

Dinosaur eggshell and tooth enamel geochemistry as an indicator of Mongolian Late Cretaceous paleoenvironments

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ABSTRACT

The Late Cretaceous fossiliferous beds of Mongolia's Gobi Desert have yielded spectacular articulated remains of a remarkable diversity of fossil mammals, lizards, turtles, birds, and non-avian dinosaurs. Paleoenvironmental interpretations of the deposits at these localities have ranged from arid wind-blown dune fields to more mesic, moist environments. Among the diversity of fossils, dinosaur eggshells and teeth are commonly found at these localities. Dinosaur eggs, like modern avian eggs, are constructed of biomineralized calcite (CaCO₃) and proteins, allowing carbon and oxygen stable isotopes to be quantified to provide information about the environment in which the egg-laying animals were living. Here it is shown that dinosaur eggshell and teeth from the Djadokhta and Nemegt Formations have not been significantly altered and reflect an environment of dry dunes during deposition of the Djadokhta Formation and a more mesic stream environment for conditions in the Nemegt Formation. Carbonate nodules from the same eggshell-bearing layers also independently reflect a similar environmental signal. This study represents the first geochemical analysis of dinosaur remains from the Cretaceous of Mongolia and illustrates the potential of utilizing dinosaur fossil geochemistry of both eggs and teeth to reconstruct Mesozoic environments.

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1. Introduction

Geochemical analysis of biological materials in fossils, such as tooth enamel, bone, and eggshell is a commonly used method for discerning paleoenvironments and paleobiology of extinct organisms and ecosystems (e.g., Fricke and O'Neil, 1996; Koch, 1998, 2007). Typically these types of studies are done on mammalian tooth enamel, but it has been shown that these methods can be used on dinosaur teeth and eggshells for paleoecological reconstruction (e.g., Cojan et al., 2003; Amiot et al., 2004, 2006; Fricke et al., 2008, 2009). Carbon in the carbonate phase of bioapatite [Ca₅(PO₄, CO₃)₃(OH, CO₃)] the material making up both teeth and bones, is reflective of organic material ingested by the organism. Oxygen in bioapatite is primarily influenced by the oxygen isotopic composition of the water an organism drinks and metabolic processes within the organism (Longinelli, 1984; Luz and Kolodny, 1985). Strontium is another trace element that can be examined in eggshell to help discern paleoenvironment and water chemistry at the locality (e.g. Erben et al., 1979; Cojan et al., 2003) and analyses of strontium on these Mongolian eggshells is forthcoming but will not be included in this paper.

Southern Mongolia is made up of flat-lying, non-marine, Upper Cretaceous rock formations. During the Late Cretaceous, the Gobi Desert region was a completely terrestrial interior continental setting, as it is 2800 km from the nearest known Cretaceous marine outcrops in

Kazakhstan (Averianov, 1997). This location provides a unique window into Central Asian Cretaceous paleoclimates that cannot be obtained anywhere else. Terrestrial paleoclimate records from the Mesozoic are especially limited, and vertebrate fossils can provide a useful proxy.

Experiments on modern bird eggshell over the past four decades have shown clearly that carbon and oxygen isotopic compositions of the calcite shells record the environmental conditions that the female was experiencing immediately prior to egg laying (Folinsbee et al., 1970; Johnson et al., 1997). Using this information, paleoenvironmental archives have been obtained from ostrich and ratite eggshell (e.g., Stern et al., 1994; Johnson et al., 1998; Segalen et al., 2002), and dinosaur eggshell from India (Sarkar et al., 1991), France (Cojan et al., 2003), China (Zhao et al., 2009) and Romania (Bojar et al., 2010), illustrating the potential of this proxy. Oxygen isotopic compositions in eggshell have been well correlated with the isotopic composition of drinking water, while carbon isotopes of the eggshell carbonate strongly reflect stable isotopic composition of ingested food material of the egg-bearer (Folinsbee et al., 1970; Erben et al., 1979; Von Schirnding et al., 1982; Schaffner and Swart, 1991).

It can be difficult to use dinosaurs for stable isotope investigation because, unlike mammals, no experimentation is possible on living non-avian dinosaurs to measure isotopic fractionations between diet, drinking water and isotopes in eggshells and bioapatite. With eggshell, it is assumed that the fractionation of oxygen and carbon isotopes in dinosaur eggshell is similar to what occurs in extant bird eggshell (Cojan et al., 2003). But in studies of dinosaur teeth, isotopic composition of tooth enamel cannot be attributed to true environmental signal because

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the exact fractionation factor is not known, an issue that has been showcased in numerous publications (e.g. Stanton Thomas and Carlson, 2004; Fricke et al., 2008).

Fricke et al. (2008) states that if certain assumptions are made, then relative differences in isotopic values among taxa from the same and/or different localities can be compared to glean important environmental information. The first assumption is that dinosaurs utilize and incorporate carbon as all extant homeothermic vertebrates do. The second assumption is that dinosaurs were homeothermic, which has been corroborated numerous times (e.g., Barrick and Showers, 1994; Fricke and Rogers, 2000). In this paper, eggshells and teeth from two different species of dinosaur from three different localities are analyzed. If our data show distinct differences or similarities in isotope values when compared between localities and species, then ancient environments with general reference to vegetation and precipitation can be characterized. One would expect distinct differences in isotopic values between species that occupy different dietary niches. Additionally, there would be isotopic differences between species inhabiting environments with different climate regimes. Similarities in isotope values could mean the animals ate similar food and occupied similar dietary niches, or that diagenesis has overwhelmed all signal and reset isotope values to be homogenous.

1.1. Background on isotopes and environment

There are numerous detailed reviews on the systematics of carbon and oxygen isotopes in ecosystems (e.g., Koch, 2007), and how they are preserved in fossils so only a brief review will be presented here. Plants utilize one of three metabolic pathways: C3, C4, and CAM. Grasses and succulents utilize the C4 and CAM pathways. Since there is no evidence for widespread C4 or CAM plants until the Cenozoic, the assumption is that only C3 plants occur in the Late Cretaceous (Sage, 2004). Carbon isotope ratios of plants depend on both photosynthetic pathways and environmental conditions (O'Leary, 1988). $\delta^{13}\text{C}$ values of organic matter in the neighborhood of -24% and higher are indicative of a semi-arid environment with low relative humidity (Kohn, 2010). It is notable that the $\delta^{13}\text{C}$ of atmospheric CO_2 can also change over time, which in turn affects the $\delta^{13}\text{C}$ of organic plant matter (Fricke et al., 2008). The $\delta^{13}\text{C}$ of atmospheric CO_2 can also differ by $\sim 1\%$ depending on the global extent of glaciation, so care must be taken in interpreting results from times when the extent of glacial cover is not known (Koch, 1998).

Oxygen isotopic ratios in water vary because of temperature, evaporation, and source of the precipitation's air mass (Dansgaard, 1964). The cause of $\delta^{18}\text{O}$ variation in precipitation is the preferential incorporation of ^{18}O into condensate as water is precipitated and removed from the cooling air mass. The same is true in terrestrial bodies of water; ^{16}O is preferentially evaporated concentrating the ^{18}O in the water body. Typically, terrestrial vertebrates do not ingest precipitation directly. Instead, most water ingestion comes from leaves, streams, ponds, and lakes that will have a different $\delta^{18}\text{O}$ than precipitation (Fricke et al., 2008). In humid areas, there may not be a large discrepancy between $\delta^{18}\text{O}$ of precipitation and $\delta^{18}\text{O}$ of water on land, but in arid regions the increased evaporation will lead to a large difference in these $\delta^{18}\text{O}$ values. Another important factor is that not all animals (e.g., desert dwelling vertebrates) are obligate water drinkers. These organisms get most of their water from plants and seeds, or they create metabolic water from the breakdown of proteins (Chew, 1961; Johnson et al., 1997, 1998). Metabolic water is formed in all organisms, but rarely does it contribute substantially to body water. Animals such as kangaroo rats never need to drink free water because their entire water budget is met by metabolic water, but larger organisms need water from other sources (Chew, 1961). It has been shown that non-passerine birds such as ostriches produce metabolic water, but the majority of their body water needs are met by drinking surface water and water contained in the plants they eat (Withers, 1983). Due to the fact non-avian dinosaurs are close relatives of modern birds, the physiology of dinosaurs could have functioned similarly to that of extant birds like ostriches, so the $\delta^{18}\text{O}$ of

their body water reflects ingested water from plants and surface reservoirs. Leaf water of plants in water stressed areas can be ^{18}O enriched relative to $\delta^{18}\text{O}$ of meteoric water because of the preferential evapotranspiration of ^{16}O (Gonfiantini et al., 1965). Because it is unknown if the dinosaurs in question were obligate drinkers or not, all of these scenarios must be taken into account when interpreting the data.

1.2. Geology and stratigraphy

The stratigraphy of Mongolia's Late Cretaceous Nemegt Basin is divided into three formations: Djadokhta, Barun Goyot, and Nemegt (from stratigraphically oldest to youngest) (Jerzykiewicz and Russell, 1991; Hasegawa et al., 2009). Evidence from geochronological studies shows that the lithologic sequence of the Nemegt Basin is essentially a semi-continuous section from Cenomanian to Maastrichtian (Jerzykiewicz and Russell, 1991; Shuvalov, 2000; Hasegawa et al., 2009). All three of the formations in this basin are known to have produced a vast array of fossil vertebrates, such as dinosaurs (e.g., Norell et al., 1994; Clark et al., 2001), mammals (e.g., Wible et al., 2007), crocodiles (e.g., Pol and Norell, 2004), turtles (e.g., Mlynarski and Narmandach, 1972), and lizards (e.g., Gao and Norell, 2000).

The localities of Ukhaa Tolgod and Bayn Dzak (Fig. 1) are assigned to the Djadokhta Formation, which is Campanian in age (Loope et al., 1998; Dashzeveg et al., 2005; Dingus et al., 2008). These localities are separated by about 187 km. The formation was first described in 1927 at the Bayn Dzak locality (Berkey and Morris, 1927). The fossil locality of Bayn Dzak, also known as the Flaming Cliffs and Shabarak Usu, was discovered by the Central Asiatic Expeditions of the American Museum of Natural History in the 1920s (Andrews et al., 1932). Dinosaurs such as *Velociraptor*, *Saurornithoides*, and *Oviraptor* were discovered in the red beds of Bayn Dzak (Osborn, 1924). Ukhaa Tolgod, discovered in 1993 by the Mongolian Academy of Sciences–American Museum of Natural History Expedition (MAE), has yielded an unprecedented diversity of extremely well-preserved specimens of birds, dinosaurs, mammals, and lizards reviewed by Dashzeveg et al. (1995). This locality is correlated to the Djadokhta Formation based on lithofacies and biostratigraphic evidence and is assigned a Campanian age (Dingus et al., 2008).

The rocks of the Djadokhta Formation at Bayn Dzak are reddish-orange medium to fine grained sandstones (Fig. 2). Some of the strata contain calcareous nodules and pockets of silty clay (Dashzeveg et al., 2005). The fossiliferous unit of the Djadokhta Formation exposed at Bayn Dzak is reddish colored, structureless, medium grained sandstone that varies between 2 m and 14 m in thickness. There is evidence of migrating dunes, with cliffs of consolidated sandstones with 5–7 m high crossbed sets. Calcareous nodules are found in both the crossbedded and structureless sandstone layers, and these white nodules often contain the bones of mammals such as multituberculates, and lizards (Dashzeveg et al., 2005). There are thin beds of concretionary calcite and lenses of siltstone and mudstone within the sandstone units, indicating an arid to semi-arid depositional environment.

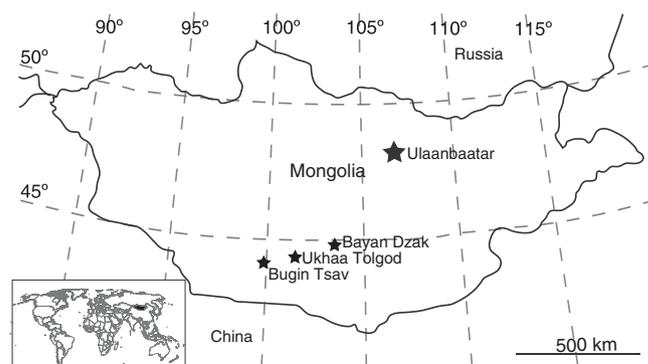


Fig. 1. Map of Mongolia. The locations of the localities are marked with stars.

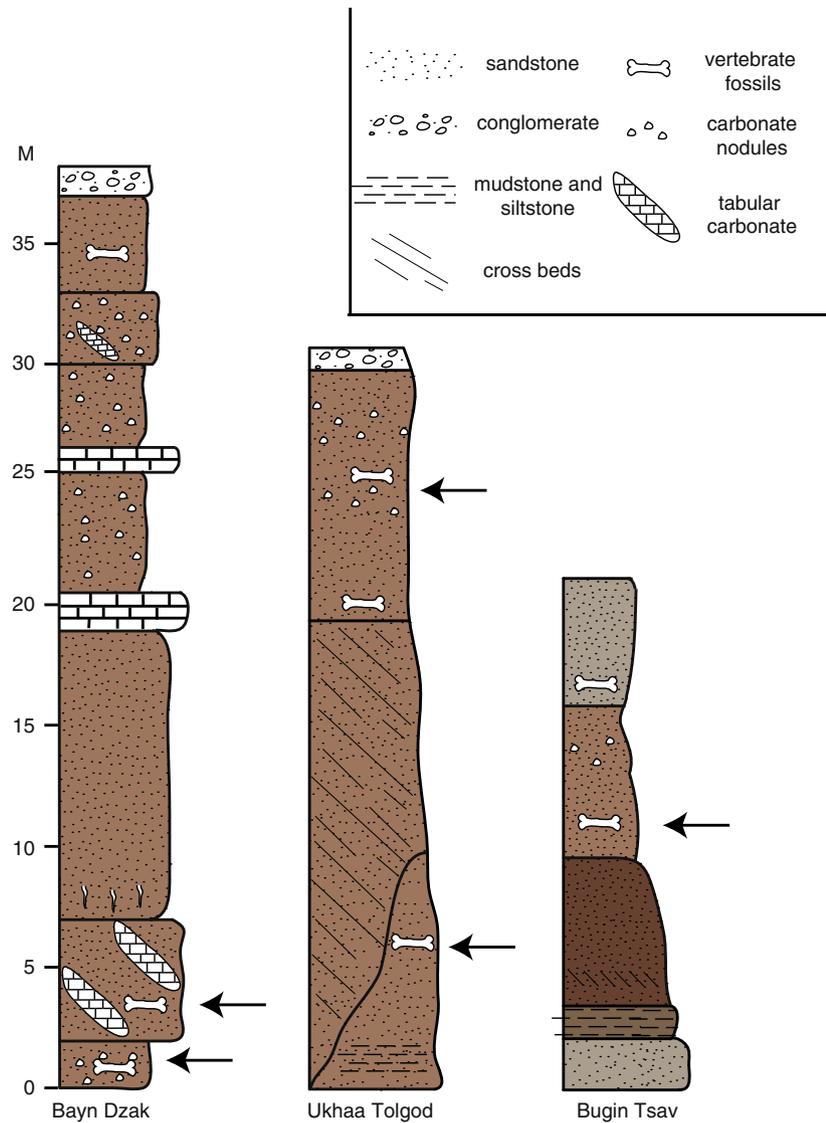


Fig. 2. Generalized stratigraphic columns showing the general structural and lithologic successions at each locality. The prevalence of aeolian and structureless sandstones indicates that the Djadokhta Formation localities, Bayn Dzak and Ukhaa Tolgod, were far drier than the Nemegt Formation locality, Bugin Tsav. The stratigraphy at Bugin Tsav indicates the presence of a fluvial system. Arrows indicate where analyzed fossils were found in each section. Columns are compiled from Dashzeveg et al., 2005 (Bayn Dzak), Dingus et al., 2008 (Ukhaa Tolgod), and Kielan-Jaworowska and Sochava, 1969 (Bugin Tsav).

At Ukhaa Tolgod, lithology similar to that seen at Bayn Dzak is observed (Fig. 2). The outcrops of fossiliferous rock are also reddish fine-grained structureless sandstones. There are non-fossiliferous cross-stratified dune deposits and siltstone deposits that are not laterally continuous (Dingus et al., 2008). The vertebrate fossils preserved at Ukhaa Tolgod often appear to be in death positions, which seem to indicate that the animals were rapidly buried in sandslides off of superhydrated collapsing dunes while they were still alive (Loope et al., 1998; Dingus et al., 2008). Calcite sheets and nodules are also present at this locality, which indicates the dunes were stable for a period of time. There are indications of small ponds in the interdune corridors during times of dune stabilization, but these were mostly ephemeral (Dingus et al., 2008). Based on these lithographic and faunal similarities, Ukhaa Tolgod is assigned to the Bayn Dzak Member of the Djadokhta Formation proposed by Dashzeveg et al. (2005) (Dingus et al., 2008).

The Bugin Tsav locality (Fig. 1) is located in the southern portion of the central Gobi Desert of Mongolia and is assigned to the Nemegt Formation, which overlies the Barun Goyot Formation (Gradzinski, 1970). It is about 126 km from the Ukhaa Tolgod locality and about 294 km from the Bayn Dzak locality. The Nemegt Formation is considered late Campanian (Weishampel et al., 2008) to Maastrichtian (Kielan-Jaworowska and

Barsbold, 1972) in age. The Nemegt Formation differs from the Djadokhta Formation in that it consists mainly of fluvial sediments deposited by braided or meandering river systems (Gradzinski and Jerzykiewicz, 1974; Jerzykiewicz and Russell, 1991). Fossiliferous sediments at the Bugin Tsav locality are yellowish-brown sands that range in grain size from very fine to very coarse. Additionally, there are thin-bedded conglomerates and sandy siltstones (Gradzinski, 1970). Features such as climbing ripples, flaser structures, and scoured surfaces are present providing additional evidence that the Nemegt Formation was deposited on an alluvial plain with a low-flow regime (Gradzinski, 1970). Remains of dinosaurs and other vertebrates like turtles (sometimes found in mass death assemblages) are commonly found in point bar deposits without much obvious reworking, so death appears to have been close to the location of burial (Weishampel et al., 2008) (Fig. 2).

1.3. Bioattribution of eggshell

Mongolian dinosaur eggs have been studied on the basis of microstructure (Grellet-Tinner and Norell, 2002; Grellet-Tinner et al., 2006; Balanoff et al., 2008), nesting behavior (Norell et al., 1995; Weishampel et al., 2008), and embryonic associations (Norell et al., 1994; Balanoff

et al., 2008), but never have stable isotopes been utilized in the analyses of these eggshells. Unfortunately, dinosaur eggshells are usually found separate from any identifiable skeletal remains, so taxonomic assignment is in most cases problematic. This has led to the development of an eggshell parataxonomic scheme (Mikhailov et al., 1996), which is used for identifying “ootaxa”. Eggshell types are characterized by a combination of size, shape, ornamentation, and microstructure (Mikhailov et al., 1996). Recent discoveries of dinosaur nests with associated remains of parents or embryos have allowed association of certain eggshell morphotypes with distinct species or groups of dinosaurs and in many cases it is no longer necessary to rely entirely on the potentially misleading parataxonomic scheme (Norell et al., 1994; Grellet-Tinner et al., 2006).

At Ukhaa Tolgod, the oviraptorid taxon known to belong to an egg morphotype is *Citipati osmolskae*. They certainly belong to the oofamily Elongatoolithidae (Grellet-Tinner et al., 2006). At Bugin Tsav, the exact identity of the egg-layer is unknown, but the microstructural and ultrastructural similarities between the eggshells from Ukhaa Tolgod and Bugin Tsav seem to indicate they are both from oviraptorids (Weishampel et al., 2008). Because this egg type has been found associated only with this group of dinosaurs in the Late Cretaceous of Central Asia, this allows us to parataxonometrically categorize them as elongatoolithid, and for this egg type to be preliminarily assigned to oviraptorids. This eggshell morphotype is characterized by an elongated egg shape, two aprismatic layers of calcite in the eggshell microstructure, and linear tuberculate ornamentation on the surface of the eggshell. In this study, only elongatoolithid type eggshell fragments were used, to provide for taxonomic control in interpreting the paleoenvironments of these localities. These fragments were mostly collected in situ weathering out of rocks or as nearly complete eggs in float.

1.4. Diagenesis in biogenic materials

All fossilized material is affected by diagenesis, even soon after burial (Trueman and Tuross, 2002). Alteration occurs when there is isotopic exchange between bioapatite and surrounding fluids at a significantly different temperature and isotopic composition than formation; alteration can also occur when there is dissolution or addition of secondary apatite or carbonate (Zazzo et al., 2004). Because diagenesis is nearly universal, it needs to be shown that the primary signal in the fossil material has not been completely obscured by secondary diagenetic alteration. The highly porous bioapatite constructed of small apatite crystals (with more surface area) found in bone seems to be more susceptible to alteration, whereas tooth enamel is more resistant due to its tightly packed, large bioapatite crystals (Sharp et al., 2000; Kohn and Cerling, 2002).

While there is no way to demonstrate definitively that diagenesis has not obscured primary signal, a suite of methods, such as cathodoluminescence and comparison of isotopic signals in biogenic carbonate to signals in authigenic carbonates, can be used to best illustrate that alteration is not completely pervasive (Cojan et al., 2003; Fricke et al., 2008, 2009; Grellet-Tinner et al., 2010). One such method is comparison of the isotopic signal of the material in question, in this case eggshell calcite and tooth enamel, with an independent proxy, such as bulk organic carbon or carbonate nodules in the same formation. If the carbon and oxygen isotopic compositions of the two substrates differ, then diagenesis, such as hydrothermal alteration or burial, have not significantly impacted the locality and altered the primary environmental signal (Sarkar et al., 1991; Cojan et al., 2003; Fricke et al., 2008). We apply this method, and when eggshells were collected, carbonate nodules weathering out from the same sedimentary layer were also collected if available.

Additionally, cathodoluminescence (CL) is used on polished thin sections of the eggs to check for zones of chemical and mineral alteration. Authors using fossil shells for geochemical analysis commonly use CL as a diagenetic indicator (Barbin et al., 1995). Pure CaCO₃ has very little

luminescence; unaltered CaCO₃ is essentially non-luminescent under CL, but has slight changes in luminescence when there are ionic substitutions in the crystal lattice (Grellet-Tinner et al., 2010). Iron and manganese most commonly replace calcium in the crystal lattice and typically diagenetic pore waters are enriched in these two elements relative to biological host fluid (Grellet-Tinner et al., 2010). Finding signs of alteration under CL gives an indication that diagenesis has occurred. Energy-dispersive spectroscopy (EDS) can also be used to create an element map of the eggshell in the SEM and obtain qualitative elemental abundance data (Grellet-Tinner et al., 2012). If there is suspicion of diagenesis under CL, EDS can be used to determine where the secondary elements have infiltrated the eggshell. If luminescence is absent, it provides evidence there has been little or no diagenetic alteration of biogenic carbonate. Another method, such as electron backscatter detection (EBSD), has been used with great success in the analysis of the chemical composition of eggshells (e.g., Grellet-Tinner et al., 2011) but was unavailable in this analysis.

2. Methods

Between 5 and 19 eggshell fragments from each locality were analyzed. Carbonate nodules from Ukhaa Tolgod were also analyzed as comparative samples, providing a test of diagenesis. Across all materials, a total of 60 samples were analyzed. Samples of eggshell were manually abraded to remove adhered sediment and subsequently crushed with a mortar and pestle. The carbonate nodules were prepared by drilling out material from each nodule with a Dremel tool. Bulk samples of protoceratopsian tooth enamel were obtained by crushing or drilling enamel flakes after they were separated from the underlying dentin. In this analysis, the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tooth enamel was analyzed from the carbonate (CO₃)₂ substituted for PO₄ in the bioapatite matrix. For carbonate samples (nodules and eggshell) approximately 250 μg of sample was obtained, and for bioapatite samples over 1000 μg was used to obtain an accurate result. Powdered samples of bioapatite were subsequently treated using 30% H₂O₂ and 0.1 N acetic acid to remove organic material and surficial carbonates; carbonate samples were treated only with H₂O₂ (see MacFadden and Higgins (2004) for detailed methods). Analyses were run on a Thermo Electron Corporation Finnegan Delta plus XP mass spectrometer in continuous-flow mode via the Thermo Electron Gas Bench peripheral and a GC-PAL autosampler housed at the University of Rochester. Carbon and oxygen isotopic results are reported in per mil (‰) relative to VPDB (Vienna Pee-Dee Belemnite) with an allowable 2-sigma uncertainty of 0.12‰ and 0.20‰ for carbon and oxygen respectively. Isotopic ratios of carbon and oxygen are expressed using the permil notation, such as: δX (per mil, ‰) = $((R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000)$, where R = ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ of an unknown sample relative to a known standard V-PDB (Coplen, 1994). Statistical analyses, such as t-tests, F-tests, Hotelling's pairwise comparisons, and MANOVA were all performed on Microsoft Excel 2011 and PAST ver. 2.14.

Thin sections made of eggshell fragments from each locality were examined under both SEM and transmitted light microscopy. Using transmitted light to view the thin sections illustrates preservation of the two distinct layers seen in unaltered oviraptorid-type eggshell. The sections were viewed under 50 \times magnification on a Nikon polarizing microscope. Photographs of the slide were captured using a Sony CCD-Iris camera with UltraTV software. These thin sections were also viewed with CL in a Hitachi S-4700 SEM equipped with a Gatan MonoCL cathodoluminescence detector. Eggshells were examined under the Zeiss EVO 60 variable pressure SEM to look at crystal structure and make elemental maps with the equipped Bruker AXS Quantax 4010 EDS. Eggshells were cleaved manually, and the freshly broken side was examined under extended pressure in the SEM chamber to see if the two eggshell layers were visible. Then, these same freshly broken shells, along with the thin sections of the same eggshell, were used to create elemental maps to discern whether secondary elements had infiltrated the eggshells. The EDS maps were made using Bruker Esprit 1.9.3

software with a wavelength between 15 and 20 kV and a collection time 5 minutes for element maps. Some images were refined in Adobe Photoshop CS5 to improve contrast and visibility of fine-scale structures.

3. Results and discussion

3.1. Eggshell microscopy

Under transmitted light, distinct structures can be seen in the eggshell thin sections. Oviraptorid eggshell is unique in that it consists of two distinct aprismatic layers of biogenic calcite as opposed to the tri-layered avian and mono-layer crocodilian eggshell (Grellet-Tinner and Makovicky, 2006; Grellet-Tinner et al., 2006). The base inorganic eggshell layer consists of acicular calcite crystals arranged in a fan-like pattern. The distinct second layer consists of calcite crystals arranged with their C crystalline axis oriented 90° in respect to the first layer (Grellet-Tinner et al., 2006). The outer surface of the shell appears wavy due to the lineartuberculate orientation of the shell. The preservation of these fine-scale structures in the shell indicates that the calcite crystals have not been significantly altered by diagenesis (Fig. 3a). In some cases, the eggshell surface appears strongly eroded, which most likely means it was exposed to some acidic environment that degraded its structure and composition. Under variable pressure SEM, the same crystal layers are seen. On freshly broken dinosaur eggshells, the radiating acicular crystals can be seen forming a separate layer (Fig. 3b). Additionally, the underside of the eggshell still clearly shows mammillary cones, all adding to the argument that these eggshells have not been severely altered (Fig. 3c).

Under CL, the thin sections did not exhibit bright luminescence. This could indicate that there is a large amount of iron in the eggshell, so the same eggshells were placed under the SEM to examine their elemental composition through EDS. A fresh ostrich egg was also placed in the SEM for comparison purposes. The ostrich eggshell showed similar structure features, like the fan-like calcite base layer, and reflected a pure calcium carbonate elemental composition with only a small amount of sodium detected in the shell, which has similarly been seen in other extant reptile and bird eggshell chemical studies (Dauphin et al., 2006; Al-Bahry et al., 2009). In the dinosaur eggshells, on the other

hand, more elements appear in some EDS spectra, such as magnesium, iron, and strontium. Silica and aluminum are present, but that is clearly due to adhered sand grains on the eggshell (see images in supplement). The amount of other elements besides Ca, C, and O in the dinosaur eggshell total <1% in each shell sampled. This supports the conclusion that there are no major elemental changes in the eggshell since burial, and their composition remains relatively pure and appropriate for stable isotopic testing.

3.2. Stable isotope paleoecology

The mean $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, number of samples, and standard deviations for each material in each locality are provided in Table 1. The Hotelling's pairwise comparisons of these means between materials and localities are presented in Table 2. F-tests and t-tests were also performed for pairwise comparisons of carbon and oxygen between substrates tested (Table 3).

3.2.1. Carbon isotopes in dinosaur remains and paleovegetation

At Ukhaa Tolgod and Bayn Dzak, both of the Djadokhta Formation localities, the $\delta^{13}\text{C}$ of eggshell ($\delta^{13}\text{C}_{\text{egg}}$) values are high with a mean of $-5.2 \pm 1.1\text{‰}$ and $-4.6 \pm 0.9\text{‰}$ respectively. The $\delta^{13}\text{C}_{\text{egg}}$ from both Djadokhta Formation sites are not significantly different (Table 3). At Bugin Tsav, the younger Nemegt Formation locality, the mean of $\delta^{13}\text{C}_{\text{egg}}$ is similarly high ($-5.6 \pm 0.65\text{‰}$) (Fig. 4). Across avian groups, eggshell calcite is enriched by $\sim 16.0\text{‰}$ relative to ingested plant fodder (Von Schirnding et al., 1982; Schaffner and Swart, 1991). If it is assumed that non-avian dinosaurs, as extinct relatives of birds, had a similar method of fractionation, then the vegetation of the paleoenvironment may be characterized. With the enrichment factor of 16.0‰ subtracted from the measured $\delta^{13}\text{C}$, the average plant $\delta^{13}\text{C}$ is found to be -21.2‰ at Ukhaa Tolgod and -20.6‰ and -21.6‰ at Bayn Dzak and Bugin Tsav respectively.

The closest modern day environmental analog to the calculated plant $\delta^{13}\text{C}$ from the eggshells in both formations is a semi-arid desert ecosystem that supports gymnosperms (*Pinus* sp.) and small shrubs (DeLucia and Schlesinger, 1991). Among modern C3 plants, it is noted that gymnosperms often have the highest $\delta^{13}\text{C}$ values (Tieszen, 1991).

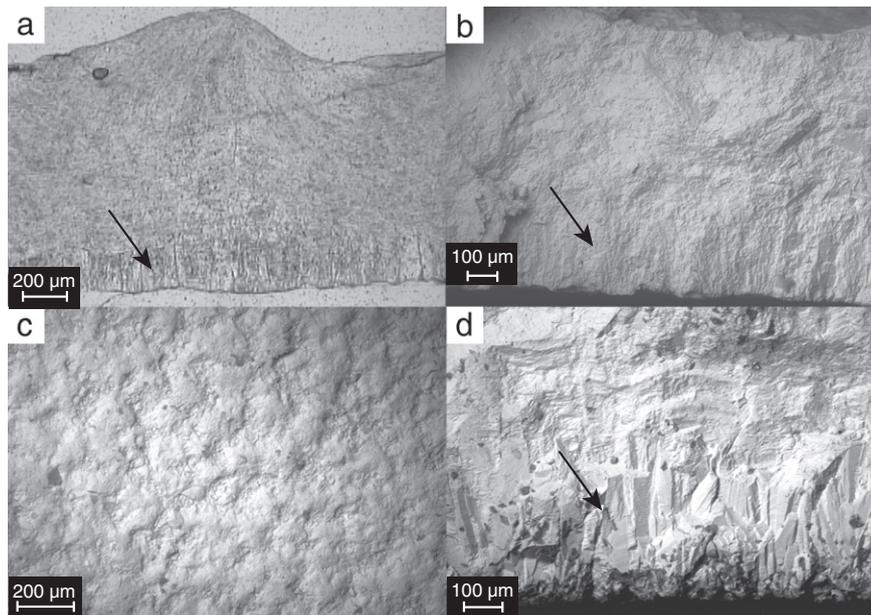


Fig. 3. Photomicrographs of dinosaur eggshell. Black arrows point to the layer of radial calcite crystals in a, b, and d. a. Transmitted light radial view of an elongatoolithid eggshell thin section (specimen IGM 100/1189) from Bugin Tsav. Note the clear delineation of the radiating acicular calcite layer from the second layer. b. Radial SEM view of IGM 100/1189 with both eggshell layers also visible. c. SEM view of IGM 100/1189 illustrating the bottom of the eggshell's mammillary cones. d. Radial SEM view of a modern ostrich eggshell that depicts the similarities in appearance of eggshell layers to the dinosaur eggshell fragments utilized in this study.

It is quite probable that gymnosperms like pine trees and small shrubs dominated the Cretaceous ecosystems of Mongolia, as they are well adapted to water stress, and the seeds from gymnosperms could have served as a food source for nesting dinosaurs. Without actual remains of Cretaceous gymnosperms, this is only an assumption and cannot yet be directly tested.

It is notable that the $\delta^{13}\text{C}$ of the dinosaur enamel in this study and others (Stanton Thomas and Carlson, 2004; Fricke and Pearson, 2008; Fricke et al., 2008) is high when compared with enamel values of modern mammals that forage on C3 plants. The $\delta^{13}\text{C}$ of enamel ($\delta^{13}\text{C}_{\text{enam}}$) of the protoceratopsian teeth from Ukhaa Tolgod has an average of $-5.39 \pm 1.53\%$. This mean is similar to what was found in Fricke and Pearson (2008) for the $\delta^{13}\text{C}_{\text{enam}}$ of herbivorous dinosaurs of the Hell Creek Formation, which was -5.9% . The diet–tissue fractionation in mammalian herbivores has been fairly well established (DeNiro and Epstein, 1978). For wild herbivorous non-avian dinosaurs, the fractionation between bulk diet and $\delta^{13}\text{C}$ of enamel apatite is obviously more difficult to physically test because the living relatives of dinosaurs do not have teeth. This ‘high’ $\delta^{13}\text{C}$ in dinosaurs could be indicative of diagenesis or, as has been suggested by Fricke et al. (2008), indicative of a different physiological fractionation in dinosaurs relative to ingested matter than mammals. Fricke et al. (2008) compared hadrosaur tooth enamel to bulk organic sediments from two different sites and consistently found a -18% difference between the $\delta^{13}\text{C}$ of organic sediment matter (diet) and the $\delta^{13}\text{C}$ of the dinosaurian tooth enamel.

If this fractionation holds true at our localities, then the *Protoceratops* diet had an average value of -23.4% . This value is not only concordant with the average value calculated from eggshell fractionation at the same locality (-21.2%) but with plants from water-stressed environments. C3 plants exposed to a high amount of sunlight have higher $\delta^{13}\text{C}$ values than those that are constantly shaded (Lockheart et al., 1998). It is also critical to remember when comparing Cretaceous to modern day $\delta^{13}\text{C}$ values that the absolute values of $\delta^{13}\text{C}$ of organic plant matter will be higher during the Cretaceous because the $\delta^{13}\text{C}$ of atmospheric CO_2 at the time was 1–2% higher than it is today, so the $\delta^{13}\text{C}$ of plants would also be higher (Hasegawa et al., 2003; Foreman et al., 2011).

3.2.2. Oxygen in dinosaur remains and paleovegetation

The oxygen isotope composition of the eggshell fragments should reflect the body water of the nesting mother (assuming she was an obligate drinker). The $\delta^{18}\text{O}$ of eggshell ($\delta^{18}\text{O}_{\text{egg}}$) values at Ukhaa Tolgod are highly variable with a mean of $-5.2 \pm 3.2\%$ and a variance of 10.5. This is the highest variance of isotope values recorded in any of the materials sampled in this study. The $\delta^{18}\text{O}_{\text{egg}}$ reflects the organism’s drinking water days before the egg was laid (Folinsbee et al., 1970; Johnson et al., 1998).

It is possible that the $\delta^{18}\text{O}_{\text{egg}}$ signature is due to physiological needs of the organisms in question. Ostriches are not obligate water drinkers – that is, they obtain enough water to survive purely through vegetation consumed. Leaf water in warm, dry regions can be ^{18}O -enriched relative to the $\delta^{18}\text{O}$ of meteoric water ($\delta^{18}\text{O}_{\text{mw}}$) because of preferential evapotranspiration of ^{16}O (Gonfiantini et al., 1965). Captive and wild experiments on ostriches in South Africa showed that while there is a

Table 1

Stable isotope results and statistics. Mean, n (sample number), standard deviation (SD), and variance for both carbon and oxygen isotope values for all materials sampled. Isotope values are presented in per mil (‰).

Material	n	$\delta^{13}\text{C}$			$\delta^{18}\text{O}$		
		Mean	SD	Var	Mean	SD	Var
Ukhaa Tolgod eggshell	19	-5.2	1.1	1.2	-5.2	3.2	10.5
Ukhaa Tolgod carbonate nodule	11	-4.2	0.9	0.7	-11.0	0.4	0.2
Bayn Dzak eggshell	5	-4.6	0.9	0.8	-10.5	1.5	2.1
Ukhaa Tolgod <i>Protoceratops</i> teeth	8	-5.4	1.5	2.3	-5.8	1.9	3.5
Bugin Tsav eggshell	17	-5.6	0.7	0.4	-9.3	0.8	0.7

Table 2

Pairwise comparisons of all materials and localities. Post-hoc Hotelling’s pairwise comparisons of eggshell and carbonate nodules within the same environment illustrate significantly different isotopic values between Ukhaa Tolgod eggshell and carbonate nodules. Significant p-values are shown in bold.

	Ukhaa Tolgod eggshell	Ukhaa Tolgod carb nodes	<i>Protoceratops</i> enamel	Bayn Dzak eggshell
Ukhaa Tolgod eggshell				
Ukhaa Tolgod carbonate nodes	0.00000258			
<i>Protoceratops</i> enamel	0.619286	0.000193258		
Bayn Dzak eggshell	0.000206455	0.712936	0.00955824	
Bugin Tsav eggshell	0.00000092	0.00303766	0.00149165	0.159946

correlation between $\delta^{18}\text{O}_{\text{egg}}$ and the $\delta^{18}\text{O}$ of drinking water, the strong correlation between these two values falls apart when the ostriches studied are wild as opposed to captive (Johnson et al., 1998). In the instance of the present study, the $\delta^{18}\text{O}_{\text{egg}}$ may be reflecting the $\delta^{18}\text{O}$ of leaf water in the plant, which can vary upwards of 14% over the course of a single day, as was supposed with wild ostriches (Johnson et al., 1998). Consequently, the equation derived from captive ostriches is not necessarily useful due to this wild variation, and for this reason it will not be used in relation to these non-avian dinosaurs. The large range of oxygen isotope values in the eggshells from this locality is probably reflective of a combination of evaporative enrichment of the water source and evapotranspiration within the leaves of food.

The $\delta^{18}\text{O}_{\text{egg}}$ from the Bayn Dzak locality of the Djadokhta Formation has a mean of $-10.5 \pm 1.5\%$ with a variance of 2.10. At the Bugin Tsav locality of the Nemegt Formation, the mean $\delta^{18}\text{O}_{\text{egg}}$ is $-9.3 \pm 0.8\%$ and has a variance of 0.7, the lowest variance of all eggshell isotopic values. The mean $\delta^{18}\text{O}_{\text{egg}}$ from Ukhaa Tolgod is significantly higher than that seen at Bayn Dzak and Bugin Tsav. While this could indicate diagenesis, the earlier findings illustrating the structural and elemental purity of the eggshell make this less likely. In fact, this sort of difference between localities and formations would be expected because there are clearly differing environments represented between an arid environment like Ukhaa Tolgod and the more mesic environment, Bugin Tsav. $\delta^{18}\text{O}$ of surface waters in areas subject to evaporative water loss are high, while in more mesic environments there is not as much variance (Sternberg et al., 1989). The mean $\delta^{18}\text{O}_{\text{enam}}$ of the protoceratopsian teeth is also high, like that from the eggshell in Ukhaa Tolgod, but less variable. It appears as though the protoceratopsians were drinking from evaporated pools, just as is indicated in the oviraptorid eggshells, but whatever they were eating and/or drinking was not as water stressed. More samples of the tooth enamel from different species at these localities are needed to confirm the microhabitat differentiation between species. The difference between the eggshell stable isotopes in oxygen values at both Djadokhta localities is most likely explained by regional variation, primarily in hydrology as reflected by $\delta^{18}\text{O}_{\text{egg}}$.

Table 3

Results from t-tests. F-tests were first performed to see if the variances between samples were equal or unequal. Depending on that result, the appropriate t-test for equal or unequal variance was performed. These t-tests show at Ukhaa Tolgod, that there is a significant difference between the $\delta^{13}\text{C}$ of the carbonate nodules and eggshell. This also holds true for the $\delta^{18}\text{O}$ for the same materials. Eggshell $\delta^{13}\text{C}$ composition from all three localities is indistinguishable, but $\delta^{18}\text{O}$ is different. Abbreviations: UT = Ukhaa Tolgod, BD = Bayn Dzak, BT = Bugin Tsav.

Variable 1	Variable 2	Test	p Value	Significant?
UT eggshell carbon	UT carbonate carbon	t-equal var.	0.02	Yes
UT eggshell carbon	BD eggshell carbon	t-equal var.	0.33	No
UT eggshell carbon	BT eggshell carbon	t-equal var.	0.14	No
UT eggshell oxygen	UT carbonate oxygen	t-unequal var.	0	Yes
UT eggshell oxygen	BT eggshell oxygen	t-unequal var.	0	Yes
UT eggshell oxygen	BD eggshell oxygen	t-equal var.	0.002	Yes
BT eggshell oxygen	BD eggshell oxygen	t-equal var.	0.03	Yes

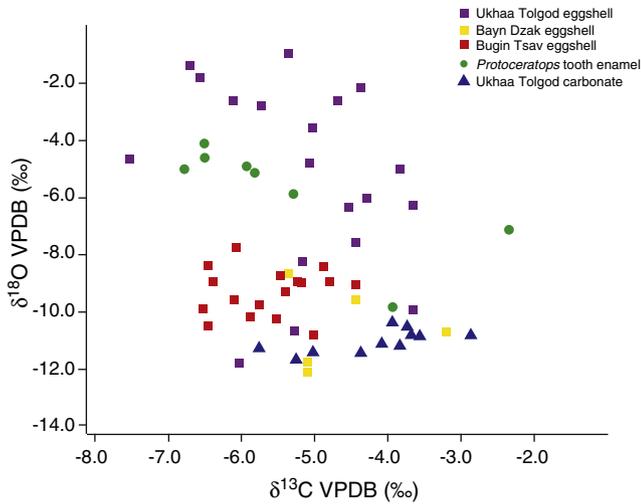


Fig. 4. Bivariate plot of oxygen and carbon, $\delta^{18}\text{O}$ vs. $\delta^{13}\text{C}$ values for eggshell, tooth enamel, and soil carbonate. Samples are marked by colored squares, circles, and triangles as noted in the legend.

3.2.3. Carbonate nodules

The carbonate nodules from Ukhaa Tolgod do not appear to be traditional paleosol carbonates. Hasegawa et al. (2009) calls the carbonate pebbles “reworked calcrete” at the Bayn Dzak locality. The fabric of the nodules is micritic, pointing to early diagenetic groundwater calcite. Eberth (1993) notes that there are similar groundwater calcrete nodules in the structureless sandstones of the contemporaneous Djadokhta Formation Bayan Mandahu locality of China’s Gobi Desert. Calcite cements like those found in the Djadokhta Formation are common in sandstones and are formed during long periods of non-deposition in semi-arid localities with less than ~760 mm per year of precipitation (Birkeland, 1999; Royer, 1999; Dingus et al., 2008).

At Ukhaa Tolgod, the carbonate nodule $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{carb}}$) mean is $-4.1 \pm 0.9\%$. These carbonate nodules appear to be contemporaneous with the fossils at the same locality. Quade and Roe (1999) state that these sorts of calcretes represent ground-water cements and can potentially be used in the same way paleosol carbonates are to reconstruct paleoclimate, but the fractionation and source of $\delta^{13}\text{C}$ found in the nodules are not well defined. If the pedogenic carbonate fractionation (-16%) from Cerling and Quade (1993) is assumed, then the average $\delta^{13}\text{C}$ of vegetation would be about -20.4% , which is in concordance with what we see preserved in the tooth enamel and eggshell $\delta^{13}\text{C}$. Although, since these carbonates are most likely early groundwater carbonate, the fractionation between vegetation and the $\delta^{13}\text{C}_{\text{carb}}$ of this type of carbonate is not precisely known (Quade and Roe, 1999). The source of carbon in the carbonate nodules and the eggs are most likely not exactly the same, so a difference between $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{13}\text{C}_{\text{egg}}$ is expected. In this case, the isotopic values of the carbonate nodules are used to compare to the other carbonate at the site (eggshell) to see if there was any mixing of the isotopic values, indicating diagenesis. There is no linear mixing of the isotopic values from different materials (Fig. 4) and the carbonate nodules and eggshells are significantly different despite the fact that they are from the same site (Table 2). This fact strengthens the assertion that the paleoenvironmental reconstruction is not affected by diagenesis.

The $\delta^{18}\text{O}_{\text{carb}}$ from Ukhaa Tolgod does not show as much scatter (mean $-11.0 \pm 0.4\%$) in the data as the eggshell fragments from the same locality. An F-test shows the variances of $\delta^{18}\text{O}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{egg}}$ are not equal. Generally, the $\delta^{18}\text{O}$ of soil carbonates is determined mainly by the meteoric water $\delta^{18}\text{O}$ (precipitation), soil temperature, and soil water evaporation (Levin et al., 2004). The fact that $\delta^{18}\text{O}_{\text{carb}}$ has such a low variance (0.2) makes sense because it is from early-diagenetic

ground-water calcrete which would not be subject to as much evaporative enrichment as more exposed water sources.

4. Comparing lithology and isotopic paleoenvironment reconstructions

The stable isotopic inferences of environment are in concordance with paleoenvironmental information that can be gleaned from the rock record. The Djadokhta Formation is largely composed of cross-bedded sandstones, representing large dunes, and structureless sandstone facies. The scarcity of small channel cuts and mud or silt stones leads one to believe the environment on the whole was devoid of abundant water sources. Our isotopic data from Ukhaa Tolgod strongly support this assumption. The high $\delta^{13}\text{C}_{\text{egg}}$ and $\delta^{13}\text{C}_{\text{enam}}$ are indicative of dinosaurs feeding on vegetation adapted to a dry environment. The oviraptorid eggshells from Ukhaa Tolgod show a large spread of oxygen isotopic values, but the *Protoceratops* teeth from the same locality tell a different story with much less $\delta^{18}\text{O}$ variation, perhaps due to differences in microhabitats of oviraptors versus protoceratopsians. It is fairly apparent from both lithological and isotopic evidence that dinosaurs at Djadokhta localities were not drinking running water from frequently replenished sources. The eolian dunes had minimal drainage, with runoff collecting in interdune ponds and streams undergoing evaporation.

Similar lithologies at the contemporaneous Bayn Dzak locality give us a similar paleoenvironmental interpretation from the rocks. The stable isotope values of the eggshell from Bayn Dzak are different from those at Ukhaa Tolgod; the $\delta^{13}\text{C}_{\text{egg}}$ means are statistically similar, but there is a substantial difference in the $\delta^{18}\text{O}_{\text{egg}}$ at these Djadokhta Formation localities. The $\delta^{18}\text{O}_{\text{egg}}$ at Bayn Dzak shows lower enrichment in ^{18}O than at Ukhaa Tolgod, which illustrates that the environment could have been less dry at Bayn Dzak representing regional hydrological variation.

On the other hand, the lithology of Bugin Tsav locality of the younger Nemegt Formation is most certainly representative of a more mesic environment than the Djadokhta Formation localities. In the Nemegt Formation, there are clear features in the sandy siltstones, such as ripples and flaser structures, that indicate the paleoenvironment was a braided stream system. Most of the fossils there are preserved in laterally discontinuous deposits of sandstone, which are indicative of point bars. The lack of carbonate nodules at this locality, which generally only form in dry conditions, also reinforces the notion that these two formations represent different types of environments. The stable isotopic evidence presented in this paper also strengthens this interpretation. The smaller variance of $\delta^{18}\text{O}_{\text{egg}}$ at Bugin Tsav (compared with Ukhaa Tolgod) (Table 3) suggests that oviraptorids were drinking from less evaporated bodies of water, such as streams. Interestingly, there is no statistical difference when Hotelling’s post-hoc comparison (Table 2) is performed between eggshell from Bayn Dzak (Djadokhta) and Bugin Tsav (Nemegt), indicating that perhaps Ukhaa Tolgod was an unusually dry environment in the Late Cretaceous in this region. This unique quality of the environment at Ukhaa Tolgod could be part of the reason for such unprecedented exceptional fossil preservation at this locality when compared with other Gobi localities (Dashzeveg et al., 1995). The consumed vegetation $\delta^{13}\text{C}$ for both formations is calculated to be $\sim -22\%$, which indicates that the type and physiological qualities of the plants present in both sorts of environments were the same. Further discovery and sampling of organic plant material from these localities is needed to confirm our isotopic inferences about the plants these dinosaurs were eating.

5. Summary

Overall, when stable isotopes are examined in dinosaur remains, environmental heterogeneity becomes apparent in both plants and surface waters when compared within the same formation and time slice (Bayn Dzak and Ukhaa Tolgod) and also between localities from two different

formations potentially spanning millions of years (Ukhaa Tolgod/Bayn Dzak versus Bugin Tsav). Comparing within and between formations and time scales helps us test the viability of our methods for reconstructing environmental change in a basin over time. While this reconstruction cannot particularly reveal whether the Mongolian fauna fell victim to either a mass-wasting event like a landslide (Loope et al., 1998) or were buried in a sudden sandstorm (Jerzykiewicz, 1998), it shows that the Gobi Desert was still a dry, harsh environment ~80 Ma. Even before the uplift of the Tibetan plateau and the Himalayas during the Cenozoic, which currently deprive the Gobi of rainfall, this ecosystem probably was only able to support sheltered areas of biodiversity where organisms could thrive and reproduce.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2012.12.004>.

References

- Al-Bahry, S.N., Mahmoud, I.Y., Al-Amri, I.S., Ba-Omar, T.A., Melgheit, K.O., Al-Kindi, A.Y., 2009. Ultrastructural features and elemental distribution in eggshell during pre and post hatching periods in the green turtle, *Chelonia mydas* at Ras Al-Hadd, Oman. *Tissue & Cell* 41, 214–221.
- Amiot, R., Lécuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., Martineau, F., 2004. Latitudinal temperature gradient during the Cretaceous Upper Campanian–Middle Maastrichtian: $\delta^{18}\text{O}$ record of continental vertebrates. *Earth and Planetary Science Letters* 226, 255–272.
- Amiot, R., Lécuyer, C., Buffetaut, E., Escarguel, G., Fluteau, F., Martineau, F., 2006. Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs. *Earth and Planetary Science Letters* 246, 41–54.
- Andrews, R.C., Nelson, N.C., Hillhouse, C., Granger, W., 1932. The new conquest of central Asia: a narrative of the explorations of the Central Asiatic Expeditions in Mongolia and China, 1921–1930. American Museum of Natural History.
- Averianov, A.O., 1997. New late Cretaceous mammals of southern Kazakhstan. *Acta Palaeontologica Polonica* 42, 243–256.
- Balanoff, A.M., Norell, M.A., Grellet-Tinner, G., Lewin, M.R., 2008. Digital preparation of a probable neoceratopsian preserved within an egg, with comments on microstructural anatomy of ornithischian eggshells. *Die Naturwissenschaften* 95, 493–500.
- Barbin, V., Brand, U., Hewitt, R.A., Ramseyer, K., 1995. Similarity in cephalopod shell biogeochemistry since Carboniferous: evidence from cathodoluminescence. *Geobios* 28, 701–710.
- Barrick, R.E., Showers, W.J., 1994. Thermophysiology of *Tyrannosaurus rex*: evidence from oxygen isotopes. *Science* 265, 222–224.
- Berkey, C.P., Morris, F.K., 1927. Geology of Mongolia: a reconnaissance report based on the investigations of the years 1922–1923, 2. The American Museum of Natural History.
- Birkeland, P.W., 1999. Soils and Geomorphology. Oxford University Press, New York, p. 372.
- Bojar, A.-V., Csiki, Z., Grigorescu, D., 2010. Stable isotope distribution in Maastrichtian vertebrates and paleosols from the Hateg Basin, South Carpathians. *Palaeogeography, Palaeoclimatology, Palaeoecology* 293, 329–342.
- Cerling, T.E., Quade, J., 1993. Stable carbon and oxygen isotopes in soil carbonates. *Geophysical Monograph Series* 78, 217–231.
- Chew, R.M., 1961. Water metabolism of desert-inhabiting vertebrates. *Biological Reviews* 36, 1–28.
- Clark, J.M., Norell, M.A., Barsbold, R., 2001. Two new oviraptorids (Theropoda: Oviraptorosauria), Upper Cretaceous Djadokhta Formation, Ukhaa Tolgod, Mongolia. *Journal of Vertebrate Paleontology* 21, 209–213.
- Cojan, I., Renard, M., Emmanuel, L., 2003. Palaeoenvironmental reconstruction of dinosaur nesting sites based on a geochemical approach to eggshells and associated paleosols (Maastrichtian, Provence Basin, France). *Palaeogeography, Palaeoclimatology, Palaeoecology* 191, 111–138.
- Coplen, T.B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure and Applied Chemistry* 66, 273–276.
- Dansgaard, W., 1964. Stable isotopes in precipitation. *Tellus* 16, 436–468.
- Dashzeveg, D., Novacek, M.J., Norell, M.A., Clark, J.M., Chiappe, L.M., Davidson, A., McKenna, M.C., Dingus, L., Swisher, C., Altangerel, P., 1995. Extraordinary preservation in a new vertebrate assemblage from the Late Cretaceous of Mongolia. *Nature* 374, 446–449.
- Dashzeveg, D., Dingus, L., Loope, D.B., Swisher III, C.C., Dulam, T., Sweeney, M.R., 2005. New stratigraphic subdivision, depositional environment, and age estimate for the Upper Cretaceous Djadokhta Formation, southern Ulan Nur Basin, Mongolia. *American Museum Novitates* 1–31.
- Dauphin, Y., Cuif, J.P., Salomé, M., Susini, J., Williams, C.T., 2006. Microstructure and chemical composition of giant avian eggshells. *Analytical and Bioanalytical Chemistry* 386, 1761–1771.
- DeLucia, E.H., Schlesinger, W.H., 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72, 51–58.
- DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42, 495–506.
- Dingus, L., Loope, D.B., Dashzeveg, D., Swisher III, C.C., Minjin, C., Novacek, M.J., Norell, M.A., 2008. The geology of Ukhaa Tolgod (Djadokhta Formation, Upper Cretaceous, Nemegt Basin, Mongolia). *American Museum Novitates* 1–40.
- Eberth, D.A., 1993. Depositional environments and facies transitions of dinosaur-bearing Upper Cretaceous red beds at Bayan Mandahu (Inner Mongolia, People's Republic of China). *Canadian Journal of Earth Sciences* 30, 2196–2213.
- Erben, H.K., Hoefs, J., Wedepohl, K.H., 1979. Paleobiological and isotopic studies of eggshells from a declining dinosaur species. *Paleobiology* 5, 380–414.
- Folinsbee, R.E., Fritz, P., Krouse, H.R., Robblee, A.R., 1970. Carbon-13 and oxygen-18 in dinosaur, crocodile, and bird eggshells indicate environmental conditions. *Science* 168, 1353–1356.
- Foreman, B.Z., Fricke, H.C., Lohmann, K.C., Rogers, R.R., 2011. Reconstructing paleocatchments by integrating stable isotope records, sedimentology, and taphonomy: a Late Cretaceous case study (Montana, United States). *Palaios* 26, 545.
- Fricke, H.C., O'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. *Palaeogeography, Palaeoclimatology, Palaeoecology* 126, 91–99.
- Fricke, H.C., Pearson, D.A., 2008. Stable isotope evidence for changes in dietary niche partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation, North Dakota. *Paleobiology* 34, 534.
- Fricke, H.C., Rogers, R.R., 2000. Multiple taxon-multiple locality approach to providing oxygen isotope evidence for warm-blooded theropod dinosaurs. *Geology* 28, 799.
- Fricke, H.C., Rogers, R.R., Backlund, R., Dwyer, C.N., Echt, S., 2008. Preservation of primary stable isotope signals in dinosaur remains, and environmental gradients of the Late Cretaceous of Montana and Alberta. *Palaeogeography, Palaeoclimatology, Palaeoecology* 266, 13–27.
- Fricke, H.C., Rogers, R.R., Gates, T.A., 2009. Hadrosaurid migration: inferences based on stable isotope comparisons among Late Cretaceous dinosaur localities. *Paleobiology* 35, 270.
- Gao, K., Norell, M.A., 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History* 1–118.
- Gonfiantini, R., Gratzu, S., Tongiorgi, E., 1965. Oxygen isotopic composition of water in leaves. *Isotopes and Radiation in Soil-Plant Nutrition Studies*, pp. 405–410.
- Gradzinski, R., 1970. Sedimentation of dinosaur-bearing Upper Cretaceous deposits of the Nemegt Basin, Gobi Desert. *Palaeontologica Polonica* 21, 147–210.
- Gradzinski, R., Jerzykiewicz, T., 1974. Dinosaur- and mammal-bearing aeolian and associated deposits of the Upper Cretaceous in the Gobi Desert (Mongolia). *Sedimentary Geology* 12, 249–278.
- Grellet-Tinner, G., Makovicky, P., 2006. A possible egg of the dromaeosaur *Deinonychus antirrhopus*: phylogenetic and biological implications. *Canadian Journal of Earth Sciences* 43, 705–719.
- Grellet-Tinner, G., Norell, M., 2002. An avian egg from the Campanian of Bayn Dzak, Mongolia. *Journal of Vertebrate Paleontology* 22, 719–721.
- Grellet-Tinner, G., Chiappe, L., Norell, M., Bottjer, D., 2006. Dinosaur eggs and nesting behaviors: a paleobiological investigation. *Palaeogeography, Palaeoclimatology, Palaeoecology* 232, 294–321.
- Grellet-Tinner, G., Corsetti, F., Buscalioni, D., 2010. The importance of microscopic examinations of eggshells: discrimination of bioalteration and diagenetic overprints from biological features. *Journal of Iberian Geology* 36, 181–192.
- Grellet-Tinner, G., Sim, C.M., Kim, D.H., Trimby, P., Higa, A., An, S.L., Oh, H.S., Kim, T.J., Kardjilov, N., 2011. Description of the first lithostrotian titanosaur embryo in ovo with Neutron characterization and implications for lithostrotian Aiptian migration and dispersion. *Gondwana Research* 20, 621–629.
- Grellet-Tinner, G., Murelaga, X., Larrasoana, J.C., Silveira, L.F., Olivares, M., Ortega, L.A., Trimby, P.W., Pascual, A., 2012. The first occurrence in the fossil record of an aquatic avian twig-nest with phoenicopteriformes eggs: evolutionary implications. *PLoS One* 7, e4697.
- Hasegawa, T., Pratt, L.M., Maeda, H., Shigeta, Y., Okamoto, T., Kase, T., Uemura, K., 2003. Upper Cretaceous stable carbon isotope stratigraphy of terrestrial organic matter from Sakhalin, Russian Far East: a proxy for the isotopic composition of paleoatmospheric CO₂. *Palaeogeography, Palaeoclimatology, Palaeoecology* 189, 97–115.
- Hasegawa, H., Tada, R., Ichinnorov, N., Minjin, C., 2009. Lithostratigraphy and depositional environments of the Upper Cretaceous Djadokhta Formation, Ulan Nuur basin, southern Mongolia, and its paleoclimatic implication. *Journal of Asian Earth Sciences* 35, 13–26.
- Jerzykiewicz, T., 1998. Okavango Oasis, Kalahari Desert: a contemporary analogue for the Late Cretaceous vertebrate habitat of the Gobi Basin, Mongolia. *Geoscience Canada* 25, 15–26.
- Jerzykiewicz, T., Russell, D.A., 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research* 12, 345–377.

- Johnson, B.J., Miller, G.H., Fogel, M.L., Beaumont, P.B., 1997. The determination of late Quaternary paleoenvironments at Equus Cave, South Africa, using stable isotopes and amino acid racemization in ostrich eggshell. *Palaeogeography, Palaeoclimatology, Palaeoecology* 136, 121–137.
- Johnson, B.J., Fogel, M.L., Miller, G.H., 1998. Stable isotopes in modern ostrich eggshell: a calibration for paleoenvironmental applications in semi-arid regions of southern Africa. *Geochimica et Cosmochimica Acta* 62, 2451–2461.
- Kielan-Jaworowska, Z., Barsbold, R., 1972. Narrative of the Polish–Mongolian palaeontological expeditions 1967–1971. *Palaeontologia Polonica* 5–12.
- Kielan-Jaworowska, Z., Sochava, A.V., 1969. The first multituberculate from the uppermost Cretaceous of the Gobi Desert (Mongolia). *Acta Palaeontologica Polonica* 14, 355–367.
- Koch, P.L., 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences* 26, 573–613.
- Koch, P.L., 2007. Isotopic study of the biology of modern and fossil vertebrates. In: Michener, R., Lajtha, K. (Eds.), *Stable Isotopes in Ecology and Environmental Science*. Blackwell Publishing, Boston, pp. 99–154.
- Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate. *Proceedings of the National Academy of Sciences* 107, 19691.
- Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. *Reviews in Mineralogy and Geochemistry* 48, 455–488.
- Levin, N.E., Quade, J., Simpson, S.W., Semaw, S., Rogers, M., 2004. Isotopic evidence for Plio-Pleistocene environmental change at Gona, Ethiopia. *Earth and Planetary Science Letters* 219, 93–110.
- Lockheart, M.J., Poole, I., Van Bergen, P.F., Evershed, R.P., 1998. Leaf carbon isotope compositions and stomatal characters: important considerations for palaeoclimate reconstructions. *Organic Geochemistry* 29, 1003–1008.
- Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and palaeoclimatological research? *Geochimica et Cosmochimica Acta* 48, 385–390.
- Loope, D.B., Dingus, L., Swisher, C.C., Minjin, C., 1998. Life and death in a Late Cretaceous dune field, Nemegt basin, Mongolia. *Geology* 26, 27.
- Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. *Earth and Planetary Science Letters* 75, 29–36.
- MacFadden, B.J., Higgins, P., 2004. Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama. *Oecologia* 140, 169–182.
- Mikhailov, K.E., Bray, E.S., Hirsch, K.E., 1996. Parataxonomy of fossil egg remains (Veterovata): principles and applications. *Journal of Vertebrate Paleontology* 16, 763–769.
- Mlynarski, M., Narmandach, P., 1972. New turtle remains from the Upper Cretaceous of the Gobi Desert, Mongolia. *Palaeontologia Polonica* 7, 95–102.
- Norell, M.A., Clark, J.M., Demberelyin, D., Rhinchen, B., Chiappe, L.M., Davidson, A.R., McKenna, M.C., Altangerel, P., Novacek, M.J., 1994. A theropod dinosaur embryo and the affinities of the Flaming Cliffs dinosaur eggs. *Science* 266, 779–782.
- Norell, M.A., Clark, J.M., Chiappe, L.M., Dashzeveg, D., 1995. A nesting dinosaur. *Nature* 378, 774–776.
- O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. *Bioscience* 38, 328–336.
- Osborn, H.F., 1924. Three new theropoda, *Protoceratops* zone, central Mongolia. *American Museum Novitates* 144, 1–12.
- Pol, D., Norell, M.A., 2004. A new gobiosuchid crocodyliform taxon from the Cretaceous of Mongolia. *American Museum Novitates* 1–31.
- Quade, J., Roe, L.J., 1999. The stable-isotope composition of early ground-water cements from sandstone in paleoecological reconstruction. *Journal of Sedimentary Research* 69, 667–674.
- Royer, D.L., 1999. Depth to pedogenic carbonate horizon as a paleoprecipitation indicator? *Geology* 27, 1123–1126.
- Sage, R.F., 2004. The evolution of C4 photosynthesis. *The New Phytologist* 161, 341–370.
- Sarkar, A., Bhattacharya, S., Mohabey, D., 1991. Stable-isotope analyses of dinosaur eggshells: paleoenvironmental implications. *Geology* 19, 1068–1071.
- Schaffner, F.C., Swart, P.K., 1991. Influence of diet and environmental water on the carbon and oxygen isotopic signatures of seabird eggshell carbonate. *Bulletin of Marine Science* 48, 23–38.
- Segalen, L., Renard, M., Pickford, M., Senut, B., Cojan, I., Le Callonnec, L., Rognon, P., 2002. Environmental and climatic evolution of the Namib Desert since the Middle Miocene: the contribution of carbon isotope ratios in ratite eggshells. *Comptes Rendus Geoscience* 334, 917–922.
- Sharp, Z.D., Atudorei, V., Furrer, H., 2000. The effect of diagenesis on oxygen isotope ratios of biogenic phosphates. *American Journal of Science* 300, 222–237.
- Shuvalov, V.F., 2000. The Cretaceous stratigraphy and palaeobiogeography of Mongolia. In: Benton, M.J., Shishkin, M.A., Unwin, D.M., Kurochkin, E.N. (Eds.), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, pp. 256–278.
- Stanton Thomas, K.J., Carlson, S.J., 2004. Microscale $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ isotopic analysis of an ontogenetic series of the hadrosaurid dinosaur *Edmontosaurus*: implications for physiology and ecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206, 257–287.
- Stern, L.A., Johnson, G.D., Chamberlain, C.P., 1994. Carbon isotope signature of environmental change found in fossil ratite eggshells from a South Asian Neogene sequence. *Geology* 22, 419–422.
- Sternberg, L.D., Mulkey, S.S., Wright, S.J., 1989. Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. *Ecology* 70, 1317–1324.
- Tieszen, L.L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *Journal of Archaeological Science* 18, 227–248.
- Trueman, N., Tuross, N., 2002. Trace elements in recent and fossil bone apatite. *Reviews in Mineralogy and Geochemistry* 48, 489–521.
- Von Schirnding, Y., Van Der Merwe, N.J., Vogel, J.C., 1982. Influence of diet and age on carbon isotope ratios in ostrich eggshell. *Archaeometry* 24, 3–20.
- Weishampel, D.B., Fastovsky, D.E., Watabe, M., Varricchio, D., Jackson, F., Tsogtbaatar, K., Barsbold, R., 2008. New oviraptorid embryos from Bugin-Tsav, Nemegt Formation (Upper Cretaceous), Mongolia, with insights into their habitat and growth. *Journal of Vertebrate Paleontology* 28, 1110–1119.
- Wible, J.R., Rougier, G.W., Novacek, M.J., Asher, R.J., 2007. Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* 447, 1003–1006.
- Withers, P.C., 1983. Energy, water, and solute balance of the ostrich *Struthio camelus*. *Physiological Zoology* 56, 568–579.
- Zazzo, A., Lécuyer, C., Sheppard, S.M., Grandjean, P., Mariotti, A., 2004. Diagenesis and the reconstruction of paleoenvironments: a method to restore original $\delta^{18}\text{O}$ values of carbonate and phosphate from fossil tooth. *Geochimica et Cosmochimica Acta* 68, 2245–2258.
- Zhao, Z., Mao, X., Chai, Z., Yang, G., Zhang, F., Yan, Z., 2009. Geochemical environmental changes and dinosaur extinction during the Cretaceous–Paleogene (K/T) transition in the Nanxiong Basin, South China: evidence from dinosaur eggshells. *Chinese Science Bulletin* 54, 806–815.