



Water utilization of the Cretaceous Mussentuchit Member local vertebrate fauna, Cedar Mountain Formation, Utah, USA: Using oxygen isotopic composition of phosphate

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ABSTRACT

While the oxygen isotopic composition of pedogenic carbonate has successfully been used to address the effects of global climate change on the hydrologic cycle, detailed regional paleohydrologic studies are lacking. Since the hydrologic cycle can vary extensively on local or regional scales due to events such as mountain building, and since pedogenic carbonates (calcite) form in a narrow moisture regime, other proxies, such as vertebrate remains, must be used to decipher local versus regional variations in paleohydrology. In this study, the oxygen isotopic composition ($\delta^{18}\text{O}_p$) of phosphatic remains from a diverse set of vertebrate fossils (fish, turtles, crocodiles, dinosaurs, and micro-mammals) from the Mussentuchit Member (MM) of the Cedar Mountain Formation, Utah, USA (Aptian to Cenomanian) are analyzed in order to determine differences among the available water reservoirs and water utilization of each taxon. Calculated changes in water reservoir $\delta^{18}\text{O}_w$ over time are then used to determine the effects of the incursion of the Western Interior Seaway (WIS) and the Sevier Mountains on paleohydrology during the MM time.

Calculation of $\delta^{18}\text{O}_w$ from the results of isotopic analysis of phosphate oxygen suggests that turtles and crocodiles serve as another proxy for meteoric water $\delta^{18}\text{O}$ that can be used as a measure of average local precipitation $\delta^{18}\text{O}_w$ similar to pedogenic calcite. Pedogenic calcites can be slightly biased toward higher values, however, due to their formation during evaporative conditions. Turtles and crocodiles can be used in place of pedogenic calcite in environments that are not conducive to pedogenic carbonate formation. Remains of fish with rounded tooth morphology have $\delta^{18}\text{O}_p$ values that predict temperatures consistent with other estimates of mean annual temperature for this latitude and time. The $\delta^{18}\text{O}_p$ of ganoid scales and teeth with pointed morphology, however, indicates that these skeletal materials were precipitated from water that is ^{18}O -enriched due to migration to either evaporatively enriched water, or ^{18}O -enriched estuarine waters of the Western Interior Seaway (WIS). Another possibility that cannot be discounted and assuming all morphological remains are from the same taxon, is that the pointed teeth and ganoid scales precipitated at different temperatures than rounded teeth. Mammal and herbivorous dinosaur $\delta^{18}\text{O}_p$ suggests they primarily drank isotopically depleted river water. Co-existence of crocodiles, turtles, and mammals allows for calculation of relative humidity from site to site and these calculations suggest humidity averaged ~58% and ranged between ~42% and ~76%.

The $\delta^{18}\text{O}_w$ values estimated from semi-aquatic taxa and pedogenic calcite suggest dominance of WIS-derived moisture during their growth. Herbivorous dinosaurs particularly indicate that altitude and catchment effects from the Sevier Mountains are seemingly important for river water $\delta^{18}\text{O}_w$ in the fall through early spring. These data suggest that temporal changes in the isotopic composition of the MM fauna are produced by the small-scale regressive–transgressive cycles of the WIS.

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1. Introduction

Numerous isotopic studies have demonstrated that the mid-Cretaceous global warming caused an intensification of the hydrologic cycle, resulting in increased regional rainout in the temperate humid belts and higher evaporation in dry belts (White et al., 2001; Ufnar et

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al., 2002; 2004; Suarez, 2009). While these studies have explored the hydrologic cycle at hemispheric to global scales, detailed regional isotopic studies are lacking. For example, the relative contribution of local *versus* regional water sources to rivers and other water bodies (e.g. lakes and ponds) can vary significantly within a particular region, but this variability is difficult to ascertain. In addition, regional events such as mountain building and transgression/regressions can affect the proximity of moisture sources and significantly alter regional moisture patterns, thereby influencing the isotopic composition of precipitation. The causes of changing isotopic compositions of precipitation are difficult to constrain using isotopic proxy records that form under a narrow moisture regime, such as pedogenic carbonates. Because of these limitations, biogenic materials are being used with greater frequency to infer paleohydrology and paleoenvironments (Dettman et al., 2001; Billon-Bruyat et al., 2005; Fricke et al., 2008). It is therefore imperative to better understand water utilization behavior of different taxa, and improve the understanding of proxy records that can provide information on the factors controlling variability in the isotopic composition of water for a given site.

Several studies have used stable isotopes in continental taxa (aquatic, semi-aquatic, and terrestrial) to determine paleoenvironmental, paleoclimatic, and paleoecologic information (Fricke and O'Neil, 1996; Billon-Bruyat et al., 2005; Lee-Thorp and Sponheimer, 2005; Fricke, 2007; Fricke et al., 2008; Amiot et al., 2009). Vertebrate taxa record the isotopic compositions of their water sources in their bone and tooth apatite [$\text{Ca}_5(\text{PO}_4)_3(\text{OH}, \text{CO}_3)$]. While both the carbonate and phosphate components of bioapatite have been used for isotopic studies, phosphate is more resistant to diagenesis than structural carbonate (Kolodny et al., 1996). Furthermore, enamel apatite and ganoin (dense upper layer of ganoid scales, similar to enamel) are more resistant to diagenetic alteration than bone apatite and are considered a more reliable source of biogenic and paleoecologic information (Kolodny et al., 1996; Trueman et al., 2003; Fricke et al., 2008).

In this study, the isotopic composition of a diverse late Early Cretaceous vertebrate fauna is measured to investigate water utilization strategies employed by different organisms. While the isotopic composition of Mesozoic land-dwelling vertebrate faunas is now more commonly used (Billon-Bruyat et al., 2005; Fricke, 2007; Fricke et al., 2008; Amiot et al., 2009), few paleoecological isotope studies of Mesozoic terrestrial ecosystems have been conducted that elucidate the water sources utilized by a wide variety of co-existing taxa. The Mussentuchit Member (MM) of the Cedar Mountain Formation (CMF) is most amenable for such a study because it preserves a diverse continental fauna including freshwater aquatic, semi-aquatic and terrestrial vertebrates (Cifelli et al., 1999). Furthermore, the vertebrate fauna contains numerous physicochemically resistant elements such as teeth, scales, and scutes that may be used for stable isotopic analysis (Billon-Bruyat et al., 2005; Fricke et al., 2008). This diverse fauna allows us to explore water utilization strategies by vertebrates and to tease out the relative contribution of local *versus* regional water sources. The isotopic composition of fish remains are used to calculate temperature and relative humidity is estimated from the isotopic composition of co-existing mammals and semi-aquatic taxa. Furthermore, temporal changes in the isotopic composition of the different water reservoirs available to the MM fauna are tracked through the Cenomanian based on detailed stratigraphic control of the available collections. By tracking these changes the impact of the Sevier Mountains and incursions of the Western Interior Seaway on paleohydrology during Mussentuchit time is constrained. The results of this study provide the most diverse phosphate O-isotopic study to date of the Mesozoic; with over 100 phosphate analyses from seven different taxonomic groups from seven different sites as well as pedogenic and cementing carbonate.

2. Geologic setting

The Cedar Mountain Formation (CMF) was deposited in Utah during the Barremian to Cenomanian and includes, from oldest to youngest,

the Buckhorn Conglomerate, Yellow Cat Member, Poison Strip Sandstone, Ruby Ranch Member, and Mussentuchit Member (MM). The focus of this study, the Mussentuchit Member, primarily crops out on the western side of the San Rafael Swell anticline. It is identifiable by its high smectitic-clay content and drab gray popcorn-weathered mudstones that form extensive badlands in the Willow Springs and Short Canyon quadrangles of central-Utah. Several ash layers present in the MM give ages that range from 98.3 ± 0.1 Ma (Cifelli et al., 1999) to 96.7 ± 0.5 Ma (Garrison et al., 2007), suggesting MM deposits are Cenomanian in age. The upper part of the MM contains abundant lignitic coal layers and is commonly interbedded with the overlying Dakota Sandstone; however, locally there are erosional unconformities between the MM and Dakota. While carbonate nodules are abundant in the underlying Ruby Ranch Member, they are less common in the MM.

The MM vertebrate fauna was sampled by field crews of the Oklahoma Museum of Natural History in the Mussentuchit Wash and Short Canyon areas (Fig. 1) via screen washing techniques. Representative stratigraphic sections (Fig. 2) illustrate the relative stratigraphic position of seven different sites. Garrison et al. (2007) suggested that these sites were deposited in a lacustrine system in which a perennial lake cyclically transgressed and regressed, while Kirkland et al. (1997) suggested that the MM represents fluvial environments with small channels and overbank deposits. Taphonomically, all the sites are microvertebrate sites from either lag concentrations of channel and floodplain-derived material or oxbow-lake deposits, and so were likely transported to some degree. However, most samples with the exception of a few are well-preserved and do not show significant signs of abrasion, suggesting they were not transported far and the sites were likely parautochthonous in nature.

In a foreland basin setting similar to that in which the Mussentuchit was deposited, there are two main sources of water that continental vertebrates can utilize: 1) local precipitation or meteoric water and 2) water in larger rivers derived from distant sources. While both of these sources are ultimately derived from precipitation, water in large rivers is influenced by precipitation in the distant portions of the rivers' catchment areas. Dutton et al. (2005) provide an extensive review of the differences between river water and local meteoric water isotopic composition. The oxygen isotopic composition ($\delta^{18}\text{O}$) of meteoric water is controlled by water vapor sources (*i.e.* ocean, or large lakes), distance from the source (continental effect), elevation (altitude effect), temperature, humidity, and evaporative effects. In general, the $\delta^{18}\text{O}$ of precipitation produced from a given air mass becomes lighter by $\sim 2\text{‰}/1000$ km of transport (Rozanski et al., 1993) assuming no elevation change. Similarly, as an air mass moves to higher elevations, the precipitation will become gradually lighter by $\sim 2.8\text{‰}/\text{km}$ of elevation (Dutton et al., 2005). Temperature and precipitation $\delta^{18}\text{O}$ are positively correlated with mean annual air temperature (e.g. Dansgaard, 1964). Humidity and evaporative effects act in concert to modify the isotopic composition of precipitation, with lower humidity resulting in greater evaporation and ^{18}O -enrichment. The isotopic composition of river water is dominantly controlled by the $\delta^{18}\text{O}$ of precipitation in its catchment area. As altitude effects result in lower $\delta^{18}\text{O}$, river water sourced at higher elevations tends to be ^{18}O -depleted relative to that of low elevation tributaries and ephemeral streams. In general, river water $\delta^{18}\text{O}$ decreases by $\sim 4.2\text{‰}/\text{km}$ of elevation change (Dutton et al., 2005). Thus, precipitation-derived water at a given elevation will be heavier than river waters at the same elevation if the river is sourced from higher elevations.

2.1. Ecologic and climatic setting

The ecologic setting of these animals was affected by two main geologic events that could have impacted local hydrology: 1) mountain building from the Sevier Fold and Thrust Belt (SFTB) and 2) the incursion of the Western Interior Seaway. The SFTB is a segment of the larger Cordilleran retroarc fold-and-thrust belt that formed during the late Mesozoic to early Cenozoic times (DeCelles and Coogan, 2006).

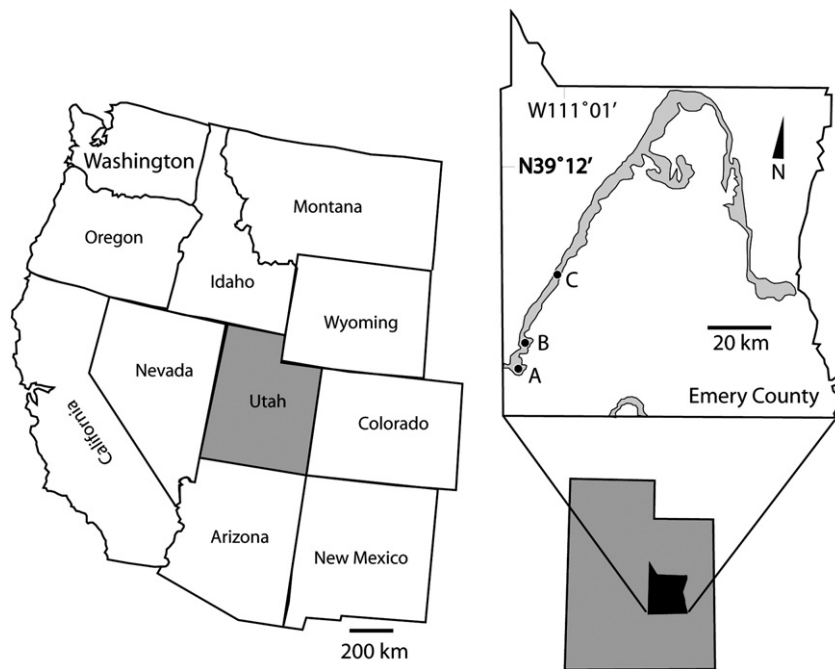


Fig. 1. Vertebrate sites from Emery County, Utah, USA. A, B, and C are the location of representative stratigraphic sections in Fig. 2. The gray shaded area within Emery County represents the outcrop belt of the Cedar Mountain Formation.

Deformation along the SFTB was syndepositional with the majority of the Cedar Mountain Formation, which is made up of sediments shed from the resulting mountains. The Mussentuchit Member was deposited in the foredeep of the foreland-basin system and its deposition is synchronous with the Pavant Thrust event (110 to 86 Ma) (Currie, 1998; DeCelles and Coogan, 2006). The resulting mountains ran northeast to southwest from central Nevada to western Utah, and by the Late Cretaceous they formed an Andean-style fold-and-thrust belt with a high-elevation, low-relief hinterland plateau. By the end of the Pavant Thrust (and end of MM deposition), paleo-elevation was likely greater than ~2.2 km in western Utah (DeCelles and Coogan, 2006). Regional paleohydrology was affected by these orogenic events because the rise of the mountains hindered westerly jet stream moisture (Poulsen et al., 2007).

Oboh-Ikuenobe et al. (2008) showed that during the early part of the WIS formation, at least two smaller-scale transgressions and regressions occurred prior to the major Greenhorn transgression (95–96 Ma) and could have brought sea water sources closer to the MM area. These small-scale transgressions and regressions could have resulted in increased humidity and ^{18}O -enriched moisture sourced from the seaway.

3. Materials and methods

3.1. *Mussentuchit* fauna

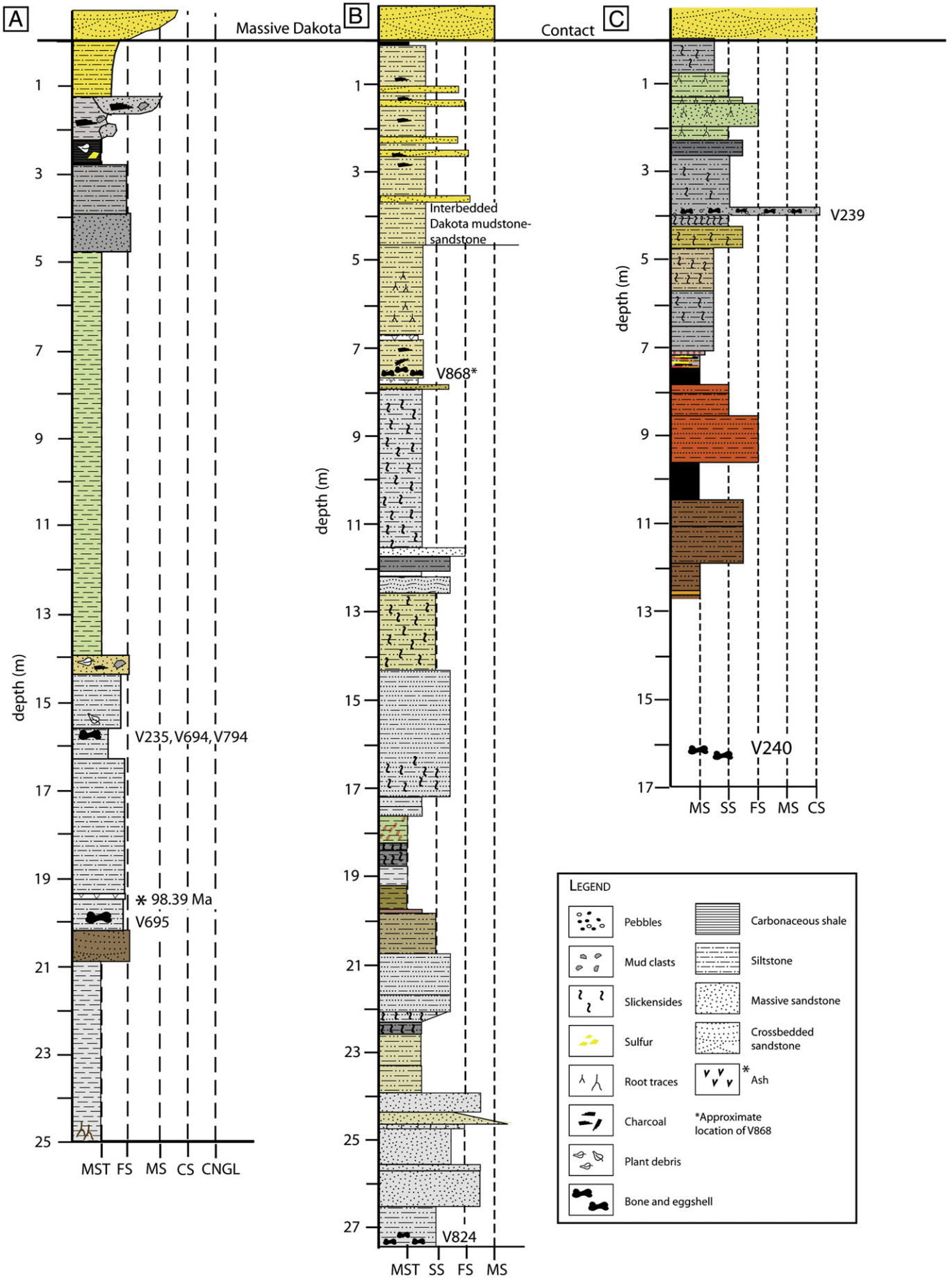
All samples used in this study were obtained from the Oklahoma Museum of Natural History's Sam Noble Museum, and were selected on the basis of the number of taxa per site, close proximity of sites, and distinct stratigraphic location (Table 1). The MM vertebrate taxa represent one of the richest vertebrate faunas described from

the early Cretaceous (Cifelli et al., 1999). The fauna appears to be a combination of older European-affiliated taxa such as *Coniophis* (snakes; not analyzed in this study), *Pachycephalosauria* (Ornithischia), and *Hesperornithiformes* (birds; not analyzed in this study), and a younger Asian-originated fauna such as the carnivorous dinosaurs Troodontidae and Tyrannosauridae, and herbivorous dinosaurs Hadrosauridae and neoceratopsians (Cifelli et al., 1999).

Fish samples were unable to be specifically identified because they were all disarticulated elements. Samples were broadly identified by OMNH personnel as *Lepisosteidae* teeth (pointed teeth) or *Osteichthyes* or *Lepidotes* teeth (rounded teeth) and *Lepisosteidae* scales (ganoid scales). In light of the lack of positive identification of fish remains, samples were grouped based on physical morphology into rounded teeth, pointed teeth, and ganoid scales. Since it is impossible to know if the scales are part of the same organism that contained either the rounded teeth or pointed teeth, isotopic composition of the scales can be compared to the teeth in order to infer which teeth likely were also from the same organism as the scales (Fig. 3A), assuming all elements were precipitated at the same temperature. Based on tooth shape, their diet can broadly be inferred. Rounded teeth probably belong to durophagous (clam-eating), fish as opposed to the smooth and pointed teeth that are likely characteristic of meat-eating fish.

Crocodylian teeth and osteoderms (scutes) include representatives of the *Goniopholididae*, *Atoposauridae*, and *Bernissartia* sp. (*Bernissartiidea*) (Fig. 3B). *Bernissartia* has durophagous dentition and has been reported from the Lower Cretaceous of Europe (Buffetaut and Ford, 1979; Mazin et al., 2006) and the Aptian–Albian of Texas (Winkler et al., 1990). Like the taxa represented by rounded teeth, it probably ate mollusks and lived in rivers and streams. *Goniopholididae*, (semi-aquatic mesosuchians) and *Atoposauridae* (small, terrestrial mesosuchians) span the Upper Jurassic to Late Cretaceous (Carroll, 1988; Marwick, 1998a;

Fig. 2. Stratigraphic sections identified in Fig. 1. Sections A and B are re-drafted from sections described by Cifelli et al. (1999). Sites V695, V234, V694, and V794 are represented in section A, V868 in section B, and V239 and V240 in section C. Locality data sheets put site V240 at ~16 m below the Dakota. However the section measured at section C in the summer of 2005 did exceed 16 m below the Dakota. Site V240 is further down the canyon where the Mussentuchit is thicker and so is projected without sedimentologic data. Site V824 is not sampled within this study, but is a major vertebrate locality and is reported as "Cifelli #2" in Garrison et al. (2007).



Martin et al., 2010). Also sampled were several small crocodylian scutes that were not specifically identified (Fig. 3B).

Most turtle specimens are broadly identified as belonging to the order Chelonia, but some samples are more specifically identified as belonging to the family Trionychidae, and few to the genus level, *i.e.* *Glyptops* sp., and *Naomichelys* sp. (Fig. 3C). All taxa are fully aquatic (Carroll, 1988; Demar and Breithaupt, 2006; Lyson and Joyce, 2009). Trionychidae, or soft-shelled turtles, were freshwater carnivores that lived at the bottom of rivers but also some small ponds (Carroll, 1988; Demar and Breithaupt, 2006). *Glyptops* sp. is an archaic genus that was a direct ancestor of the family Baenidae that is a clade of the paracryptodirian turtles endemic to North America (Lyson and Joyce, 2009). It is common in both the underlying Morrison Formation and overlying Dakota Formation (Cifelli et al., 1999). Since most baenids were river-dwelling, it is likely that *Glyptops* was a bottom-dwelling, riverine turtle. *Naomichelys* sp. is a member of the family Solemydidae. It is distinguishable by its pustulate shell ornamentation and has been identified in brackish water deposits near the bottom of the Upper Cretaceous Iron Springs Formation (Milner et al., 2006) and in riverine deposits of the Mesaverde Formation (Demar and Breithaupt, 2006).

Dinosaur teeth from the site are broadly identified as Hadrosauridae, Ornithischia, or Theropoda (Fig. 3D). The Hadrosauridae teeth are from basal (primitive) hadrosaurs, though some have been identified as the advanced iguanodontid, *Eolambia caroljonesa* (Kirkland, 1998). Other ornithischian teeth belong to hypsilophodontids such as *Orodromeus*, nodosaurids such as *Animantarx*, and the marginocephalians: Neoceratopsia and pachycephalosaurs. Of the theropod dinosaurs, all teeth are only broadly identified as Theropoda. Most of the teeth represent troodontidae, dromaeosaur, or tyrannosaurid teeth. Most theropods teeth sampled in this study are dromaeosaur. Tooth morpho-species include *cf. Paronychodon* and *cf. Richardoestesia*. Some very small and slender sauropod teeth have also been recovered from the MM, however they are rare and were not sampled for isotopic analysis.

Mammalian teeth sampled are broadly identified as “Mammalia” but are sometimes more specifically identified as Multituberculata or Tribosphenida (Fig. 3E). Cifelli et al. (1999) suggest most of the Multituberculata are representatives of the genus *Paracimexomys*. The samples of Tribosphenida were probably from the marsupial-like genus *Kokopellia* (Cifelli, 1993). Both types of sampled mammals are hypothesized to have been omnivorous. All of the mammalian remains were thus grouped together and sampled as “mammalia.”

3.2. Methods

When possible, at least 10 individuals per taxon were analyzed in attempts to determine the range in seasonal variability (Clementz and Koch, 2001; Levin et al., 2006; Kohn and Dettman, 2007). When 10 individuals were not samples, at least 3–5 serially sampled teeth were analyzed which is required to resolve the seasonal variability and range in $\delta^{18}\text{O}_p$ of a particular taxa per stratigraphic level (Clementz and Koch, 2001; Levin et al., 2006; Kohn and Dettman, 2007). This is also the minimum number required to get an error of $\sim 1.3\%$ which is the average standard deviation of $\delta^{18}\text{O}_{\text{enamel}}$ (Levin et al., 2006). For some of the smallest teeth and scales, samples were glued to slides for better control while micro-drilling. Enough enamel or ganoine was milled to yield 200–500 μg of powder. Phosphate samples were converted to silver phosphate following the method of O’Neil et al. (1994) as modified by Bassett et al. (2007). Silver phosphate samples were analyzed at the W. M. Keck Paleoenvironmental and Environmental Stable Isotope Laboratory at the University of Kansas, Department of Geology, on a Thermo high temperature conversion elemental analyzer (TC/EA) connected to a ThermoFinnigan MAT 253 continuous flow mass spectrometer. Phosphate $\delta^{18}\text{O}$ is reported in parts per thousands (‰) relative to V-SMOW using standard δ -notation, and calculated using several

laboratory standards that include IAEA 601 benzoic acid (22.40 ± 0.28), Acros silver phosphate (14.11 ± 0.24), Sigma Cellulose (26.92 ± 0.36), and ANU Sucrose (36.25 ± 0.30). NIST 120c was not used as a calibration standard because of ambiguity of an accepted value between laboratories depending on both the analysis method and preparation method as pointed out by several workers (Vennemann et al., 2002; Lécuyer, 2004). Instead, precision was monitored via analysis of NIST 120c as a quality control standard and is better than $\pm 0.3\%$ V-SMOW, producing an average value of $22.5 \pm 0.3\%$.

Bulk pedogenic and diagenetic carbonate samples from a few MM sections near the vertebrate sites were analyzed for C and O isotopic composition. Approximately 50 μg of carbonate was milled and vacuum-roasted at 200 °C to remove volatiles. Samples were then analyzed by reaction with 100% H_3PO_4 at 75 °C using a Kiel III carbonate reaction device interfaced to the inlet of a ThermoFinnigan MAT 253 dual inlet mass spectrometer. Carbonate isotope data are reported relative to V-PDB and $\delta^{18}\text{O}$ values were converted to V-SMOW for comparison to phosphate O-isotope data. Precision was monitored through the daily analysis of NBS-18 and NBS-19 and is better than 0.10‰ for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$.

The isotopic fractionation between ingested water and bioapatite is controlled by the body temperature at which the bone forms and by vital fractionations that occur during the transfer of ingested water to body water (Longinelli and Nuti, 1973; Kolodny et al., 1983; Longinelli, 1984; Luz et al., 1984; Kohn, 1996). For homeotherms such as mammals, precipitation of bone and tooth apatite occurs at a constant temperature of $\sim 37 \pm 1$ °C (Bryant et al., 1996). Reptiles can control and maintain their temperature through basking and will only grow their teeth, shells, scutes, and bones when their body is at optimal temperature for growth (Barrick et al., 1999; Pough et al., 2002; Amiot et al., 2007). For crocodiles this temperature ranges from 26 to 36 °C with an average of 29 ± 3 °C (Amiot et al., 2007), and for turtles the range is from 20 to 35 °C with an average of 27 ± 4 °C (Barrick et al., 1999). These semi-aquatic taxa have been shown to document meteoric (precipitation) water $\delta^{18}\text{O}$ (Barrick et al., 1999; Amiot et al., 2007; Coulson et al., 2008). Since, aquatic faunal elements (*i.e.*, fish) do not thermoregulate; their isotopic composition is dependent on two unknown factors (water composition and temperature). As a result, one of those factors must be estimated. Therefore, the $\delta^{18}\text{O}$ of water calculated from turtles is used to estimate temperature in order to determine if these values are reasonable with other estimates of mean annual temperature at this time. If the values are reasonable, fish lived in water similar to that of turtles, if they are abnormal, then fish either precipitated their elements at different temperatures or lived in water with a different isotopic composition than turtles.

Ingested/living water isotopic composition was calculated from equations presented by Barrick et al. (1999) for turtles, Amiot et al. (2007) for crocodiles and Kohn (1996) for omnivorous mammals. The equation from Amiot et al. (2007) was generated from phosphate data that used a value of 21.7‰ for NIST 120c as a calibration standard. Since values of 22.5‰ for NIST 120c were consistently obtained, the published equation was corrected by subtracting 0.8‰ from the equation to correct for this difference in calibration standard:

$$\delta^{18}\text{O}_w = 0.82\delta^{18}\text{O}_p - 19.93. \quad (1)$$

Coulson et al. (2008) expand on the work of Barrick et al. (1999) and they report that Barrick used a value of 22.6‰ for NIST 120c. Because the difference is only 0.1‰ for their values of NIST 120c, the equation for the turtle water-phosphate fractionation was not altered:

$$\delta^{18}\text{O}_w = 1.01\delta^{18}\text{O}_p - 22.3. \quad (2)$$

Table 1
Oxygen isotopic composition of phosphate relative to V-SMOW.

Site	Taxa	N_{specimen}	N_{samples}	Min ‰	Max ‰	Avg‰ $\pm 1\sigma$	
V239 (SC1) depth: 4 m	Ganoid scale	9	9	15.3	16.7	16.0 ± 0.4	
	Rounded teeth	10	10	11.8	14.7	13.8 ± 0.8	
	Crocodylia:	8	10	15.9	18.5	16.7 ± 0.7	
	Atoposauridae + Goniopholididae						
	Turtle: "Chelonia" + <i>Naomichelys</i> sp.	2	11	14.7	16.4	15.4 ± 0.7	
	Ornithischia	5	7	15.4	18.6	16.9 ± 1.1	
	Theropoda	4	10	15.6	20.0	18.3 ± 1.8	
V868 (WS27) depth: 8 m	Mammalia	10	10	15.1	17.4	16.2 ± 0.7	
	Ganoid scale	10	14	15.4	17.8	16.4 ± 0.7	
	Rounded teeth	8	9	13.1	17.7	15.4 ± 1.8	
	Crocodylia:	9	13	16.4	18.6	17.1 ± 0.5	
	Atoposauridae + Goniopholididae						
	Turtle: "Chelonia"	4	17	15.0	16.9	16.2 ± 0.6	
	Ornithischia	3	14	15.5	17.4	16.5 ± 0.6	
V794 (WS13) depth: 15 m	Hadrosauridae	3	21	14.0	17.5	16.6 ± 0.9	
	Mammalia	10	12	13.8	17.4	16.3 ± 0.9	
	Ganoid scale	5	7	15.1	17.3	15.8 ± 0.7	
	Pointed teeth	10	10	14.6	18.0	15.8 ± 0.9	
	Rounded teeth	10	11	12.3	16.7	15.0 ± 1.2	
	Crocodylia:	5	21	14.4	18.3	16.3 ± 1.0	
	Goniopholididae						
	Turtle: <i>Naomichelys</i> sp.	10	10	14.9	17.1	16.0 ± 0.7	
	Ornithischia	1	10	14.8	16.1	15.5 ± 0.8	
	Hadrosauridae	2	9	15.2	17.4	16.2 ± 0.9	
	Theropoda	4	11	16.4	19.8	18.3 ± 1.0	
V235 (WS4) depth: 15 m	Mammalia:	11	12	14.8	17.5	16.4 ± 0.9	
	Multituberculata						
	Ganoid scales	9	9	14.6	17.1	15.9 ± 0.7	
	<i>Lepidotes</i> sp. teeth	7	8	15.0	16.6	15.8 ± 0.6	
	Rounded teeth	5	6	15.1	16.8	15.9 ± 0.8	
	Crocodylia scutes	4	12	15.1	16.6	15.8 ± 0.5	
	Crocodylia teeth:	14	15	15.8	18.7	17.0 ± 1.0	
	Goniopholididae + Atoposauridae						
	Hadrosauridae	3	9	15.2	17.9	16.6 ± 1.0	
	Theropoda	10	10	15.4	18.5	17.0 ± 1.1	
	V694 (WS9) depth: 15 m	Mammalia:	14	14	14.4	17.6	16.5 ± 0.8
Tribosphenida + Multituberculata							
Ganoid scales		10	10	14.9	16.5	15.7 ± 0.6	
Pointed teeth		10	10	14.8	17.9	16.4 ± 1.1	
rounded teeth		10	12	12.5	16.2	14.4 ± 1.3	
Crocodylia:		11	12	14.9	17.6	16.1 ± 0.8	
Goniopholididae + Atoposauridae							
Mammalia		10	10	15.8	17.7	16.7 ± 0.8	
V240 (SC2) depth: 16 m		Ganoid scales	10	11	16.0	18.8	17.2 ± 0.7
		Pointed teeth	10	11	14.6	21.0	17.2 ± 2.2
		Rounded teeth	10	12	13.3	19.7	15.4 ± 2.1
	Crocodylia: <i>Bernissartia</i> + Goniopholididae + Atoposauridae	13	14	15.5	19.5	17.5 ± 1.3	
	Turtle: "Chelonia"	1	9	15.5	17.2	15.4 ± 1.6	
	Hadrosauridae	3	6	14.5	17.1	16.1 ± 0.9	
	Theropoda	10	12	15.3	18.2	16.5 ± 0.9	
V695 (WS10) depth: 19 m	Ganoid scales	10	10	15.5	16.9	16.2 ± 0.5	
	Pointed teeth	10	10	15.0	18.6	16.5 ± 1.0	
	Rounded teeth	7	7	12.5	17.1	15.4 ± 1.5	
	Crocodylia scute	8	12	13.5	16.9	15.5 ± 0.8	
	Turtle: <i>Glytrops</i> sp. + <i>Trionychidae</i> + <i>Naomichelys</i> sp.	7	20	14.5	16.4	15.7 ± 0.6	
	Ornithischia	11	11	15.4	18.4	17.3 ± 0.9	
	Mammalia			14.8	18.0	16.3 ± 1.2	

The water compositions derived from turtles were then used to calculate the ambient temperature during enamel (teeth) and ganoine (scales) precipitation for fish remains using the Longinelli and Nuti (1973) and Kolodny et al. (1983) equation relating

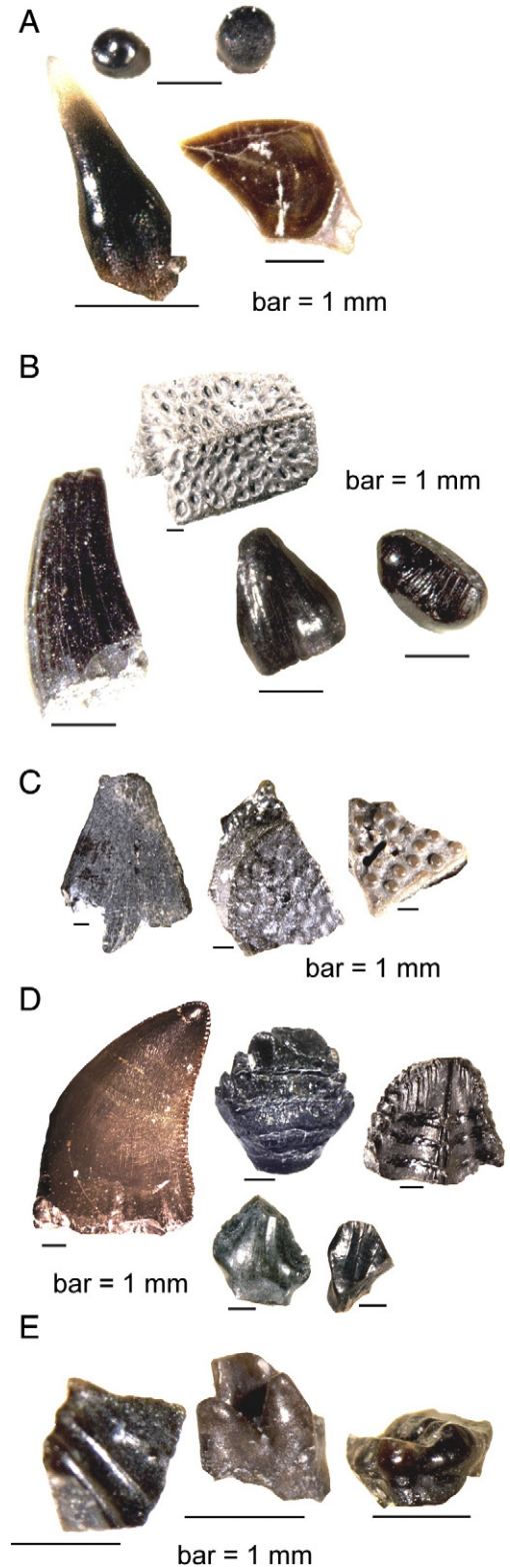


Fig. 3. Examples of tooth, scale, and osteoderm specimens sampled. (A) Representative fish remains. *Lepidotes* (top left), "rounded" teeth (top right), "Pointed" teeth (bottom left), and ganoid scales (bottom right). (B) Representative crocodile remains: from left to right, Goniopholididae, Atoposauridae, *Bernissartia* sp. and an osteoderm or scute (top). (C) Representative turtle shell fragments from left to right: Trionychidae, *Glytrops* sp., and *Naomichelys* sp. (D) Representative dinosaur teeth: dromaeosaurid theropod (top left), polacanthine nodosaur (top center), *Eolambia caroljonesa* (top right), and two types of unidentified basal ornithopod teeth (bottom). (E) Representative mammalian teeth: two morphologic types of specimens broadly identified as mammalian teeth and Multituberculata (far right). Scale bars = 1 mm.

temperature, isotopic composition of water, and isotopic composition of phosphate:

$$T(^{\circ}\text{C}) = 111.37 - 4.3(\delta^{18}\text{O}_p - \delta^{18}\text{O}_w). \quad (3)$$

In the case of terrestrial taxa, water is sourced by a combination of rivers, local precipitation, and food. The $\delta^{18}\text{O}$ of phosphate ($\delta^{18}\text{O}_p$) of herbivorous taxa is influenced not only by the $\delta^{18}\text{O}$ of their drinking water ($\delta^{18}\text{O}_w$), but also by processes that influence the isotopic composition of their ingested plant water. Water in plant leaves tends to be ^{18}O -enriched over local meteoric water as evaporation occurs in the leaves (Ehleringer and Dawson, 1992). The lower the humidity, the more ^{18}O -enrichment occurs in leaf water. Therefore, herbivorous taxa will tend to produce phosphate having $\delta^{18}\text{O}$ values higher than those of carnivorous taxa (Kohn, 1996). The relationship between humidity, $\delta^{18}\text{O}_p$ and $\delta^{18}\text{O}_w$ also allows for estimations of relative humidity by using equations for rodents derived by Kohn (1996). Because bone and tooth $\delta^{18}\text{O}$ of Mesozoic archosaurs (e.g., dinosaurs) is primarily controlled by their ingested water and atmospheric oxygen isotopic composition (both O_2 and water vapor oxygen) (Fricke et al., 2008), and because they precipitated their bone/teeth at a constant or at least a restricted temperature range of $\sim 37^{\circ}\text{C}$ (Barrick and Showers, 1994, 1995; Barrick et al., 1996; Fricke and Rogers, 2000; Amiot et al., 2006), the $\delta^{18}\text{O}$ of herbivorous dinosaur tooth enamel can be used to calculate ingested water. This is crucial for comparison to other meteoric water proxies, such as turtles, crocodiles, and pedogenic calcite.

Mammalian and multituberculate ingested water was calculated assuming a body temperature of 38°C using equation 20 for omnivorous rodents from Kohn (1996):

$$\delta^{18}\text{O}_w = 1.56\delta^{18}\text{O}_p - 35.47 + 6.09h \quad (4)$$

where h = relative humidity.

Herbivorous dinosaur-ingested water was estimated using biological parameters for herbivorous birds as presented by Kohn (1996). The Kohn (1996) bird equation was modified to account for a sustained body temperature of 37°C as suggested by Amiot et al. (2006). Because there currently is not a well constrained carnivorous bird equation relating $\delta^{18}\text{O}_p - \delta^{18}\text{O}_w$ theropod ingested water was not calculated. The following equation is then used to calculate the $\delta^{18}\text{O}$ value of herbivorous dinosaur ingested water:

$$\delta^{18}\text{O}_w = 1.41\delta^{18}\text{O}_p + 12.11h - 41.59. \quad (5)$$

Suarez (2009), in modeling water $\delta^{18}\text{O}$ -paleo-latitude gradients as calculated from 2°S – 75°N using Albian pedogenic carbonates, modeled a humidity of $\sim 47\%$ using a zonal mean annual temperature (MAT) estimated from leaf physiognomy for the CMF paleo-latitude at 34°N . Thus, h is estimated as 0.47 for all equations. MAT is 23°C for CMF paleo-latitude (~ 34 – 35°N) based on leaf physiognomy data of Wolfe and Upchurch (1987) and Spicer and Corfield (1992). This MAT was used to calculate the isotopic composition of meteoric water from carbonates.

Some modern continental taxa are water dependent and spend most of their time in water (e.g. hippopotamus) and are considered to be insensitive to evaporative conditions; i.e., their isotopic composition is not greatly affected by humidity changes (Levin et al., 2006). Conversely, the isotopic composition of taxa that are drought tolerant (e.g., Dikdik and Grant's Gazelle) is considered to be evaporation sensitive because they get their water from evaporatively-influenced sources such as plants and evaporative pools, and are thereby strongly influenced by evaporative conditions. Levin et al. (2006) used co-existing terrestrial taxa $\delta^{18}\text{O}_{\text{enamel}}$ to calculate the isotopic enrichment (ϵ) between taxa to determine evaporative sensitivity. The ϵ ($\epsilon_{\text{ES-EI}}$)

values between evaporative sensitive and insensitive taxa should be high, while ϵ ($\epsilon_{\text{EI-EI}}$) between two evaporative insensitive taxa or ϵ ($\epsilon_{\text{ES-ES}}$) between two similar evaporative sensitive taxa should be low from site to site. Therefore, one can test the evaporative sensitivity of two particular taxa. If, for example, two taxa are suspected of being evaporative insensitive, then the ϵ calculated between the two should be low from site to site. The maximum enrichment should be observed between the most evaporative insensitive and evaporative sensitive taxa, and ϵ is correlated to the degree of aridity (water deficit). Epsilon (ϵ) was calculated between taxa using the Levin et al. (2006) equation:

$$\epsilon = \left(\frac{0.001 \delta^{18}\text{O}_{p1} - 1}{0.001 \delta^{18}\text{O}_{p2} - 1} \right) * 1000 \quad (6)$$

where $\delta^{18}\text{O}_{p1}$ represents the average phosphate isotopic composition of one taxon and $\delta^{18}\text{O}_{p2}$ represents the average composition of the other taxon. Although the correlation between aridity index and epsilon was generated using mammals that precipitate their teeth at approximately the same temperature, it can generally be applied to Cretaceous archosaurs. It is recognized that the difference in enamel precipitation temperature can affect the ϵ values that are calculated; however, if temperature is the dominant cause of changes in ϵ from site to site, the ϵ value will be the same for each site. This is not the case. Also, the goal of the ϵ calculations were to determine relative changes in aridity over the course of Mussentuchit deposition, not as a means to get precise water deficit values as is done by generating an aridity index number in Levin et al. (2006). Levin et al. (2006) suggest calculations of ϵ represent the enrichment between leaf or body water and meteoric water since $\delta^{18}\text{O}_{\text{enamel}}$ of evaporative sensitive taxa represents leaf water, while the $\delta^{18}\text{O}_{\text{enamel}}$ of evaporative insensitive taxa represents meteoric water. Since turtles and crocodiles generally record meteoric water (Barrick et al., 1999; Amiot et al., 2006) turtles and crocodiles should be considered as evaporative insensitive taxa. This is further tested by measuring pedogenic carbonate (also known to represent meteoric water) from the Mussentuchit. Another way to test evaporation sensitivity is to calculate epsilon between two suspected insensitive taxa ($\epsilon_{\text{EI-EI}}$) and epsilon between two suspected sensitive taxa ($\epsilon_{\text{ES-ES}}$) from site to site. As suggested by Levin et al. (2006) the $\epsilon_{\text{EI-EI}}$ or $\epsilon_{\text{ES-ES}}$ from site to site with differing water deficit should not significantly change. As such, $\epsilon_{\text{turtle-crocodile}}$ and $\epsilon_{\text{herbivores-carnivores}}$ were calculated. Other requirements suggested by Levin et al. (2006) such as sample number and comparison of samples from the same time interval are also met.

4. Results

Results of individual analyses can be found in Supplementary data Table 1. A summary of these data (average and standard deviations per taxa per site) are presented in Table 1 and graphically in Fig. 4. Of the material from aquatic taxa, rounded teeth have the lowest $\delta^{18}\text{O}_p$ (average of $15.0 \pm 1.6\%$) and range from a minimum of 13.8% at V239 (-4 m) to a maximum of 15.8% at V235 (-15 m) (Table 1, Fig. 4). Pointed teeth and ganoid scales tend to be very similar in isotopic composition. Scales average $16.2 \pm 0.8\%$ and range from a minimum individual measurement of 15.7% at V794 and V694 (both at -15 m) to a maximum of 17.2% at V695 (-19 m). Pointed teeth average $16.4 \pm 1.4\%$ and range from a minimum individual measurement of 14.5% at V794 (15 m) to a maximum of 20.6% at V240 (16 m).

Of the two semi-aquatic taxa (turtles and crocodiles), turtles consistently have the lowest isotopic compositions and range between 15.4% at V239 (-4 m) to 16.6% at V240 (-16 m) and have an average composition of $16.0 \pm 0.7\%$. Crocodiles range from a minimum of 16.1% at site V694 (-15 m) to a maximum of 17.5% at site V240 (-16 m) with an average composition of $16.6 \pm 1.0\%$.

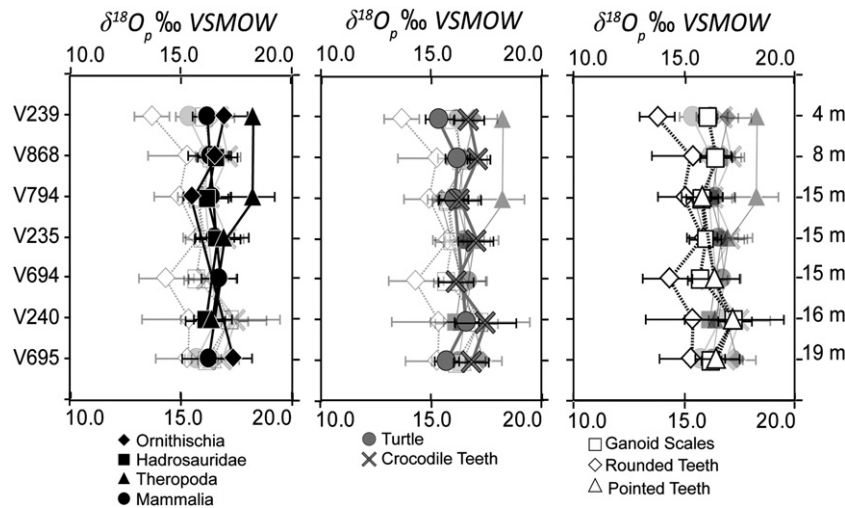


Fig. 4. Average oxygen isotopic compositions of phosphate relative to V-SMOW ‰ per site for each taxa sampled. Sites are positioned in relative stratigraphic order. Sites V794, V235, and V694 are at the approximate same stratigraphic level. (A) Terrestrial taxa overlain on semi-aquatic and aquatic taxa data, (B) semi-aquatic taxa overlain on terrestrial and aquatic taxa data, and (C) aquatic taxa (fish remain morphotypes) overlain on terrestrial and semi-aquatic taxa data. Error bars represent one standard deviation. Black symbols = terrestrial; dark gray symbols = semi-aquatic taxa, white symbols = aquatic taxa. Axis on the far right indicates meters below the Dakota Formation.

As site V695 lacks crocodile teeth, crocodylian tooth $\delta^{18}\text{O}$ was estimated based on the observation that for coexisting teeth and scutes at site V235, scutes tend to be on average 1.3‰ lower than teeth. This phenomenon has been also documented in Jurassic crocodylians from Western Europe (Billon-Bruyat et al., 2005) and in living crocodylians from the Oubangui River, Central Africa (Lécuyer et al., 2003). Therefore, the isotopic composition of teeth at V695 can be estimated as $\sim 16.8\%$.

Mammal enamel does not significantly vary from site to site (see Supplementary data, Table 2) but there is a slight trend towards lower $\delta^{18}\text{O}$ values from site V694 (-15 m) to the top of the MM at site V239 (Fig. 4). Mammal isotopic compositions range from a minimum of 16.3‰ at site V695 (-19 m) to a maximum value of 16.7‰ at V694 (-15 m). Their average composition is $16.4 \pm 0.9\%$.

Theropods tend to have the isotopically heaviest enamel of all the sampled dinosaurs. They average $17.5 \pm 1.4\%$ and range between a minimum of 16.5‰ at site V240 to a maximum value of 18.3‰ at both sites V239 (-4 m) and V793 (-15 m). Ornithischian enamel averages $16.6 \pm 1.0\%$ and range from 15.5‰ at site V794 (-15 m) to 17.3‰ at site V695 (-19 m). Hadrosaurs range from 16.1‰ at site V240 (-16 m) to 16.6‰ at both sites V868 (-8 m) and V235 (-15 m) with an average composition of $16.5 \pm 0.9\%$ (Table 1, Fig. 4).

The $\delta^{18}\text{O}$ value of pedogenic carbonate is converted from values relative to V-PDB to V-SMOW for comparison to phosphate data. The average pedogenic carbonate value is $23.3 \pm 1.9\%$, and ranges from 19.9‰ for the carbonate cemented sandstone at 15 m below the Dakota Formation to a maximum of 24.3‰ at 6 m below the Dakota. All values are found in Table 2.

Water $\delta^{18}\text{O}$ values (relative to V-SMOW) calculated from turtle $\delta^{18}\text{O}_p$ average $-6.2 \pm 0.7\%$ and range from -6.7% at site V239 to -5.5% at site V240 (Table 3). Water $\delta^{18}\text{O}$ values (relative to

V-SMOW) calculated from crocodiles average $-6.0 \pm 0.8\%$, with a minimum of -6.6% at site V694 and a maximum at of -5.4% at site V240. Calculated mammal-ingested water averages $-7.0 \pm 1.4\%$ and ranges from a minimum of -7.3% at site V239 to a maximum of -6.5% at site V694. All of the herbivorous dinosaur taxa yield water values that are extremely light in isotopic composition. Ornithischian ingested water averages $-12.5 \pm 1.4\%$ and ranges from a minimum of -14.1% at site V794 to a maximum of -11.5% at site V695. Hadrosauridae ingested water averages $-12.7 \pm 1.3\%$ and ranges from a minimum of -13.2% at site V240 to a maximum of -12.4% at site V868 (Table 3, Fig. 5). Water $\delta^{18}\text{O}$ values estimated from carbonate range from -9.1% for the sandstone at 15 m below the Dakota Sandstone to -4.9% at 6 m below the Dakota (Table 4). The average oxygen isotopic composition of water that precipitated micritic calcite from MM is $-5.8 \pm 1.8\%$.

The temperatures calculated from rounded teeth, using the water composition calculated from turtles, range from a minimum of 16.6 °C at V235 to a maximum of 23.5 °C at V239 and average $20.3 \pm 2.5\text{ °C}$ (Table 5). Since ganoid scales and pointed teeth were not significantly different from each other at each site, ganoid scales were used for calculations of temperature since they were present at each site. Temperature calculated from ganoid scales are much lower than rounded teeth, and range from 13.6 °C at V240 to a maximum of 17.6 °C at V694 and average $15.5 \pm 1.7\text{ °C}$.

5. Discussion

5.1. Preservation of biologic records

Kolodny et al. (1996) outlined criteria for the selection of vertebrate fossil material for isotopic study of paleoecosystems. First, they suggested that the more diagenetically resistant biominerals, enamel and ganoine, rather than bone or dentine be used. In this study, with the exception of turtle shell, only enamel and ganoine are used. Second, they suggested that if using bone, only materials with micron-scale preservation be used. Although bone is not used, intermediate scale structures such as growth banding in tooth enamel and in ganoine scales are preserved in most samples. The separation of $\delta^{18}\text{O}$ values of vertebrate remains along physiological lines (e.g. aquatic versus terrestrial taxa) has also been used to indicate preservation of original biogenic signals (Lécuyer et al., 2003; Fricke et al., 2008; Amiot et al., 2009). For example, Lécuyer et al. (2003) analyze a wide diversity of Late Cretaceous taxa from the Laño locality of

Table 2
Oxygen isotopic composition of micritic calcite relative to V-SMOW.

Depth (m)	Sedimentology	$\delta^{18}\text{O}_c\%$ – VSMOW
4	Nodule	23.9
6	Mudstone	24.2
6	Mudstone	24.3
15	Sandstone	19.9
26	mudstone	24.2

Table 3
Calculated oxygen isotopic composition of water (‰V-SMOW) from phosphate.

Site	Depth (m)	Turtle	Crocodile	Mammalia	Ornithischia	Hadrosauridae
		$\delta^{18}O_w = 1.01 * \delta^{18}O_p - 22.3$ (Barrick et al., 1999)	$\delta^{18}O_w = 0.82 * \delta^{18}O_p - 19.93$ (Amiot et al., 2007)	$\delta^{18}O_w = 1.6 * \delta^{18}O_p - 35.5 + 6.1 h$ (Kohn, 1996)	$\delta^{18}O_w = 1.41 \delta^{18}O_p + 12.11 h$ –41.59 (modified, Kohn, 1996)	
V239	4	–6.7 ± 0.7	–6.1 ± 0.6	–7.3 ± 1.1	–12.0 ± 1.5	
V868	8	–5.9 ± 0.5	–5.7 ± 0.4	–7.1 ± 1.5	–12.6 ± 0.9	–12.4 ± 1.3
V794	15	–6.1 ± 0.7	–6.4 ± 0.8	–7.0 ± 1.4	–14.1 ± 0.6	–13.0 ± 1.2
V235	15		–5.8 ± 0.7	–6.8 ± 1.3		–12.5 ± 1.5
V694	15		–6.6 ± 0.6	–6.5 ± 1.2		
V240	16	–5.5 ± 0.6	–5.4 ± 1.2			–13.2 ± 1.4
V695	19	–6.4 ± 0.6	–6.1 ± 0.7	–7.2 ± 1.9	–11.5 ± 1.2	

$h = 0.47$.

Northern of Spain and report $\delta^{18}O_p$ values for crocodile teeth (19.2‰), an *Iguanodon* tooth (19.3‰), *Ankylosaurus* tooth (19.3‰), fish scale (19.7‰), turtle shell (19.5‰), alligator teeth (19.5‰), *Titanosaurus* tooth (19.4‰), theropod tooth (19.1‰), shark tooth (19.4‰) and ray tooth (18.7) with no more than 1.0‰ difference between taxa, suggesting poor preservation of original biogenic information. Since differences in isotopic composition between taxa of different physiologies of MM taxa (e.g. rounded teeth (13.8‰) versus theropod teeth (18.3‰)) are observed in this data set (see statistical results in Supplementary data Tables 2 and 3), it is suggested that the MM vertebrates do preserve original biogenic isotopic signals.

5.2. Paleocological interpretation and implications

Based on the calculated $\delta^{18}O_w$ for the MM vertebrates and carbonates, reasonable interpretations on the past habitats of the different taxa can be made. Water $\delta^{18}O$ values calculated from pedogenic carbonate $\delta^{18}O$ for the entire member average -5.8 ± 1.8 ‰ and represent soil water. Pedogenic calcite forms under precipitation deficit (Breecker et al., 2009) and therefore its composition is that of precipitation slightly influenced by evaporation. Given that water calculated from aquatic turtles is -6.2 ± 0.7 ‰ and crocodiles is -6.0 ± 0.8 ‰ their compositions also represent local meteoric water but represent a short time-scale average for meteoric water while pedogenic calcite represents slightly ^{18}O -enriched meteoric water

on long-term time scales. As turtles tend to grow their shells in the summer months (Barrick et al., 1999; Pough et al., 2002) it is likely that the calculated $\delta^{18}O_w$ is biased toward summer water composition. It cannot be ascertained if turtles inhabited locally recharged streams and rivers or were simply recording base flow composition of regional rivers.

Crocodiles yield water $\delta^{18}O$ values that were similar to water $\delta^{18}O$ values calculated from turtles (-6.0 ± 0.8 ‰ avg.) and slightly lower than water $\delta^{18}O$ calculated from pedogenic calcite. Though the Cretaceous crocodiles (mesosuchians) are extinct taxa, their habitat was probably very similar to that of extant crocodiles (eusuchians). Modern crocodiles spend much of their time as sit-and-wait predators in shallow water near the shore of rivers, lakes, and ponds (Marwick, 1998b; Pough, et al., 2002) influenced by a combination of meteoric water and water draining from highlands. Thus, Cretaceous crocodile data agree with the interpreted habitat of modern crocodiles. Based on the similarity in calculated living/ingested water, crocodiles (Amiot et al., 2007) inhabited similar bodies of water to turtles.

The average $\delta^{18}O_w$ value calculated from the mesosuchian *Bernissartia* is -6.2 ± 1.1 ‰ at V240. This is slightly lower than $\delta^{18}O_w$ calculated from co-existing Atoposauridae (-5.3 ± 0.8 ‰) and Goniopholididae (-5.1 ± 1.1 ‰) suggesting *Bernissartia* spent more time in slightly ^{18}O -depleted water than Atoposauridae and Goniopholididae. The durophagous dentition of *Bernissartia* sp. indicates they likely spent more time in the water grazing the river and stream bottoms for clams, and thus would not be subject to evaporative effects to the same extent as co-existing crocodiles. This is consistent with the interpretation that *Bernissartia* was a small freshwater crocodile and Atoposauridae and Goniopholididae were terrestrial mesosuchians. The $\delta^{18}O_p$ of crocodiles from this site has captured slight differences in habitat preference (Buffetaut and Ford, 1979; Mazin et al., 2006).

A relative humidity of 47%, estimated by Suarez (2009) for the CMF paleolatitude (34°N), was used to estimate water ingested by the micro-mammals. Their drinking water $\delta^{18}O$ value (-7.0 ± 1.4 ‰) was relatively lower than the one ingested by crocodiles and turtles. Modern small mammals show a wide variety of drinking habits that is highly dependent on their habitat (Chew, 1951; McManus, 1974; Smith et al., 2002; Hamilton, 2009). Small mammals from humid or riparian areas tend to get their drinking water from

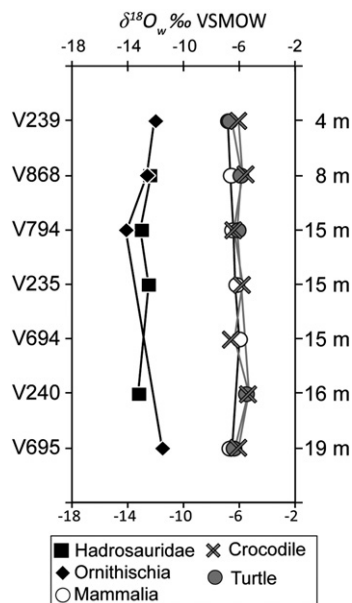


Fig. 5. Average calculated ingested water composition from Table 3. Humidity is held constant at 47% throughout the section and dinosaur body temperature is assumed to be 37 °C (Amiot et al., 2006).

Table 4
Calculated oxygen isotopic composition of water from micritic calcite.

Depth (m)	T (K)	$10^3 \ln \alpha$	α	Sedimentology	$\delta^{18}O_w$
	295.82	$10^3 \ln \alpha = 2.78$ $(10^6/T^2) - 2.89$			$\delta^{18}O_w = ((\delta^{18}O_c + 10^3)/\alpha) - 10^3$
4		28.878	1.0293	Nodule	–5.3
6				Mudstone	–4.9
6				Mudstone	–4.9
15				Sandstone	–9.1
26				Mudstone	–5.0

Table 5

Calculated temperatures of fish scale and tooth formation.

Site ^a	Depth (m)	Ganoid scales	Pointed teeth	Rounded teeth
		$t^{\circ}\text{C} = 111.4 - 4.38 * (\delta^{18}\text{O}_p - \delta^{18}\text{O}_w)$ (Kolodny et al., 1983)		
V239	4	14.0 ± 1.5		23.5 ± 3.4
V868	8	15.5 ± 3.1		20.0 ± 7.6
V794	15	17.5 ± 3.1	17.1 ± 4.0	20.5 ± 5.1
V235	15	16.6 ± 3.1 ^a		16.6 ± 3.5 ^a
V694	15	17.7 ± 2.6 ^a	14.9 ± 4.6 ^a	23.3 ± 5.4 ^a
V240	16	13.6 ± 3.2	13.6 ± 9.7	21.4 ± 9.2
V695	19	14.4 ± 2.4	13.0 ± 4.3	17.5 ± 6.5

^a No turtles preserved at V235 or V694; used V794 turtles.

surface water such as streams and lakes (Chew, 1951; Tütken et al., 2006; Hamilton, 2009) whereas small mammals that inhabit dry climates can get almost all of their water from their diet (McManus, 1974; Huertas et al., 1995). Mammals from both habitats do get some portion of water from rain and dew, though the proportions are dependent on rainfall amounts, temperature, and relative humidity (Chew, 1951). Based on the types of MM vertebrate fauna preserved (including frogs and lizards) and sedimentologic evidence (rare carbonate formation) humidity was likely higher than 47%. Calculations (using 47% humidity) suggest that the micro-mammals in the MM ingested water that was more ¹⁸O-depleted than water ingested by turtles or crocodiles and was from isotopically ¹⁸O-depleted river water or dew. Their water was not solely from food water (Smith et al., 2002; Tütken et al., 2006; Hamilton, 2009) as this would result in relative ¹⁸O-enrichment over local meteoric water.

Calculated ingested water $\delta^{18}\text{O}_w$ for herbivorous dinosaurian taxa is isotopically much lighter than the $\delta^{18}\text{O}_w$ calculated from the aquatic/semi-aquatic taxa (as low as -15.2%). This depletion (at least for the dinosaurs) is perplexing at first considering modern terrestrial taxa should be enriched relative to river water due to evaporative enrichment of body water and of their diet (Kohn, 1996; Fricke, 2007). The calculated ingested water values depend significantly on the humidity used in the calculation (Eqs. (2) and (3)). High humidity should result in lower $\delta^{18}\text{O}$ of body water and of the precipitated phosphate (Kohn, 1996). Therefore, if the CMF humidity of 47% is used, the calculated ingested water could result in an under estimation of dinosaurian ingested water than those of the aquatic and semi-aquatic taxa. As suggested by the sedimentology and fauna preserved in the MM, it is likely that humidity was higher during MM time relative to older units of the CMF. Since small mammals and rodents tend to be greatly affected by humidity (Huertas et al., 1995; Kohn, 1996) the isotopic compositions of MM mammal teeth are used to constrain humidity, in attempts to get a new estimate of relative humidity related solely to the MM. Rather than calculating mammal drinking water from their isotopic composition of phosphate, the equation for omnivorous rodents presented by Kohn (1996) is used (Table 6) to solve for humidity using water calculated from the potential drinking water reservoirs (calculated from semi-aquatic taxa). Isotope values calculated from crocodile and turtle phosphate were used to calculate humidity over the course of the MM (average humidity $\sim 58\%$). Depending on which water source is used, the average humidity is as low as $\sim 42\%$ (using crocodile-ingested water at V694) to as high as $\sim 76\%$ (using turtle ingested water at site V235). Using new relative humidity calculated per site, the calculated isotopic composition of ingested water ranges from -9.2% for hadrosauridae at V235 when using turtle ingested water to calculate humidity to -13.5% for ornithischians at V7945 when using crocodile ingested water to calculate humidity (Table 6, Fig. 6). These values are still more negative than those of the calculated water from aquatic taxa. This suggests that dinosaurs ingested water that was greatly composed of isotopically depleted river water, and that the high relative humidity resulted in less evaporative enrichment of body water. As it has been suggested that dinosaurs were

Table 6Effects of calculated humidity on isotopic composition of dinosaur-ingested water ($\%$ V-SMOW).

Site	h^a (turtle)	Ornithischia (%)	Hadrosauridae (%)	h^b (croc.)	Ornithischia (%)	Hadrosauridae (%)
V239	0.50	-11.9		0.63	-10.3	
V868	0.64	-10.7	-10.6	0.67	-10.3	-10.2
V794	0.58	-12.9	-11.9	0.53	-13.5	-12.5
V235	0.76		-9.2	0.60		-11.1
V694	0.47			0.42		
V240						
V695	0.56	-10.6		0.61	-10.0	
Avg.	0.59			0.58		

^a h (turtle) = $0.16 * \delta^{18}\text{O}_{w\text{-turtle}} - 0.26 * \delta^{18}\text{O}_{p\text{-mammalia}} + 5.82$.^b h (croc) = $0.16 * \delta^{18}\text{O}_{w\text{-croc}} - 0.26 * \delta^{18}\text{O}_{p\text{-mammalia}} + 5.82$.

endotherms (Amiot et al., 2006), then their apatite synthesis was not limited to the narrow summer window which reptiles and other ectothermic aquatic taxa are constrained to. Dinosaurs probably drank water year round so they are most likely to record seasonal fluctuations in river water $\delta^{18}\text{O}$ values, such as the ¹⁸O-depleted melt-water during the late spring to early summer as well as the ¹⁸O-enriched water during the summer (Fan and Dettman, 2009). Snow-melt derived water $\delta^{18}\text{O}$ values for the higher latitude, Aptian–Albian Kootenai Formation, Montana, USA has been calculated using bivalve shells to be as negative as -16.13% (Glancy et al., 1993). Similar, though perhaps not as negative values should be expected to feed large rivers depositing the CMF units. A modern analog at a latitude that has a MAT of 23°C (as is predicted for the Cedar Mountain Formation at 34°N paleo-latitude) are the Mexican Sierra Madre Mountains. Isotopic composition of precipitation in the Sierra Madres ranges between -10.9% at elevations greater than 3 km (Cortés et al., 1997) and -6.5% for springs that drain low-elevation precipitation (Johannesson et al., 2004). Thus the greater range with a lower average isotopic composition recorded by dinosaurs relative to the aquatic taxa indicates that dinosaurs are better recorders of regional water values.

The inferred habitats of the fish remains are difficult to interpret because of the lack of identification of isolated fish remains. It is

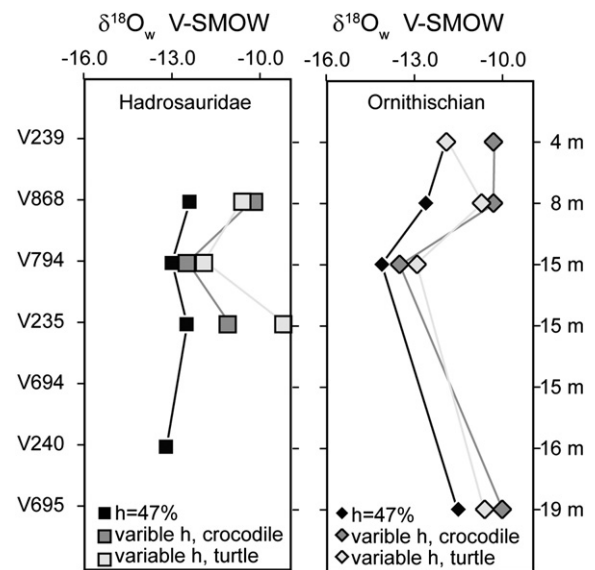


Fig. 6. Re-calculated ingested water for dinosaurs using variable humidity. Humidity is calculated by solving for humidity in the mammal equation (Eq. (4)) and using water calculated from turtles and crocodiles (see also Table 6). Note the large increase in $\delta^{18}\text{O}_w$ of dinosaurs using variable humidity at site V868, 8 m below the Dakota Sandstone.

impossible to know with certainty if the scales came from the same taxon as the teeth without a body fossil. However, the similarity in isotopic composition between the ganoid scales and pointed teeth suggests they may have come from the same taxon. Conversely, rounded teeth and the few identified *Lepidotes* teeth have a lower isotopic composition than ganoid scales and pointed teeth (as much as 2.2‰ and on average 1.1‰). This suggests that either the rounded teeth are from a different fish than the fish with ganoid scales and pointed teeth and the two have different habitats (and therefore lived in water with different isotopic compositions) or the fish contained all of the morphological types of fish remains but precipitated their phosphate at different temperatures.

The temperature of precipitation for the fish remains is calculated using Eq. (3), to determine if they are consistent with suggested MAT for this time period and paleolatitude. *Lepidotes* and rounded teeth return paleotemperatures (20.3 ± 2.5 °C) that are consistent with Suarez (2009). Ganoid scales (and pointed teeth) however, are more enriched than rounded teeth and therefore calculated temperatures are much lower ($\sim 15.5 \pm 1.7$ °C) than for rounded teeth by 4.8 °C. Domingo et al. (2009) showed that phosphate from scales along the body of a lepisosteid did precipitate at different temperatures (as much as 4.6 °C). In their data set, the average of anterior scales is 1.1‰ greater than dorsal scales. For the MM data, the maximum difference between ganoid scales and rounded teeth is 2.2‰ at V239 and a minimum of 0.1‰ at V235, with the average difference of 1.1‰. Without a body fossil to confirm that all fish remains, pointed teeth, rounded teeth, and ganoid scales came from the same taxon it is impossible to be certain that MM fish precipitate their remains at different temperatures or if they came from different fish that precipitated their remains in different isotopic composition waters (e.g. brackish water versus freshwater). Due to these uncertainties, besides confirming that the MM fish were primarily freshwater fish, few conclusions can be made from the fish data.

5.3. Evaporative sensitivity

Based on habitats of the reptiles the semi-aquatic taxa (turtles and crocodiles) are defined as evaporative insensitive taxa and the terrestrial taxa (dinosaurs) as evaporative sensitive. The low range in $\epsilon_{\text{crocodile-turtle}}$ indicates that crocodiles and turtles exhibit the same sensitivity (or lack thereof) to evaporative conditions (Fig. 7A). Likewise, the low range in $\epsilon_{\text{average herbivorous dinosaur-theropod}}$ indicates similar sensitivity to evaporative conditions for the dinosaurs (Fig. 7B). Therefore, crocodiles and turtles are defined as “evaporative insensitive” and the dinosaurs are defined as “evaporative sensitive”.

The stratigraphic changes in ϵ values between evaporative sensitive and insensitive taxa are used to infer changes in moisture and the causes of these changes (Fig. 8). Overall trends include a decrease in ϵ from site V695 to V240, followed by a significant increase in ϵ from site V240 to V235 and an increase in ϵ between sites V794 to V239 with the exception of $\epsilon_{\text{theropod-crocodile}}$. These increases in ϵ are interpreted as being caused by a combination of humidity changes and composition of water reservoirs (input of orographically depleted water drained to rivers) and are discussed below.

5.4. Climatic interpretation and implications

Based on the isotopic composition of the various taxa and the calculated ϵ , climatic changes are interpreted through the MM. As it is unlikely that the paleo-westerlies delivered significant amounts of moisture to the leeward side of the Sevier Mountains, it follows that moisture was mostly derived from air masses from the WIS. The proximity of the WIS also resulted in the relatively high humidity ($\sim 58\%$) estimated over the course of the MM as calculated from the micro-mammals. Contributions of the Sevier Mountain melt waters are only detected in the isotopically light values of river water recorded by dinosaurs.

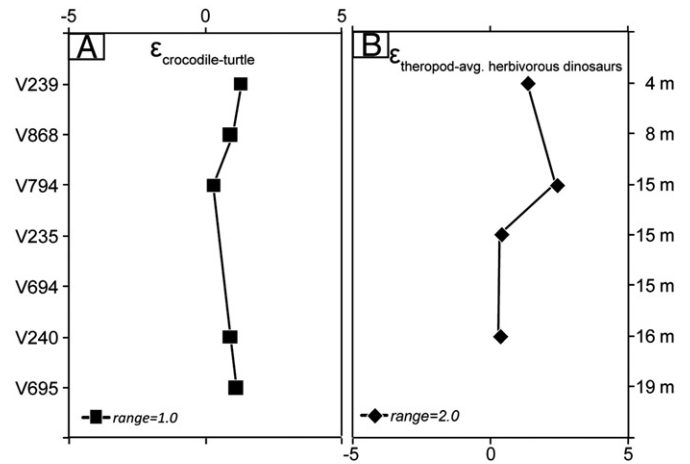


Fig. 7. Calculated epsilon (ϵ) values between taxa. (A) Evaporative insensitive taxa. (B) Evaporative sensitive taxa. Ranges are low when compared to $\epsilon_{\text{ES-EI}}$ in Fig. 8. Low range in epsilon between sites confirms evaporative insensitive and evaporative sensitive taxa since changes in aridity will affect all evaporative sensitive and evaporative insensitive taxa similarly.

Oxygen isotopic compositions of semi-aquatic taxa (and their calculated body water $\delta^{18}\text{O}$ value) increase from site V695 (–19 m) to site V240 (–16 m) and herbivorous taxa show a decrease in their $\delta^{18}\text{O}_p$. This results in the significant decrease in ϵ between average herbivores and evaporation insensitive taxa (Fig. 8) from V695 to V240 and is interpreted as an increase in humidity. Since only 3 mammal teeth were analyzed for V240, there are not enough data to be confident in the $\delta^{18}\text{O}_p$ of mammals for this site. However, if these few values are used, the average value (15.2‰), obtains an extremely high humidity ($>90\%$). While this value is most likely too high and an artifact of the small sample size, it does indicate that conditions during deposition at V240 were very humid.

This increase in humidity is attributed to the incursion of the WIS, possibly the sequence 3.1 transgression of Oboh-Ikuenobe et al. (2008) (Figs. 9A, B, 10). The proximity of the sea would have delivered sufficient humidity to allow for relatively low values of $\delta^{18}\text{O}_p$ of terrestrial taxa and abundant precipitation that was isotopically heavy (as recorded by semi-aquatic taxa).

There is a dramatic decrease in relative humidity at site V694 ($\sim 53\%$). Unfortunately, no dinosaur taxa were available for V694, to confirm arid conditions. There is, however, a decrease in the $\delta^{18}\text{O}_w$ calculated from the semi-aquatic taxa. This change suggests a retreat

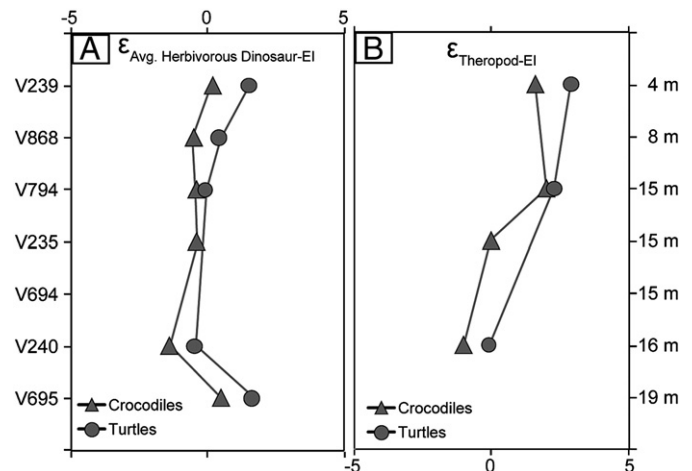


Fig. 8. Epsilon (ϵ) between evaporative sensitive and evaporative insensitive taxa. (A) Epsilon between theropods and the evaporative insensitive taxa. (B) Epsilon between the average herbivorous dinosaurs and evaporative insensitive taxa.

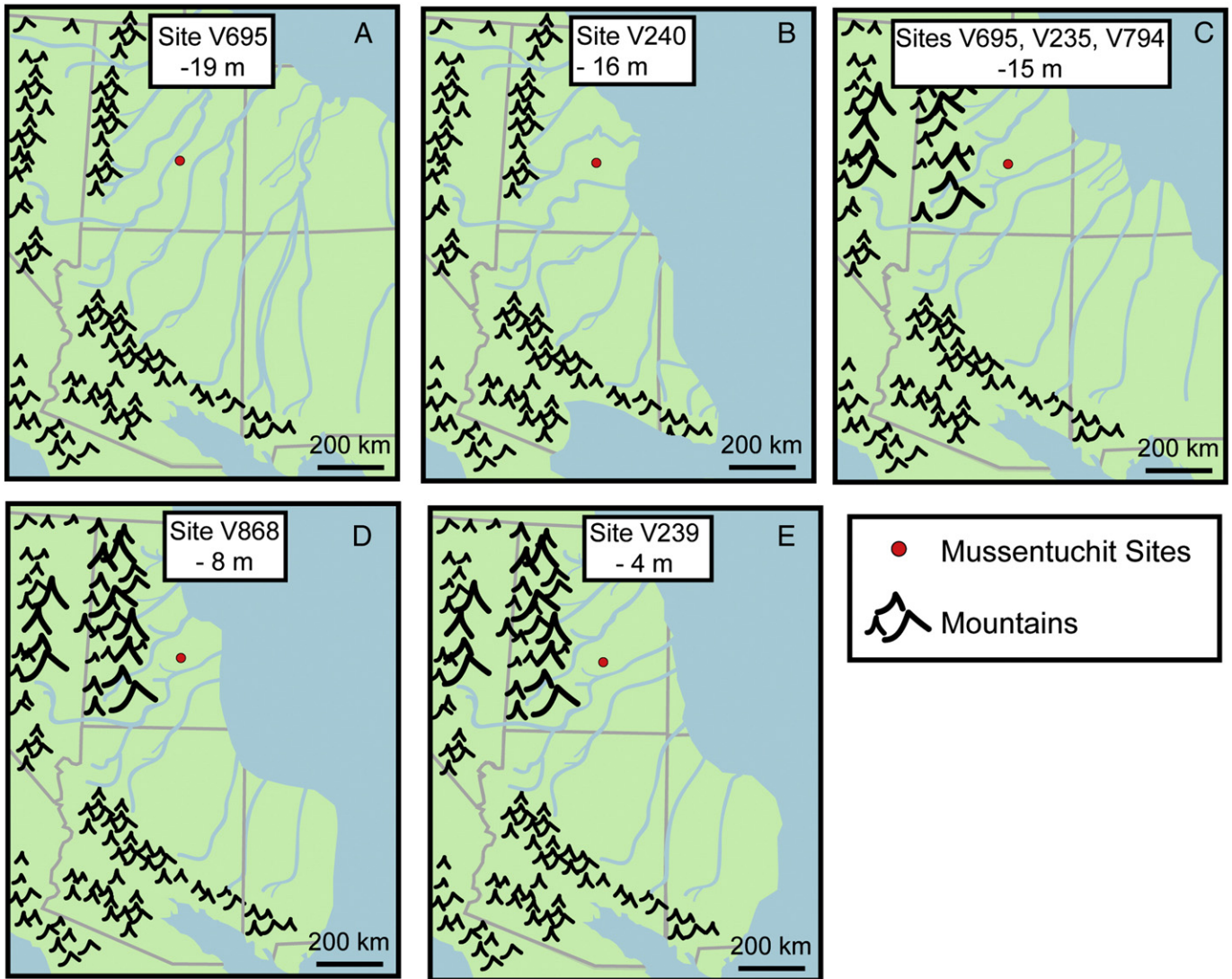


Fig. 9. Hypothetical paleogeographic maps at different times during the Mussentuchit Member deposition. (A) Paleogeography at the oldest site (V695). WIS moisture was not as prominent as it was later in the deposition. (B) Incursion of the WIS at site V240 suggested by the negative ϵ , high $\delta^{18}\text{O}_w$ values of semi-aquatic taxa and low $\delta^{18}\text{O}_w$ values of terrestrial taxa. (C) Retreat of the seaway and increased elevation of the Sevier Mountains at sites V694, V235, and V794 as suggested by decreased humidity calculated from mammal data. (D) Incursion of the WIS at V868 as suggested by an increase in humidity, decrease in dinosaur water, and increase in meteoric water determined from turtle. (E) Retreat of the WIS and increased elevation of the Sevier Mountains, as suggested by a decrease in humidity a decrease in aquatic taxa ingested water. Increase in evaporative conditions experienced by dinosaurs off-sets depletion from ingested isotopically depleted river water (modified from Blakey, NAU Geology).

of the WIS (sequence boundary SB 3.2 of [Obloh-Ikuenobe et al. \(2008\)](#)) and consequently a decrease in isotopically heavier moisture. It is also possible that the changes are caused or magnified by increased contributions of isotopically light melt-water from the Sevier Mountains, possibly resulting from increased elevation of the orogen ([Fig. 9C](#)).

From the sites 15 m below the Dakota (V694, V235, and V794) to site V868 (8 m below the Dakota), an increase in average humidity from ~60% to ~64% is calculated when using turtle-ingested water to calculate humidity and ~51% to ~67% when using crocodile-ingested water to calculate humidity. Epsilon between average herbivorous dinosaurs–turtle increases and slightly decreases for average herbivorous dinosaurs–crocodile. Isotopic compositions of water derived from turtles and crocodiles increase relative to sites 15 m below the Dakota to V868 (–8 m), but increase for dinosaurs. Therefore, from 15 m to 8 m below the Dakota, incursion of the WIS increased the input of more ^{18}O -enriched meteoric water (turtles and crocodiles), while increasing humidity and reducing the magnitude of evaporative enrichment of terrestrial taxa (dinosaurs) ([Figs. 9D, 10](#)). The re-calculated

$\delta^{18}\text{O}_w$ ingested by dinosaurs using variable humidity also increases, suggesting input of enriched meteoric water and humid conditions ([Fig. 6](#)). This may be correlated to the sequence 3.2 transgression documented by [Obloh-Ikuenobe et al. \(2008\)](#).

Finally, there is a significant, and consistent increase in ϵ from site V868 (–8 m) to site V239 (–4 m). The dramatic increase in ϵ is due to a significant depletion between $\delta^{18}\text{O}_p$ of semi-aquatic taxa (though the decrease is greater in turtles than crocodiles) and either a slight enrichment or no change in dinosaurs $\delta^{18}\text{O}_p$. Calculated humidity decreased from ~67% to ~63% when calculated using crocodile-ingested water and decreased from ~64% to ~50% when using turtle ingested water. Therefore, it is suggested that a significant rise in the elevation of the Sevier Mountains resulted in an increase in the catchment effect on rivers ([Dutton et al., 2005](#)), producing the isotopically lighter water of the local river and streams as is recorded by the turtles and crocodiles living in those waters. If river $\delta^{18}\text{O}_w$ was influenced by catchment effects, then dinosaurs should also document this decrease in isotopic composition. However, the decrease in humidity would offset the more depleted river water consumed

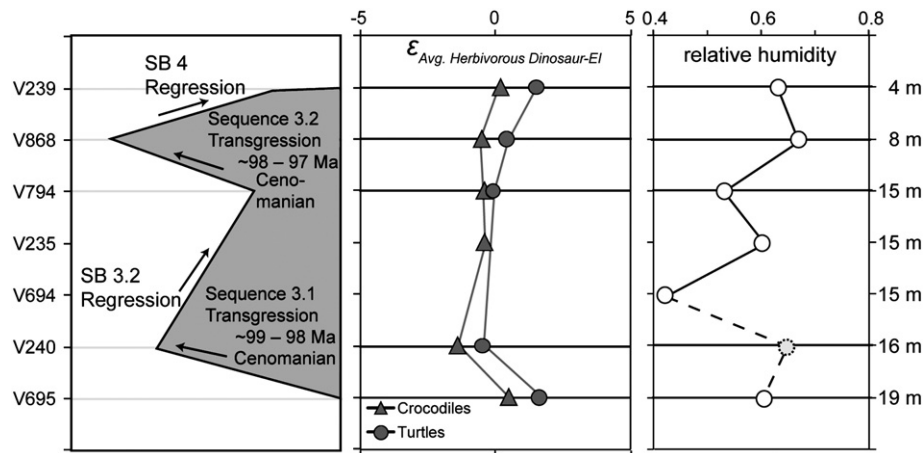


Fig. 10. Correlation between the transgressive/regressive cycles as described by [Oboh-Ikuenobe et al. \(2008\)](#), relative humidity (as calculated from mammal and crocodile phosphate), and ϵ between average herbivorous dinosaurs and evaporative insensitive reptiles (turtles and crocodiles). Landward advance and retreat of the seaway is correlated with increase and decreases in humidity (respectively) and decreases and increases in ϵ (respectively). Note that the humidity at V240 (dotted-gray circle) is relative. Only three mammalian teeth were available for sampling at V240. The calculated relative humidity was $>90\%$ which is too extreme. Likely the excessive humidity is due to the small sample size. SB = sequence boundary.

by dinosaurs because lower humidity results in greater evaporative enrichment of the dinosaurs (as it is recorded in the increased ϵ from site V868 to V239). These data are interpreted to imply that the Sevier Mountains were nearing their maximum height, and the WIS retreat caused a decrease in humidity (Fig. 9E), with the retreat possibly correlated to sequence boundary SB4 ([Oboh-Ikuenobe et al., 2008](#)).

Recent uses of pedogenic carbonate (calcite and siderite) isotopes suggest that mid-Cretaceous global warming caused an intensified and accelerated hydrologic cycle. Although meteoric water $\delta^{18}\text{O}$ values calculated from the oxygen isotope composition of pedogenic carbonates are consistently more positive relative to meteoric water $\delta^{18}\text{O}$ values recorded by turtles and crocodiles (as is expected), meteoric water predicted by turtles and crocodiles are within the range of isotopic compositions of meteoric water predicted for the zonal average at 34°N paleo-latitude. This suggests that turtles, crocodiles, and pedogenic carbonates are consistent proxies of local meteoric water. The offsets of water recorded by turtles and crocodiles versus water predicted by pedogenic carbonate are explained by the behavior of the animal to control their temperature and so can be used to confirm the intensified hydrologic cycle predicted by other researchers ([Ufnar et al., 2004](#); [Suarez, 2009](#)). Since dinosaurs seem to record isotopically depleted river water, significant offsets between turtles and dinosaurs and pedogenic carbonate and dinosaurs can be used to identify times when regional river water is affected by catchment effects and snow-melt (dinosaur water). In the case of the MM carbonates, crocodiles and turtles predict $\delta^{18}\text{O}_w$ values that are more positive than those of dinosaur-ingested water (Tables 3 and 4) and so represent local meteoric water or summer base flow rather than isotopically light river water recorded by dinosaurs that includes the pulse of isotopically light melt-water contributed over the late spring. Sampling of co-existing pedogenic carbonate, turtles, and dinosaurs are powerful proxies that help unravel regional climate dynamics during the Mesozoic.

6. Conclusions

Oxygen isotopic analyses of continental fauna are valuable tools for deciphering terrestrial paleoecology and paleoclimate. Isotopic compositions of a large variety of taxa with differing physiologies for the MM vertebrate fauna reveal differences in environmental water sources, and help identify regional climatic effects produced by the Sevier Orogeny and the incursion/retreat of the Western Interior Seaway. This study indicates that turtles and crocodiles lived in

ivers, streams, or ponds and records average local (lowland) meteoric water, similar to pedogenic carbonate, although pedogenic carbonate is influenced by evaporative enrichment and tends to be enriched by $\sim 0.4\%$ relative to turtles and crocodiles. Based on these proxies, local meteoric water in the MM ranged from -4.9 to -6.7% . Herbivorous dinosaur $\delta^{18}\text{O}_p$ record river $\delta^{18}\text{O}_w$ values that are more negative than those of local meteoric water suggesting they record yearly averages of rivers that included isotopically depleted snow-melt from higher elevations (catchment effect) as low as -13.5% . Calculation of humidity using mammal $\delta^{18}\text{O}_p$ and crocodile-derived ingested water isotopic values suggest the MM was significantly more humid than the rest of the CMF (58%). The approach used in this study allows for quantitative estimates of humidity in the geologic record, and provide constraints for the boundary conditions used in general circulation models (GCMs), and should translate to improved modeling of ancient climates.

Documentation of local meteoric water recorded by turtles and crocodiles for the MM, as a whole, corroborates the predicted zonal meteoric water predicted by pedogenic carbonates at 34°N paleo-latitude ([Ufnar et al., 2002, 2004](#); [Suarez et al., 2009](#)) as $\sim -6.0\%$. This suggests that $\delta^{18}\text{O}$ values of turtle and crocodiles can be used as an additional proxy to determine global paleohydrology. Differences from site to site within the member can be used to determine small-scale perturbations in regional climate such as orogenic effects.

The major control on the small-scale changes in isotopic composition of water recorded by MM fauna from site to site was the incursion of the Western Interior Seaway, with the Sevier Orogeny (Pavant Thrust event) contribution only recorded in larger vertebrates. At least two incursion/retreat cycles are documented by MM fauna (Figs. 9, 10): 1) incursion from site V695 (-19 m) to site V240 (-16 m), followed by a retreat of the seaway from V240 (-16 m) to the sites 15 m below the Dakota (V694, V235, V794) and 2) incursion from 15 m below the Dakota to site V868 (-8 m) followed by a retreat of the seaway at V239 (-4 m). These incursion/retreats (Fig. 10) are correlated to the transgression/regression cycles documented by [Oboh-Ikuenobe et al. \(2008\)](#).

Analysis of a variety of vertebrate taxa has allowed the range of water compositions for the Cretaceous MM as well as the effects of regional climate change on those water sources to be differentiated. Similar analysis from strata used to interpret global paleoclimate and that may also document regional climate change (due to events such as mountain building) should be conducted to distinguish between the global and regional climate effects.

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Appendix A. Supplementary data

Supplementary tables

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