mean=3.88). Variation occurs in the ulna, which is transitional between stages 3 and 4 due to the presence of more abundant long-grained texture on the epiphyses, as opposed to the rest of the long bones, which tend to be smoother (growth stage 4).

Ontogenetic dietary trends

Tooth wear has been shown to vary ontogenetically in hadrosaurids, possibly indicative of dietary differences. In the lambeosaurine *Hypacrosaurus stebingeri*, tooth shape changes from inclined and cup-like in neonates, to shearing teeth in subadults, and finally to a combination of slicing and crushing morphologies in the adults (Erickson and Zelenitsky, 2014). These authors suggested that these tooth-shape changes may correlate with ontogenetic shifts in diet, though they do cautioned that histological tissues in the teeth do not vary greatly between stages. Hadrosaurids, however, possess a highly derived dental battery that may require multiple developmental steps to fully grow. *Tenontosaurus* retains a more primitive dental arrangement, with only one active tooth per alveolus, and approximately one to two replacement teeth in the jaw. Teeth are replaced lingually in *Zahnreihen,* and are said to show uneven and concentrated wear within a single individual (Thomas, 2015).

Fully erupted teeth in large individuals show high degrees of wear (Table 3). OMNH 10132 has wear on 68% of its preserved teeth, with wear angles ranging from 60–82° with an average of 73.45° total (n=11; 60–82°, 77° average, n=6 for the upper teeth; 68–70°, 69.2° average, n=5 for the lowers). The earliest growth stage also shows wear, but not as dramatically developed as in the more mature individuals. OMNH 10144 has only 20% of its preserved teeth worn, with wear angles ranging from 61–74° and an average of 69.25° (n=4; 74° range and average, n=2 for the upper teeth; 61–68°, 64.5° average, n=2 for the lower teeth). Due to the small sample size for the smallest growth stage, little can be claimed for the few degrees of difference at this time.

In order to better reconstruct food and water ingestion, carbonate samples were analyzed for ^{13}C and ^{18}O isotopes. For both δ^{13}C and δ^{18}O there is a statistical difference between the matrix and that of the tenontosaurs ($p<0.01$ for both), but no significant difference between the two individuals (δ^{18}O $p=0.175$; δ^{13}C $p=0.796$). The error rate based on duplicates was greater for δ^{18}O (mean = 9.98%, n=4) than δ^{13}C (mean = 1.87%, n=4), meaning more variation likely exists between the data for oxygen than for carbon. Even so, this study is the first account of *Tenontosaurus* geochemistry and thus is deserving of more thorough discussion.

The δ^{13}C for the two specimens shows substantial overlap, with OMNH 10132 ranging from -12.94‰ to -12.20‰ and OMNH 10144 ranging from -14.52‰ to -12.86‰ (Table 4). This most-depleted value in OMNH 10144 is seemingly an outlier as the other readings all sit above -13‰. Since adults are presumably herbivorous and trophic increases normally move values in the positive direction (see background), the overlapping and somewhat more negative values of δ^{13}C in this juvenile indicates that young tenontosaurs had a very similar diet as the presumably herbivorous adults.

Similarly δ^{18}O does not show any statistical difference between the two growth stages. The juvenile ranged between -11.88‰ and -11.01‰, while the adult ranged from -13.42‰ to -11.37‰ (Table 5). On average juveniles are slightly more enriched in ^{18}O, but not substantially. Given the small sample size, these small differences can currently be disregarded but may prove important in a larger sample. Differences in ^{18}O uptake are related to the isotopic composition of digested water, as well as the internal temperature of the organism. Given the massive difference in size between these two individuals (see Figure 1), it is very probable that their water sources differed. Younger individuals may have ingested more water from smaller pools. Since these pools are affected more substantially by evaporation, they would become relatively-enriched in ^{18}O relative to larger water sources. Alternatively, it may be possible that juveniles and adults obtain differing amounts of water from food rather than from different meteoric sources. Body size and internal metabolic temperatures will also affect δ^{18}O ratios. If *Tenontosaurus* was poikilothermic, it could be envisioned that smaller individuals would go through more substantial shifts in temperature as compared to adults based on the thermal inertia related to surface area vs. volume decreases with ontogeny. Nonetheless, the lack of a significant difference and the relatively high error rate, mean that all of these hypotheses are tentatively less parsimonious than natural variation between two individuals with the same behavior and physiology.

Ulna rugosity

Werning (2012) noted the presence of an oval rugosity on the posterior side of the shaft of the ulna in OMNH 34191 (here growth stage 4). Werning (2012) noticed that this rugosity occurred in roughly half of all larger material in the OMNH collections and that it can be found in specimens from both the Antlers and Cloverly formations. Further, lacking other pathological features, Werning (2012) discounted the possibility that these rugosities are related to injuries. Indeed, pathological specimens are extremely rare among *Tenontosaurus* specimens, with only one described individual showing evidence of multiple healed injuries (Hunt, 2018). This rugosity was not witnessed in the least skeletally mature growth stages (1 OMNH 10144 and 2 OMNH 63525) or in the more mature growth stages 5 and 7 (OMNH 58340 or OMNH 10132). It can be seen, however, in the skeletally adult OMNH 62990 (here deemed stage 7 or above, based on size) and in growth stage 2 (represented by BB1). Though a definitive diagnosis of this rugosity cannot yet be made, it is reasonably certain that its presence is not dictated by ontogeny alone.

CONCLUSIONS

Ontogenetic reconstructions of skeletal maturity show consistency with multiple other proxies, including bone histology, bone texture analysis, and size. Though additional specimens and coding would likely create a more complicated tree topology (due to the inclusion of more individual variation), the current hypothesis can be used as a generalized formula for quickly determining the relative maturity of *Tenontosaurus* without the need for more detailed analysis. Furthermore, this study lays the groundwork for more intensive dietary analysis. The current isotopic work contained only two sampled teeth from two individuals, which happened to be the least and most mature specimens on the ontogram. Undoubtedly, more individuals will be discovered that fall on all parts of the ontogenetic spectrum and should be tested further for more detailed dietary changes with growth. At the very least, this study supports the consistency of multiple ontogenetic proxies and demonstrates that, in at least two contemporaneous specimens, by growth stage 1 (likely before the first year of life) individuals were capable of having the same diet as adult tenontosaurs.

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Table 1. Character transitions in growth stages for *Tenontosaurus tilletti* for Figure 2. Characters consistent between ACCTRAN and DELTRAN optimization are in bold.

Node	*ACCTRAN*	*DELTRAN*
A	• **Rostrodorsal edge of scapula straightens** • **Humeral head develops** • **Metatarsal length in respect to femur shortens** • Rugose and scarred distal ischium texture develops	• **Rostrodorsal edge of scapula straightens** • **Humeral head develops** • **Metatarsal length in respect to femur shortens**
B	• **Cranial and lateral coronoid process of ulna make an obtuse angle** • Dorsal bump on the ilium develops • Preacetabular process points ventrally • Kink develops on the prepubic blade of the pubis • Femur becomes longer than the tibia	• Rugose and scarred distal ischium texture develops • **Cranial and lateral coronoid process of ulna make an obtuse angle**
C	• **Caudal ilium border thickens** • **Ischium thickens distally and becomes longitudinally bowed** • **Obturator process of the ilium becomes crescentic in shape** • Intercentrum of axis becomes partially fused • Sacral neural spines thickened and rugose	• **Caudal ilium border thickens** • Dorsal bump on the ilium develops • Preacetabular process points ventrally • Kink develops on the prepubic blade of the pubis • **Ischium thickens distally and becomes longitudinally bowed**

	• Sacral neural spines thickened and rugose	• **Obturator process of the ilium becomes crescentic in shape**
D	• **Ulnar and radial condyles of humerus become rugose** • **Radius distal condyle becomes square-shaped** • **Femur straightens** • Greater and lesser trochanters begin to fuse on the femur •	• Intercentrum of axis becomes partially fused • Sacral neural spines thickened and rugose • Scapula caudal border convex • **Femur straightens**
E	• **Ulnar and radial condyles of humerus become rugose** • **Radius distal condyle becomes square-shaped**	• **Ulnar and radial condyles of humerus become rugose** • **Radius distal condyle becomes square-shaped** • Greater and lesser trochanters begin to fuse on the femur • Femur becomes longer than the tibia
F	• **Ilium develops a supracetabular shelf** • Odontoid completely fused to axis • Axis intercentrum completely fused • Axis neural spine completely fused • Scapula caudal edge and glenoid surface become rugose • Coracoid cranial edge becomes rugose and develops a large scar for M. biceps • Deltopectoral crest elongates to +50% length of humerus	• **Ilium develops a supracetabular shelf**

	and develops a large medial groove	
G	• **Forth trochanter of the femur becomes thickened**	• Odontoid completely fused to axis • Axis intercentrum completely fused • Axis neural spine completely fused • Scapula caudal edge and glenoid surface become rugose • Coracoid cranial edge becomes rugose and develops a large scar for M. biceps • Deltopectoral crest elongates to +50% length of humerus and develops a large medial groove • **Forth trochanter of the femur becomes thickened**

Table 2. Spearman Rank Correlation between bone texture class and size rank.

Element	r_s	***P***	***n***
Humerus	0.953	0.001	7
Ulna	0.916	0.001	8
Femur	0.971	0.001	6
Tibia	0.893	0.016	6

Table 3. Tooth wear for associated adult and juvenile *Tenontosaurus* specimens from the Cloverly Formation.

Specimen	***Tooth pos.***	***n***	***% worn***	***Avg. Wear angle***
OMNH 10132	U	12	0.83	77
	L	13	0.54	69.2
OMNH 10144	U	14	0.14	74
	L	6	0.33	64.5

Table 4. δ^{13}C values for adult and juvenile *Tenontosaurus* specimens from the Cloverly Formation.

Specimen	***n***	***Mean ‰***	***S. dev.***
OMNH 10132	4	-12.693	0.337
OMNH 10144	4	-13.253	0.852
Matrix V184	4	-24.998	1.895

Table 5. δ^{18}O values for adult and juvenile *Tenontosaurus* specimens from the Cloverly Formation.

Specimen	***n***	***Mean ‰***	***S. dev.***
OMNH 10132	4	-12.363	0.855
OMNH 10144	4	-11.588	0.404
Matrix V184	4	-14.18	0.183

FIGURE LEGENDS

Figure 1. Representative skeletons for OMNH 10132 (left) and OMNH 10144 (right). Skeleton reconstruction based on mounted specimens at the Sam Noble Oklahoma Museum of Natural History.

Figure 2. Ontogram showing the relative maturity of eight *Tenontosaurus tilletti* specimens as well as synontomorphies supporting each node.

Figure 3. Humeri of *Tenontosaurus tilletti* from four growth stages with character coding. Scale bar = 10 cm.

Figure 4. Graph of growth stage vs. femur length (as compared to the largest individual femur) in *Tenontosaurus tilletti*. Age is based on tibial LAG counts from Werning (2012).

Figure 5. Bone texture classes for *Tenontosaurus tilletti*. A. Femur, OMNH 34785; B. humerus, OMNH 63525; C. humerus, OMNH 58340, D. humerus, OMNH 58340. Images taken at 7x zoom.

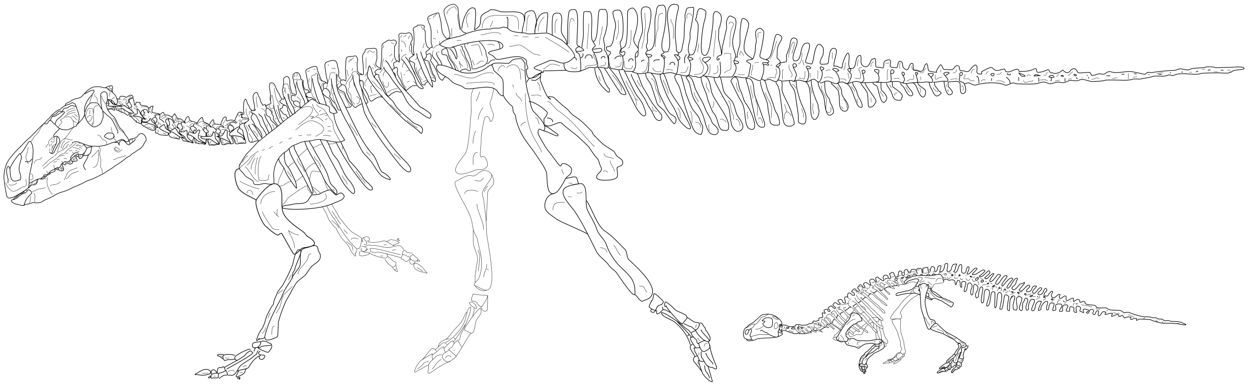

Figure 1. Representative skeletons for OMNH 10132 (left) and OMNH 10144 (right).

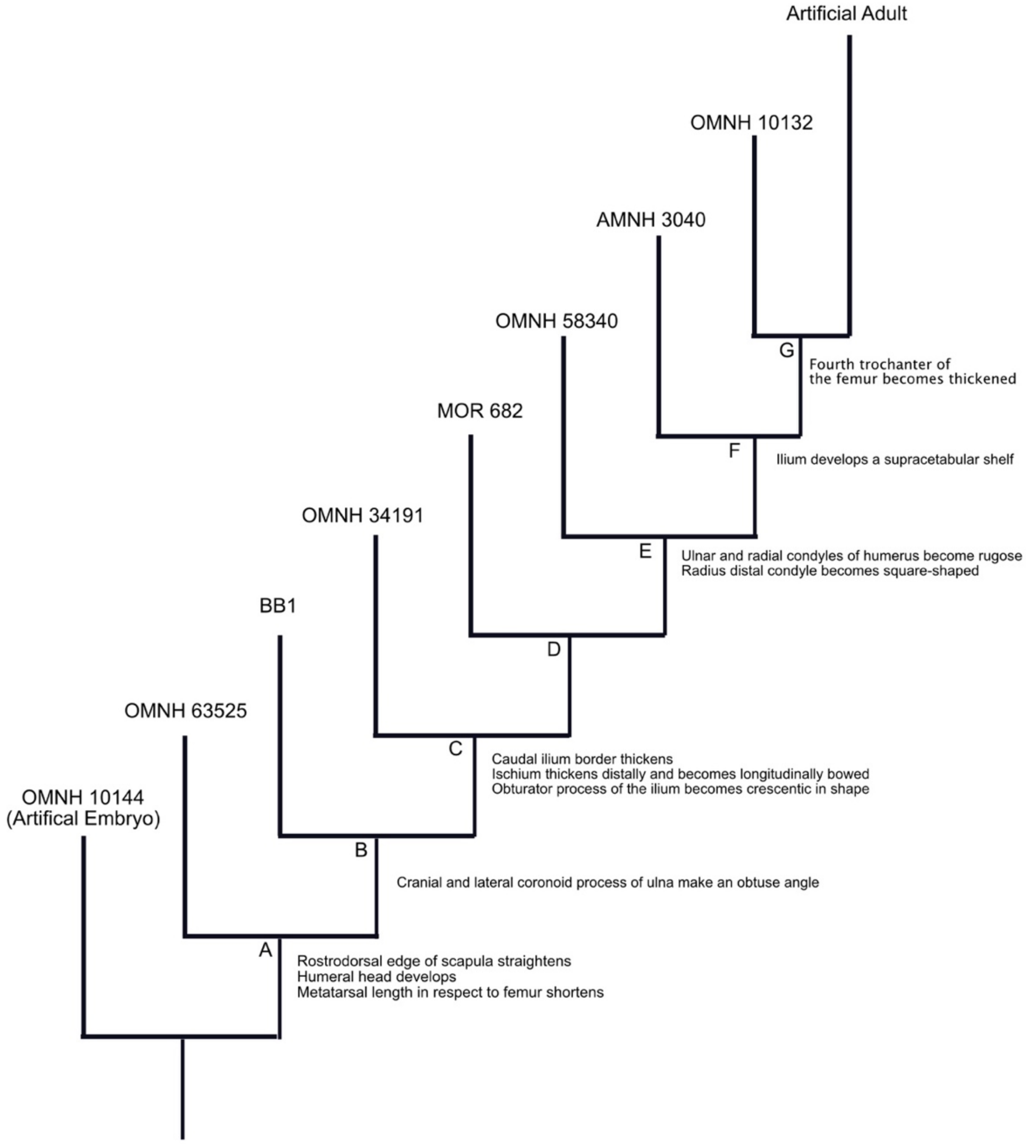

Figure 2. Ontogram showing the relative maturity of eight *Tenontosaurus tilletti* specimens as well as synontomorphies supporting each node.

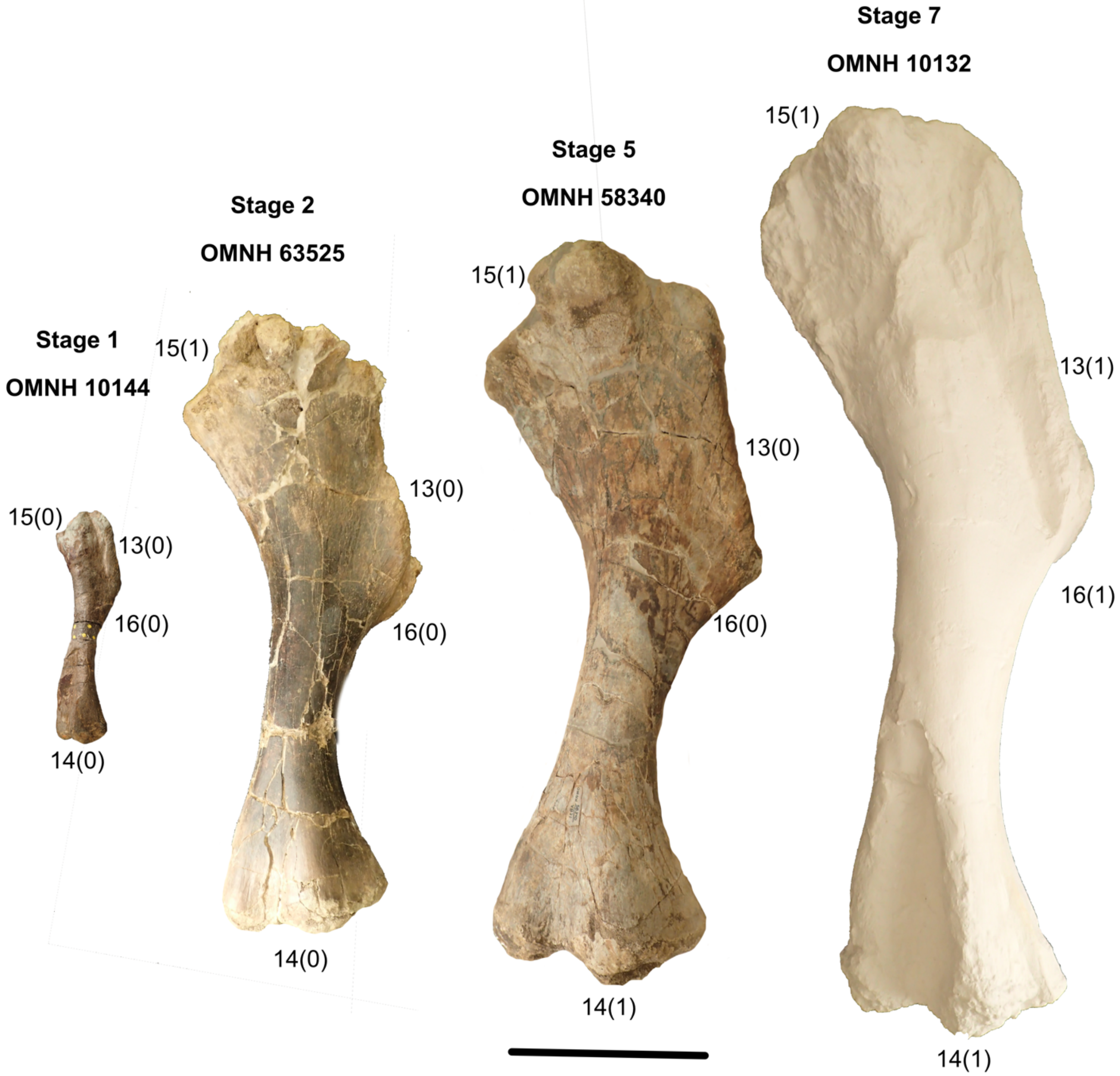

Figure 3. Humeri of *Tenontosaurus tilletti* from four growth stages with character coding. Scale bar = 10 cm.

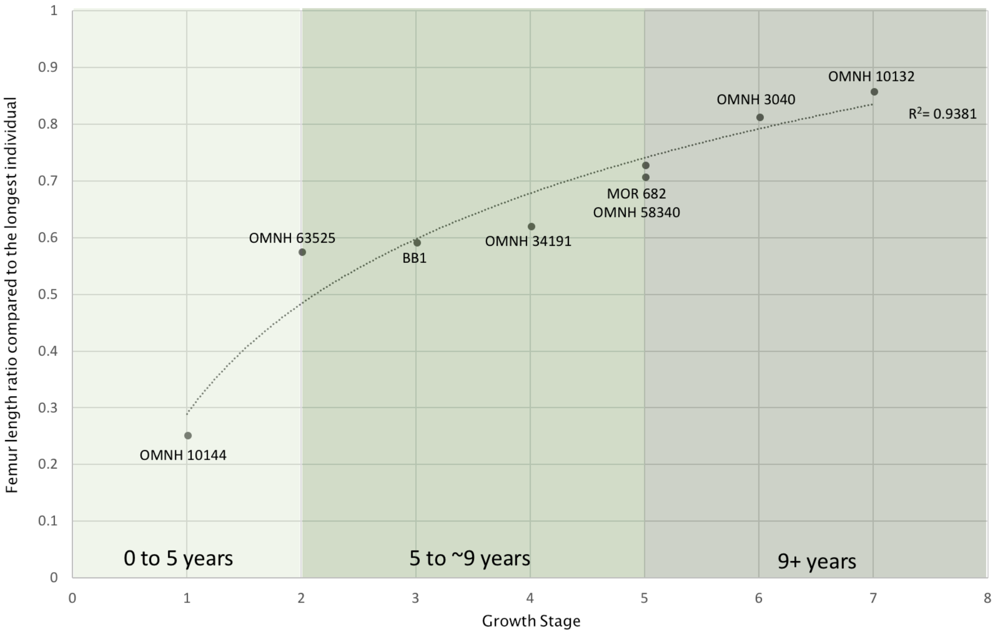

Figure 4. Graph of growth stage vs. femur length (as compared to the largest individual femur) in *Tenontosaurus tilletti*. Age is based on tibial LAG counts from Werning (2012)

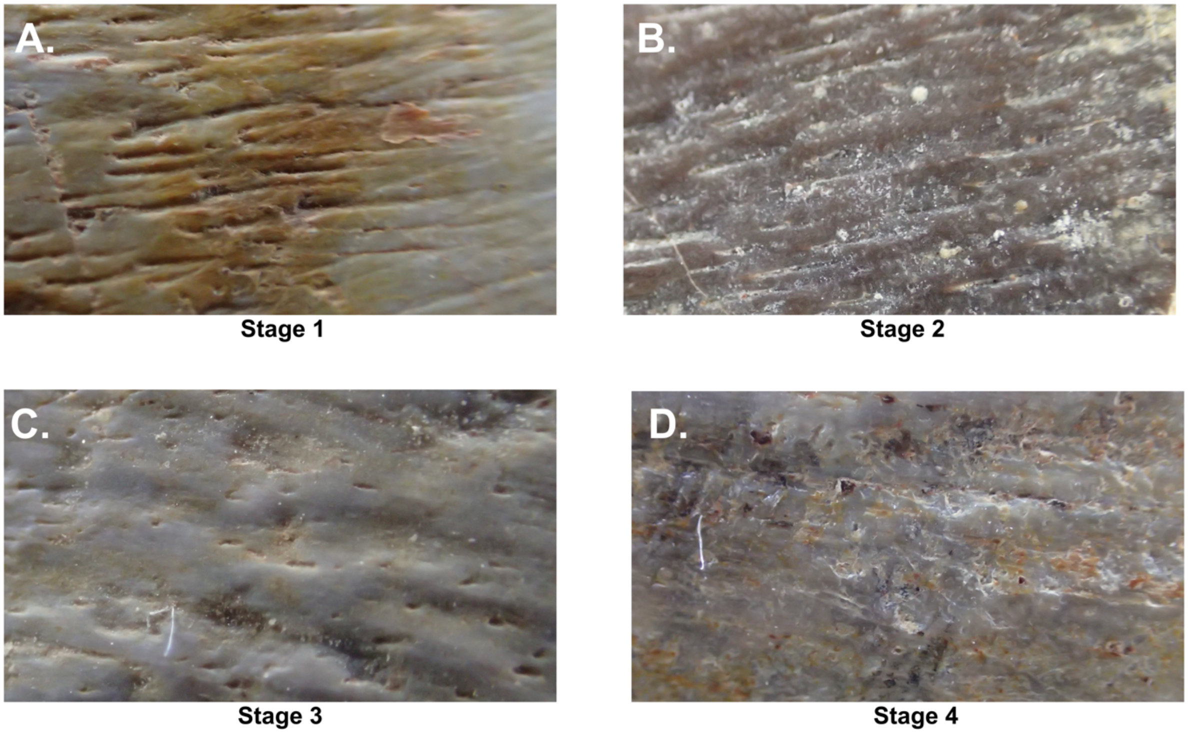

Figure 5. Bone texture classes for *Tenontosaurus tilletti*. A. Femur, OMNH 34785; B. humerus, OMNH 63525; C. humerus, OMNH 58340, D. humerus, OMNH 58340. Images taken at 7x zoom.

SUPPLEMENTARY DATA

Table 6. Bone textural classes used in this paper derived from Tumarkin-Deratzian, (2009).

Texture Class	***Midshaft Surface Characters***
1	Long-grained present Porous present Dimpled/grooved absent Isolated smooth areas
2	Long-grained present Porous present Dimpled/grooved present Isolated smooth areas
3	Long-grained usually absent Porous absent Dimpled/Grooved dominant Smooth variable
4	Long-grained usually absent Porous absent Isolated dimpled/grooved areas Smooth dominant

Table 7. Isotopic data for this analysis.

Sample	$\delta^{13}C$	$\delta^{18}O$
10144	-12.95	-11.85
10144	-12.68	-11.01
10144	-12.86	-11.61
10144	-14.52	-11.88
10132	-12.2	-13.42
10132	-12.76	-12.12
10132	-12.87	-12.54
10132	-12.94	-11.37
Matrix	-25	-14.01
Matrix	-23.82	-14.38
Matrix	-27.67	-14.04
Matrix	-23.5	-14.29

Table 8. Character list for ontogram.

1. Odontoid; fusion to axis: unfused (0), partially fused (1), completely fused (2).
2. Axis; intercentrum fusion: unfused (0), partially fused (1), completely fused (2).
3. Axis, neural spine, fusion to centrum: Unfused to partial fusion (0), complete fusion (1):
4. Sacral vertebrae; neural spines: smooth and not thickened (0), apex thickened and rugose (1)
5. Sacral vertebrae; neural spines, fusion: unfused (0), coalesced (1).
6. Sacral, fusion of centra to each other: unfused all (0), some fusion (1).
7. Scapula; caudal border, shape: flat (0) convex (1).
8. Scapula; rostrodorsal edge: concave (0), straight (1).
9. Scapula; caudal edge: smooth (0), rugose (1).
10. Scapula: glenoid surface: smooth (0), rugose (radiating lines) (1).
11. Coracoid: cranial and ventral border; texture: smooth (0), rugose (1).
12. Coracoid; scar for m. biceps: poorly developed (0); well-developed (1).
13. Humerus; deltopectoral crest, length: 49.9% or less (0), 50 or more (1)
14. Humerus, ulnar/radial condyle, texture: smooth (0), rugose (1).
15. Humerus, head: flat or poorly developed (0), well-developed (1)
16. Humerus, deltopectoral crest, caudal surface, groove: very shallow (0), well-defined (1).
17. Ulna, cranial coronoid process dorsal angle with lateral coronoid process angle: acute (0), obtuse (1)
18. Radius, distal head shape: elliptical (0), more-square (1).
19. Ilium, caudal border, lateral thickness: uniform (0); thickened (1) (thickened, makes a L with a rounded mass in middle at the caudal border in posterior view).
20. Ilium, supraacetabular shelf/rim: absent (0), present (1).
21. Ilium, dorsal border: (0) straight, noticeable dorsal bump at the postacetabular process (1)
22. Ilium, direction of the point of the preacetabular process: rostral (0), ventral (1)
23. Pubis; prepubic blade; ventral kink, presence: absent (0), present (1).
24. Ischium; shape; shaft: straight with only slight lateral or dorsoventral flare at the distal tip (0), abrupt ventral bend approximately two-thirds down the shaft accompanied by increased lateral thickening and flaring at the tip (1).
25. Ischium, shape, dorsal view: straight (0), bowed longitudinally (1).
26. Ischium, obturator process, shape: rounded (0), square or crescentic (1).
27. Ischium, distal texture: smooth (0), rugose and/or scarred (1)
28. Femur, greater and lesser trochanters, fusion: unfused (0), partially to completely fused (2).
29. Femur, 4th trochanter, size: small, finger-like (0), robust and thick (1).
30. Femur, shaft: bowed (0), straight (1).
31. Tibia; length in respect to the femur: longer or equal (0), shorter (1).
32. Tibia; length in respect to the femur: longer or equal (0), shorter (1).
33. Metatarsal III; length in respect to femur: 0.44 or large (0); 0.43 or smaller (1).

Table 9. Data matrix for coded *Tenontosaurus tilletti* specimens in the present analysis.

					5					10					15					20					25					30		
OMNH 10144	?	?	?	?	?	0	0	0	0	0	?	?	0	0	0	0	0	0	?	?	?	?	0	0	0	0	0	0	0	0	0	0
OMNH 63525	?	?	0	?	?	?	0	1	0	0	0	?	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	1
BB1	0	0	0	0	?	?	?	?	?	?	0	0	?	0	1	0	1	0	0	0	?	?	?	0	0	0	1	?	?	?	?	?
OMNH 34191	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	1	1	1	1	1	1	1	0	?	0	?	?
MOR 682	1	1	0	1	1	?	1	1	0	0	0	0	0	0	?	0	1	0	?	0	1	1	1	1	1	1	1	?	0	1	?	?
OMNH 58340	0	1	0	1	0	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0	1	?	1	1	1	1	1	1	?	1	1	1
AMNH 3040	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	1	1	1	1	1	1	1	0	1	?	?
OMNH 10132	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	?	1	1	1	1	1
Artificial embryo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Artificial adult	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

CHAPTER IV: ONTOGENETIC DIETARY SHIFTS IN *DEINONYCHUS ANTIRRHOPUS* (THEROPODA; DROMAEOSAURIDAE): INSIGHTS INTO SOCIAL BEHAVIOR IN RAPTORIAL DINOSAURS.

Joseph A. Frederickson, Michael H. Engel, and Richard L. Cifelli

INTRODUCTION

Pack-hunting in raptors is the most among the most prevalent hypotheses about the behavior of dinosaurs. The pack-hunting hypothesis was first proposed by Ostrom (1969), to explain the co-occurrence of multiple individuals of the dromaeosaur *Deinonychus antirrhopus* mixed with the larger hypothetical prey species, *Tenontosaurus tilletti* from the YPM 64-75 quarry from the Early Cretaceous, Cloverly Formation of Montana. Although a trophic relationship between these two species seemed certain, Ostrom (1969; 1986) could not envision a single *Deinonychus*, weighing approximately 70 to 100 kg (Seebacher, 2001), being capable of dispatching a one-ton *Tenontosaurus* alone (Ostrom, 1969; Forster, 1984; Maxwell and Ostrom, 1995; Roach and Brinkman, 2007). Based on the taphonomic associations of at least three individuals at YPM 64-75, he proposed that *Deinonychus* was a pack hunter, similar to modern canids. Since then, dozens of sites have been discovered with associated *Tenontosaurus* and *Deinonychus* remains in both the Cloverly (Maxwell and Ostrom, 1995) and the contemporaneous Antlers Formation of Oklahoma (Brinkman et al., 1998). The prevalence of this association almost certainly suggests that *Tenontosaurus* was a chief food source for *Deinonychus* (Ostrom, 1969; Forster, 1984; Maxwell and Ostrom, 1995), however, the dynamics of *Deinonychus* hunting capabilities are still hotly debated.

Ostrom's (1969; 1986) suggestion that *Deinonychus* had a canid-like pack-hunting strategy, is rather intuitive. *Deinonychus* was certainly morphologically similar to canids in some of its predatory adaptations, characterized by cursorial, elongate limbs, specialized for speed and agility (Ostrom, 1969). Further, this species possessed a relatively large brain by dinosaurian standards (Balanoff et al., 2013), a necessary prerequisite for handling the cognitive challenges associated with social structure. Even Ostrom's (1969) original evidence based on the *Deinonychus*-*Tenontosaurus* size differences is a highly reasonable suggestion, as this predator/prey size disparity is not unlike that of many wild canids, including the African Wild Dog *Lycaon pictus*. These 20-25 kg predators work in small to medium-sized groups to capture and kill prey up to 200 kg in size. These tactics are highly efficient, with a success rate up to 85% in some populations, where group size is correlated with an increased success rate, shorter hunts, increased prey size, and increased prey yield. In addition to benefits related to hunting, larger groups increase the ability of the pack to steal carcasses from other predators as well as provide greater protection for their pups (Creel and Creel, 1995).

The most substantial refutation of the *Deinonychus* pack hunting hypothesis came from Roach and Brinkman (2007), who upon re-evaluation of YPM 64-75, found evidence that at least one of the *Deinonychus* was killed by conspecifics. These authors go on to note that cooperative behavior in modern archosaurs is relatively rare and that a more suitable analog should be used to approximate *Deinonychus* behavior. Indeed, modern crocodilians show only the most rudimentary forms of cooperation during hunting (Pooley and Ross, 1989). In birds, group coordination is more common, yet pack hunting large-bodied prey is almost non-existent. In the few notable species that do practice cooperative hunting, close kinship bonds and extreme environmental conditions may contribute to this atypical behavior (McIlhenny, 1939; Buckley, 1999; Roach and Brinkman, 2007; see chapter I). Given these differences, Roach and

Brinkman (2007) hypothesized a lifestyle for *Deinonychus* more similar to the modern Komodo dragon *Varanus komodoensis*, a highly asocial species capable of hunting prey much larger than itself. Even though multiple individuals congregating around a kill is common in this species, a strict hierarchical feeding structure is followed based largely on size. Smaller lizards must wait on the periphery, while the youngest individuals are excluded altogether, forcing these animals to rely on a different food source than the others (Auffenberg, 1981; Diamond, 1992). It is this pattern between the diet of young and old agonistic species that we believe holds the key to understanding *Deinonychus* social behavior.

Like in *V. komodoensis*, ontogenetic dietary changes are widely documented in modern animals and are especially common in organisms that are gape-dependent feeders (Werner and Gilliam, 1984a). For example, juvenile crocodilians are incapable of killing the larger prey species favored by adults, and scavenging is often too dangerous because older individuals will often cannibalize the young (Grigg and Kirshner, 2015). Instead, young crocodilians go through a transition during ontogeny, initially consuming mostly invertebrates and gradually replacing this with a diet of fish, followed occasionally by an additional switch to large-bodied terrestrial or semiaquatic vertebrates (Blomberg, 1976; Wallace and Leslie, 2008). Conversely, pack hunting eusocial mammals do not show such diversity in diet through ontogeny. In these animals, such as the Grey Wolf (*Canis lupus*), the protection of the pack allows all members to feed upon similarly sized prey items (Bryan et al., 2006). Although small deviations likely occur, the bulk diet of juveniles can be hypothesized to derive largely from the diet of the rest of the group. This can be visualized in ontogenetic studies of dietary-derived carbon isotopes in the social bottle nose dolphin *Tursiops truncatus*, in which besides a small enrichment while nursing, there is minimal variation throughout life (Knoff et al., 2008). Unfortunately, due to the unique lifestyle of marine mammals, many of the isotopic studies of diet and growth are unsuitable for comparison with terrestrial dinosaurs.

More appropriately, isotopic studies of ontogenetic differences in birds are largely correlated with the parental feeding behavior. In some marine seabirds, such as some procellariiforms, adults feed the young a different diet than their own, leading to isotopically lower dietary signal in the juveniles; however this observation is based on relatively small differences and is not seen in all seabirds (Kojadinovic et al., 2008). Even still, this phase of life is relatively short-lived in modern birds, as most altricial young grow rapidly (Varricchio and Jackson, 2016). Conversely, non-avian dinosaurs likely had multi-year growth rates, increasing the potential for differing dietary signals with maturity. Even in fast-growing birds, however, these dietary differences can extend beyond the nestling phase and can be directly attributed to the hunting behavior differences between age classes. White-tailed eagles *Haliaeetus albicilla* , for example, show marked differences in the isotopic composition of fully-sized but immature individuals as compared to mature adults. The difference is likely attributable to the better hunting experience, range defense, and dietary diversity in mature birds (Soutullo et al., 2006).

By looking at the ontogenetic dietary pattern, we believe a rough approximation of social structure can be distinguished for medium to large-bodied carnivorous vertebrates. In this hypothesis, the canid-style pack hunting hypothesis of Ostrom

(1969; 1986) is represented by an organism with a dietary pattern that is relatively unchanging between juveniles and adults; while the Komodo dragon-style asocial hypothesis of Roach and Brinkman (2007) is found in a species that changes abruptly between small and large individuals (Figure 1). Here, we use stable isotope analysis as a proxy for diet to test for ontogenetic niche changes in *Deinonychus* teeth derived from two separate microsites in the Antlers Formation of Oklahoma and the Cloverly Formation of Montana.

METHODS

Teeth from two roughly contemporaneous OMNH microsites, V706 from the Antlers Formation of southeastern Oklahoma and V1075 from the Cloverly Formation of southcentral Montana (see supplementary information), were sorted for complete and diagnostic *D. antirrhopus* teeth. These teeth were identified based on their (1) lateral compression, (2) greatly enlarged posterior denticles (as compared to the anterior denticles), and (3) apically-curved denticles on the posterior margin. Specimens were then measured using photographs and ImageJ software for crown height, basal length, basal width, and the degree of curvature from the gumline to the apex of the tooth. Between the populations crown height was found to be significantly different using a t-test ($t=2.14$; $p=0.0176$), with teeth from the Antlers Formation being slightly larger (9.42 mm) than those from the Cloverly Formation (7.50 mm). There was no difference based on gum line angle (avg. 54.87° to 54.01°) ($t=-0.41$; $p=0.341$), indicating that there may be a size bias between sites independent of tooth position. Using images of *Deinonychus* and the closely related *Velociraptor mongoliensis* from Ostrom (1969) and

Norell et al. (2006), we determined that in a single specimen, near fully-erupted teeth differ in crown height by less than 50% regardless of tooth position, meaning that teeth that are 2x the size of others are unlikely to come from the same individual (Table 1). A representative sample was chosen composed of specimens falling into two bins equally, < 4.5 mm and > 9 mm in crown height, each with five teeth (Table 2). Specimens were chosen to best fill equally into the two bins; specimens were then subject to a Grubbs outlier test for gum line angle and crown width/height, those shown to be outliers were specifically excluded from the study. Last, comparisons were made to a similar sample of goniopholidid teeth from V1075 (three bins of <5 mm, 5–10 mm, and >10 mm). These neognathosuchians likely went through ontogenetic dietary shifts similar to modern crocodilians (see above), thus making them an ideal control within one of the same formations for the isotopic analysis. Teeth were sampled and treated following a modified technique of Koch et al. (Koch et al., 1997). Enamel was separated from the teeth to the best ability of the authors. To counter the effects of pedogenic carbonate intrusion, specimens were powdered and treated for one day using a 2% solution of NaOCl, washed five times with distilled water and then allowed to dry overnight. This was followed by a three-day treatment of 0.1 M acetic acid solution, after which samples were then washed 10 times with distilled water and allowed to dry for three days. The rest of the sample preparation and execution follows the procedure outlined in chapter II.

RESULTS AND DISCUSSION

Goniopholidid diet

Cretaceous goniopholidid crocodylians, like their modern counterparts, showed a distinct transition in diet with increased growth (Figure 2). Teeth smaller than 5 mm in height, are relatively enriched (mean=-9.32, SD=1.35, n=5) in ^{13}C, with only one specimen showing depletion overlapping with the next size class. The medium teeth (6 to 10 mm in height) are more depleted (mean=-11.20, SD=0.84, n=5) and show less variance than the other two size classes (V=0.701). The largest class (10.1+ mm crown height, n=6) are intermediate in ^{13}C values between the previous two classes (mean=-10.12, SD=1.20). An ANOVA with a Tukey's pairwise test show only a slight difference between all three groups (p=0.067), though individual comparison between the smallest and medium-sized classes cross the statistical threshold (p=0.049). Error is relatively small, duplicates from this data set show a 3.9% (n=2) difference for δ^{13}C. Unsurprisingly, measurements of δ^{18}O showed less difference between groups (p=0.489) , though the middle size-class are on average slightly more depleted in ^{18}O (mean=-13.56) than the small or large classes (mean=-12.84 and -12.73). Error, however, was higher with an average difference of 8.3% (n=2). Since we assume these animals were living in close proximity and likely in aquatic to near-aquatic environments, the small differences in δ^{18}O will not be discussed further.

Our δ^{13}C results for Cretaceous goniopholidids from Montana match well with observed dietary patterns of modern crocodilians. Analysis based on gut contents show a clear transition in diet in multiple modern species. Platt et al. (2006) found that insects and arachnids make up a large portion (97.1 to 95.1%) of the diet in hatchling and small juvenile Morelet's crocodile (*Crocodylus moreletii*), while in adults these prey items made up a substantially smaller portion of the dietary intake (12.5%). Instead, adult individuals shifted towards gastropods, fish, and crustaceans (70.8%, 31.2%, and 20.8% respectively) as the mainstay of their diets. Similarly, the Australian freshwater crocodile (*Crocodylus johnstoni*) begins post-hatching life with a diet largely of insects and spiders, before steadily transitioning to a diet of more fish and even terrestrial vertebrates in the largest individuals (Tucker et al., 1996). This change in resource partitioning is not only related to body-size increases. Erickson et al. (2003) found in a study of American alligators (*Alligator mississipiensis*) that bite force increased with positive allometry relative to body size, which is hypothesized to compensate for the larger and stronger prey items favored by adults.

In the Nile crocodile (*Crocodylus niloticus*) these same body-size/diet transitions in δ^{13}C occur at approximately 130 cm SVL (the tip of the snout to the first scale row after the cloaca) and 240 cm SVL respectively (Radloff et al., 2012). Small *C. nilocticus* transition between a diet composed of insects to a more fish-based diet with increasing size. The largest individuals have relatively depleted δ^{13}C signature, largely the result of eating a large quantity of C4 grass-feeding animals. These same changes in the diet appear to be manifested in the Cretaceous goniopholidid δ^{13}C record presented here as well. The smallest teeth are enriched in ^{13}C, similar to the smallest individuals documented by Radloff et al. (2012). There is also a similar decline in the middle size class, in which a distinct dietary transition occurred in *C. niloticus*. Surprisingly, the largest individual tooth (length of 31 mm) is more depleted in ^{13}C (-10.68 ‰) than was observed in the modern crocodile study. This, however, could be explained by the source of large terrestrial herbivorous prey between the modern and ancient environments. The Cloverly and Antlers formation's dominant terrestrial herbivore is *Tenontosaurus tilletti*. Isotopic studies of teeth from this dinosaur are relatively depleted in ^{13}C (average -12.97‰; n=8; SD=0.670; see chapter III), meaning incorporation of *Tenontosaurus* into the diet of large size-class goniopholidids, could produce the relatively lower ^{13}C values in these individuals. This is directly opposed to the more enriched-C4 herbivores present in the diet of modern large *C. niloticus*.

Deinonychus diet

The isotopic data show a significant difference between size classes in the Antlers Formation *Deinonychus* teeth (p=0.0037) (Large mean=-10.96; SD=0.572) (Small mean=-9.38; SD=0.814). Cloverly Formation size-classes are not statistically different (p=0.1243) (Large mean=-9.80; SD=1.74) (Small mean=-8.61; SD=1.244), but do show a similar pattern, with juveniles more depleted on average than the adults (Figure 3). As in the Antlers Formation, small teeth from the Cloverly do not generally have δ ^{13}C values below 10‰. Adults can far exceed this depletion, with individuals reaching -11.45 and -11.71 in the Antlers and Cloverly, respectively. As in the goniopholidids, juvenile *Deinonychus* are relatively more enriched than the adults, with these adults matching more closely to that of *Tenontosaurus* than to their conspecific juveniles. Like in the goniopholidids, $\delta^{18}O$ shows no significant difference between size classes for either the Antlers (p=0.338) (Large mean=-6.95 ; SD= 3.245) (Small mean=-6.30; SD=0.761) or Cloverly (p=0.186) (small mean=-11.32; SD=2.787) (large mean=-12.52; SD=0.564) formation *Deinonychus*. The difference in $\delta^{18}O$ between the

Antlers and Cloverly samples may represent the latitudinal gradient, as the Cloverly Formation is about 10 to 15° of latitude north of the Antlers Formation (Werning, 2012) or the difference could represent a more-depleted source of water (such as montane meltwater) for the more northern theropods than the southern ones.

Niche partitioning in Deinonychus

Based on carbon isotope data, juvenile and adult *Deinonychus* likely consumed different prey regardless of where they lived. This pattern is far closer to the Komodo Dragon ontogenetic dietary pattern of Roach and Brinkman (2007) than the canid pattern proposed by Ostrom (1969; 1986). Though we lack skeletal evidence that juvenile and adult *Deinonychus* occupied the same environments, isolated teeth from individuals varying in size are found in close proximity suggesting that the young and old were not physically separated. Given that gregariousness, even among different sized individuals, is not rare in theropods (Currie and Eberth, 2010), there is little reason to assume that *Deinonychus* would not also demonstrate a level of social tolerance at least as advanced as that seen in crocodilians (see chapter I). Because individuals of all sizes likely occupied the same environment, young animals must have behaved differently than adults, at least with respect to food preferences. We can presume based on taphonomic association of *Deinonychus* teeth with *Tenontosaurus* remains (see Forster, 1984; Maxwell and Ostrom, 1995; Brinkman et al., 1998) and the close average dental δ^{13}C, that adult *Deinonychus* were feeding-upon *Tenontosaurus* to some degree. However, some large-crowned *Deinonychus* teeth from the Cloverly also show a more depleted ^{13}C signature (-7.3 to -9.5) overlapping with the range of values for smaller individuals, implying that adults were not monophagous.

The varying adult diet of *Deinonychus* is indicative of a dynamic and opportunistic hunter. Unsurprisingly, this pattern is reminiscent of modern large-bodied carnivores, where prey preference falls largely into an optimum size range, but other organisms will be consumed when available (e.g., lions prefer prey weighing around 350 kg [Hayward and Kerley, 2005]). Larger variation between large crowned teeth in Cloverly than in the Antlers samples imply a geographical difference in diet, possibly correlated with availability of food (e.g., Fryxell et al., 1988). In their reinterpretation of dromaeosaur pedal morphology, Fowler et al. (2011) proposed the Raptor Prey Restraint (RPR) model which envisioned winged, adult *Deinonychus* acting more similar to modern accipitrids, using the large, recurved D-II pedal phalanx for small prey immobilization, supplemented by wing-flapping to maintain stability. For larger game, such as subadult *Tenontosaurus*, the D-II may have acted more as a crampon for sustained “prey-riding”. A climbing, rather than a slashing function for the D-II foot claw was also proposed by Manning et al. (2006) through robotic modeling.

Alternatively, juveniles might have been much more limited in their trophic abilities. Their enamel ^{13}C signature was relatively more enriched in both formations than the larger individuals, including more than 4‰ increase compared to tenontosaurs from the Cloverly Formation. Even small tenontosaurs were unlikely food for these juvenile predators, as juvenile *Tenontosaurus* show no statistical difference in ^{13}C (or even a slight depletion) from their adult counterparts (see chapter III). Further, the smallest juvenile tenontosaurs have been found in association with adult individuals

(Forster, 1990), making hunting such animals an even more dangerous task. Based on the ^{13}C values, it seems far more likely that these small *Deinonychus* ate a diet consisting of more minuscule, but likely trophically-higher prey than the adults.

A better analog

The life history of non-avian dinosaurs is imperfectly preserved in the fossil record. Based on the evidence at hand, all dinosaurs are currently viewed as being oviparous and most-likely exhibiting some form of parental care of their young. Most species grew over a multi-year period before reaching sexual maturity and possibly congregated in juvenile or mixed-aged groupings (Varricchio, 2011). The degree of parental care and social behavior in *Deinonychus* are relatively ambiguous. Parental care can only be assumed based on the evidence from other species, while social interactions are largely supported by bonebed composition. The evidence presented here shows that small (presumably young) *Deinonychus* did not have the same diet as the adults, meaning if parental feeding were occurring it had concluded before the offspring were large enough to sustain a typical adult diet.

In their reevaluation of social behavior in *Deinonychus*, Roach and Brinkman (2007) used examples of high levels of intraspecific aggression and cannibalism in modern archosaurs and Cretaceous theropods as evidence against higher social coordination (though the complete validity of this argument did not go unchallenged [Currie and Eberth, 2010]). In modern cannibalistic species lacking parental care, juveniles actively avoid their adult predators by seeking out adult-free environmental zones (Foster et al., 1988; Werner et al., 1983; Keren-Rotem et al., 2006). Beyond providing safety from larger conspecifics, these separate habitats often provide a higher availability of more-ideal sized prey. Both of these factors are demonstrated in the hypothesized *Deinonychus*-analog Komodo Dragon, in which hatchlings are highly arboreal, a habitat providing relative safety from nonarboreal, cannibalistic adults and a ready supply of small insects and lizards. Only with the onset of larger sizes do these individuals take on a more terrestrial lifestyle (Imansyah et al., 2008; Auffenberg, 1981).

In this sense, it is not unreasonable to hypothesize a similar niche for hatchling to juvenile *Deinonychus*. Their small size and enlarged, DII foot claw conceivably lent itself to climbing trees more than climbing large-bodied prey. Evidence for arboreal dromaeosaurs is relatively strong, especially amongst the Microraptoria, a small-bodied basal group from China, some of which possess wings on both the arms and legs in a biplane arrangement (Senter et al., 2004). Moreover, Parsons and Parsons (2015) hypothesized that, like some of these microraptorians, juvenile *Deinonychus* were volant. In their description of a juvenile *Deinonychus* from the Cloverly Formation, these authors note that the morphology of the pectoral girdle would have allowed increased rotation in the small individual as compared to the adult. Further, an enlarged and cranially oriented olecranon on the ulna meant the forearm could be extended further in juveniles. Even so, dromaeosaurs lacked many of the adaptations for flight, such as a triosseal canal, which would have made an avian-style wing stroke extremely difficult. Wing flapping in modern juvenile birds is not strictly used for flight, however. Juvenile Galliformes, which could not yet fly, have been shown to use flapping action to assist climbing steep inclines in laboratory settings (Dial et al., 2006). This action has been hypothesized as a precursor to the behavior that was later co-opted for flight in avians, It is possible that this wing-assisted incline running behavior extends to the origins of dinosaurian flight. If so, juvenile *Deinonychus* may have used wing flapping assistance to traverse inclines in order to reach the relative safety of the canopy.

This hypothetical lifestyle, however, contradicts the relatively common occurrence of juvenile theropods found alongside adults (Currie and Eberth, 2010). Indeed, purported dromaeosaur ontogenetic series are known from individual bonebeds, including a recently described site containing the remains of at least one ‘baby’, one juvenile, and one adult *Utahraptor ostrommaysorum* from the Early Cretaceous of Utah preserved in a natural mud-trap (Kirkland et al., 2016). Although it is possible these represent unrelated individuals that were captured by chance, it is more probable that this site represents a social, likely related group. If the latter, then this suggests that dromaeosaurs, and possibly other theropods, were gregarious and exhibited some degree of post-nestling care. If so, juvenile or young animals found alongside adults imply an absence or reduced presence of the cannibalistic avoidance behavior, making an analogy with the Komodo dragon less palpable. Though *Deinonychus* shows ontogenetic diet partitioning, differentiating itself from the highest-level of cooperative eusocial mammalian behavior, the lack of spatial separation from adults likely indicates that these dromaeosaurs had hunting strategies on par with many of the avian raptors (Ellis et al., 1993). In avian raptors post-fledgling behavior can range from completely asocial to relatively gregarious with cooperative hunting, even within a single species. Further, dromaeosaurs likely showed paternal parental care, similar to modern Paleognathes (Varricchio et al., 2008). This type of rearing is typified by extended protection by the father, where feeding time is reduced and predator vigilance is increased in this parent (Fernández and Reboreda, 2003). It is very possible that dromaeosaurs showed more ratite-like parental care rather than the complete agonistic relationship seen in Komodo dragons. In this scenario, parental *Deinonychus* may have reduced feeding efficiency due to their inability to both protect their young and hunt large-sized prey. The young, being precocial, would have maintained dietary independence based on their own foraging and/or small fare provided by the parent.

CONCLUSIONS

Through isotopic analysis of different-sized *Deinonychus* teeth, we indirectly find support for Roach and Brinkman's (2007) alternative hypothesis against pack-hunting in dromaeosaurids. Taken as a whole, the evidence for canid-like social behavior in raptors is not supported by modern archosaurian behavior or fossil data. Though high coordination and cooperation during hunting is unlikely in any non-avian dinosaur, gregariousness and other social behavior may have still occurred. Even in cannibalistic species, intraspecific tolerance can be relatively high when natural prey is abundant (Fox, 1975). In this sense, it is reasonable to picture *Deinonychus* living in groups based on a strong social hierarchy, but acting in their own independent interests when finding and hunting prey.

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Table 1: Relative crown height difference for upper and lower teeth in velociraptorine dinosaurs. Data from Norrell et al., 2006; Ostrom, 1970

Genus	***Velociraptor***			***Deinonychus***
Specimen #	AMNH FR 6516	*IGM 100/25*	*IGM 100/982*	*YPM 5205*
Upper : Lower tooth count	5:5	5:1	6:0	7:3
Max upper difference	64.44%	64.29%	59.09%	56.99%
Max lower difference	75.81%	n/a	n/a	57.93%
Max upper and lower difference	51.85%	64.29%	59.09%	50.98%

Table 2: Full dataset summary statistics for *Deinonychus antirrhopus* teeth from two localities in different rock formations vs. the sampled data set for isotopic analysis.

Formation	*Data set*	*n*	*Mean Crown height (mm)*	*SD*	*Min – Max (mm)*
Antlers	All V706	36	9.42	4.35	1.70 – 19.33
	sampled	10	8.39	1.92	1.92 – 19.33
Cloverly	All V1075	30	7.50	3.52	2.35 – 13.58
	sampled	10	7.01	1.25	3.04 – 12.77

FIGURE LEGENDS

Figure 1. A hypothetical pattern of average ^{13}C isotope values through ontogeny in social (Knoff et al., 2008) vs. asocial organisms (Radloff et al., 2012). The varying isotopic values (and thus diet) of adult asocial organisms is based on the possibility that smaller size-classes can be included in the diet of larger organisms (Werner and Gilliam, 1984b).

Figure 2. $\delta^{13}C$ analysis for small (<5 mm crown height), medium (5 to 10 mm crown height), and large (11+ mm crown height) goniopholidid teeth from V1075 in the Cretaceous Cloverly Formation, Montana.

Figure 3. $\delta^{13}C$ for small (<4.5 mm crow height) and large (> 9 mm crown height) *Deinonychus* teeth from the Antlers (upper) and Cloverly (lower) formations, Oklahoma and Montana, respectively.

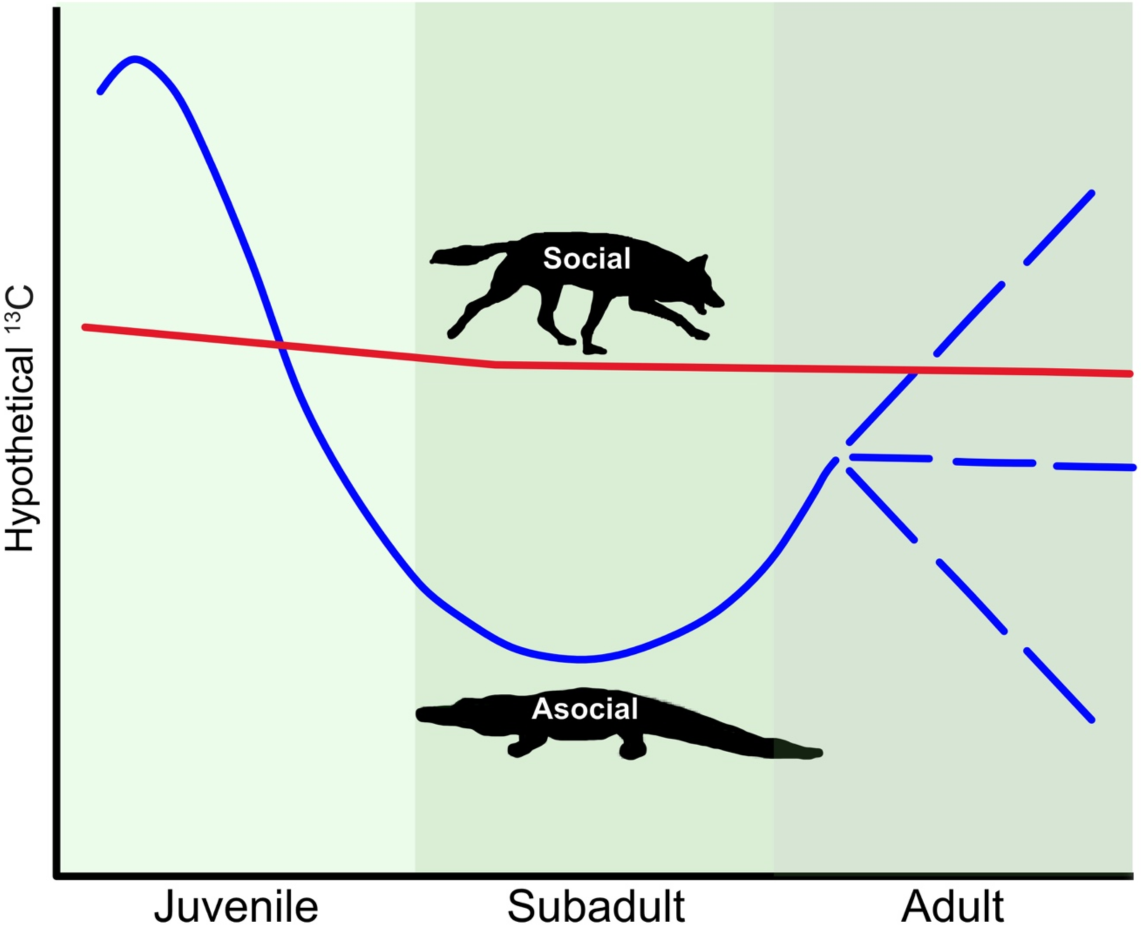

Figure 1. A hypothetical pattern of average ^{13}C isotope values through ontogeny in social (Knoff et al., 2008) vs. asocial organisms (Radloff et al., 2012).

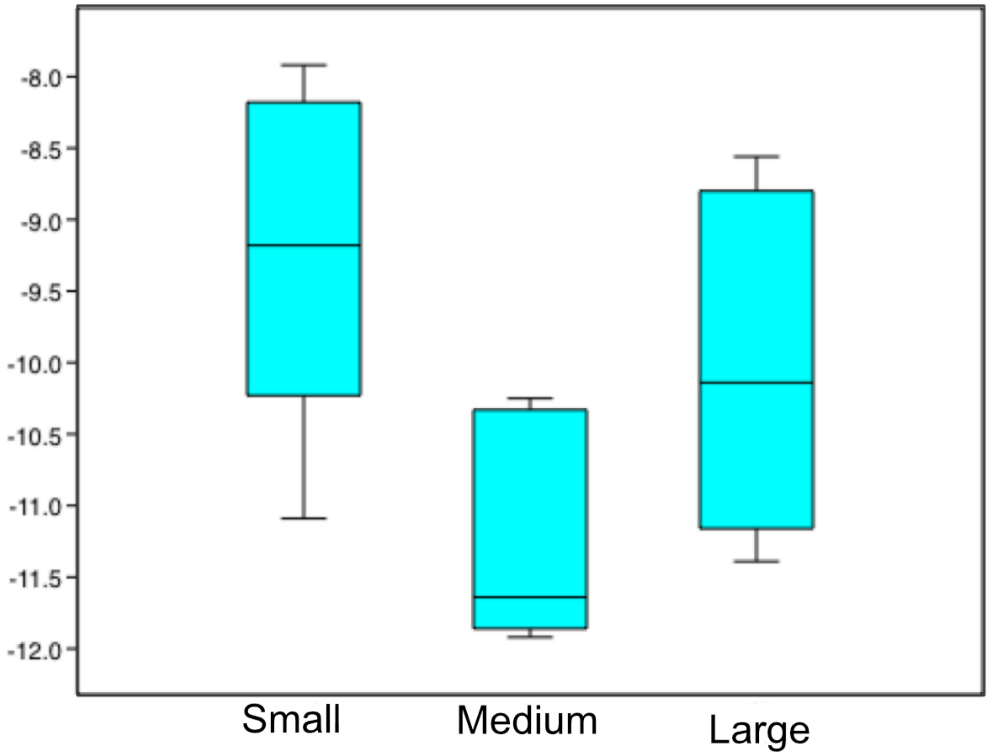

Figure 2. $\delta^{13}C$ analysis for goniopholidid teeth from V1075.

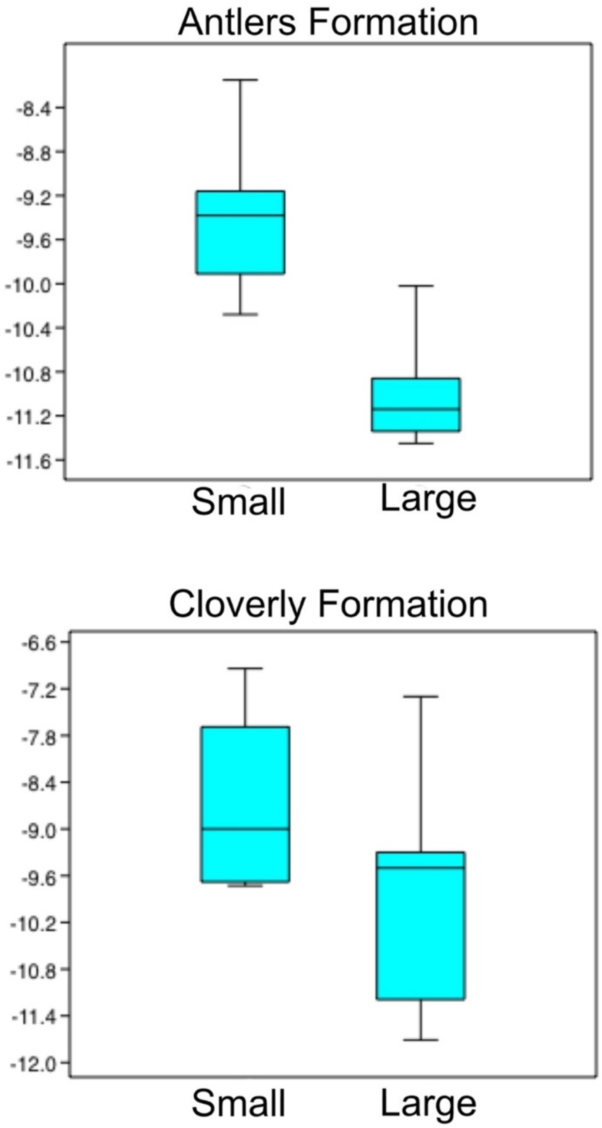

Figure 3. δ^{13}C for *Deinonychus* teeth from the Antlers (upper) and Cloverly (lower) formations.

SUPPLEMENTARY INFORMATION

Geologic notes

Specimens used in this study come from V706 and V1075 collected by the Sam Noble Oklahoma Museum of Natural History. V706 is in the Antlers Formation of SE Atoka County, Oklahoma. This microsite was found approximately 1.5 m beneath a layer containing abundant dinosaur remains, including the first definitive *Deinonychus* fossils found outside of Montana and Wyoming. The microsite was preserved in a mottled and nodule-rich mudstone, interpreted as an overbank fluvial lag. Geographically, the Antlers Formation represents a low-lying floodplain near the eastern shore of the encroaching gulf arm of the Western Interior Seaway. To date, thousands of specimens have been identified from this site, representing a highly diverse fauna, including freshwater fishes, sharks, amphibians, lizards, crocodilians, mammals, and dinosaurs (Cifelli et al., 1997). In total, 37 diagnostic *Deinonychus* teeth were recovered from this bonebed. V1075 is located in Ostrom's (1970) unit VII of the Cloverly Formation, roughly 36 km ESE of Pryor, Bighorn County, Montana. Unit VII is composed largely of sloped, colored mudstones and interbedded channel sandstones. Environmentally, unit VII represents a tropical-semitropical environment at the edge of the encroaching Arctic arm of the Western Interior Seaway (Nydam and Cifelli, 2002). Like in the Antlers, the Cloverly fauna is known from an equally robust fossil record, with V1075 containing a major representation of this sample, with tens of thousands of recovered fossils from this site. In total, 41 complete teeth were identified as *Deinonychus*.

Table 3: Measurements for Cretaceous goniopholidid teeth from V1075, Cloverly Formation, Montana.

ID	*Height*	$\delta^{13}C$	$\delta^{18}O$
SC1	0.3	-11.09	-12.38
SC5	0.3	-8.18	-13.1
SC2	0.4	-7.92	-11.45
SC3	0.4	-10.23	-13.83
SC4	0.4	-9.18	-13.42
61317A	0.7	-10.25	-12.56
61299B	0.8	-11.64	-14.16
61317C	0.8	-10.33	-13.63
61317B	0.9	-11.86	-12.84
61297B	1	-11.92	-14.63
61299A	1.3	-11.39	-13.31
BC2	1.3	-10.14	-13.46
61297A	1.4	-8.56	-9.84
61298	1.5	-11.16	-13.22
BC1	1.6	-8.8	-12.48
60442	3.1	-10.68	-14.08

Table 4: Measurements for *Deinonychus* teeth used in this experiment.

ID	***Bonebed***	***Class***	***Height***	***Width***	***Length***	***Gum angle***	$\delta^{13}C$	$\delta^{18}O$
34972	706	small	1.37	0.85	1.92	54.74	-9.91	-6.66
32427	706	small	1.46	0.88	2.85	64.63	-10.28	-5.85
34032	706	small	1.9	0.93	3.2	68.43	-8.15	-6.36
34033	706	small	2.16	0.86	3.46	64.99	-9.16	-5.33
34879	706	small	2.5	1.02	4.07	54.71	-9.38	-7.32
34205	706	Large	4.66	2.35	9.9	59.68	-11.45	-6.4
52711	706	Large	6.56	3.14	11.98	50.9	-11.34	-5.38
49412	706	Large	7.35	3.52	13.04	52.4	-10.86	-5.19
34115	706	Large	7.42	3.81	14.13	59.2	-10.02	-5.1
17709	706	Large	9.13	4.46	19.33	62.44	-11.14	-12.68
69433	1075	Small	1.9	0.76	3.04	61.7	-6.94	-12.45
69431	1075	Small	2.32	0.87	3.12	64.6	-7.69	-13.05
69432	1075	Small	2.32	0.89	3.36	57.8	-9.73	-6.36
69430	1075	Small	2.59	1	3.56	61.8	-9	-12.43
69434	1075	Small	2.74	1.08	3.72	50.6	-9.68	-12.3
69435	1075	Large	5.67	3.28	9.24	51.4	-11.19	-13.18
69441	1075	Large	6.22	2.85	10	51.9	-9.5	-12.45
69436	1075	Large	6.79	2.75	11.31	56.3	-9.3	-12.3
69437	1075	Large	7.55	3.71	12.77	62.69	-7.3	-11.74
69442	1075	Large	n/a	n/a	10	n/a	-11.71	-12.94