# STABLE ISOTOPIC COMPOSITION, PALEOECOLOGY, AND HABITAT OF THE AMMONITE *SPHENODISCUS LOBATUS* IN THE LATE CRETACEOUS (MAASTRICHTIAN) WESTERN INTERIOR SEAWAY

James D. Witts[1], Neil H. Landman[2], J. Kirk Cochran[3], Corinne E. Myers[4]

1 – Natural History Museum, London, United Kingdom.
james.witts1@nhm.ac.uk
2 – Division of Paleontology (Invertebrates), American Museum of Natural History, New York, USA
landman@amnh.org
3 – School of Marine & Atmospheric Sciences, Stony Brook University, Stony Brook, New York, USA
kirk.cochran@stonybrook.edu
4 – Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, New Mexico, USA
cemyers@unm.edu

This article has undergone peer-review and was accepted for publication in 2022 as part of a special volume: Slattery JS, Larson NL, Bingle-Davis M, Graham FC, eds. 'Insights into the Cretaceous: Building on the Legacy of William A. Cobban (1916–2015)'. To be published by the *American Association of Petroleum Geologists and Wyoming Geological Association*. https://archives.datapages.com/data/browse/wyoming-geological-association/ Subsequent versions of the manuscript may appear with slightly different content.

# STABLE ISOTOPIC COMPOSITION, PALEOECOLOGY, AND HABITAT OF THE AMMONITE *SPHENODISCUS LOBATUS* IN THE LATE CRETACEOUS (MAASTRICHTIAN) WESTERN INTERIOR SEAWAY

James D. Witts[1,2], Neil H. Landman[2], J. Kirk Cochran[3], Corinne E. Myers[2]

1 – Natural History Museum, London, Cromwell Road, London SW7 5BD, United Kingdom.

2 – Department of Earth and Planetary Sciences, University of New Mexico, Albuquerque, New Mexico 87131

3 – Division of Paleontology (Invertebrates), American Museum of Natural History, New York, 10024

4 – School of Marine & Atmospheric Sciences, Stony Brook University, Stony Brook, New York 11794

**Abstract**

Despite their abundance as fossils, the life histories of ammonites are still poorly understood. We analyzed the oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotopic composition of well-preserved shell material taken from different growth stages of the streamlined oxyconic ammonite species *Sphenodiscus lobatus* from the Upper Cretaceous (Maastrichtian) Pierre Shale and Fox Hills Formation of South Dakota. Pairing isotopic data with an analysis of the distribution of this species through a range of shallow marine environments allows us to reconstruct the life history and habitat of this ammonite in the Western Interior Seaway (WIS). When plotted ontogenetically using whorl height (WH) as a proxy for growth stage, $\delta^{18}O$ values in the early ontogeny of *S. lobatus* are consistently depleted (-3 to -4‰), irrespective of facies and stratigraphic position. These results suggest a warm surface water habitat with lowered salinity. A distinct positive shift at a WH of ~40 mm in all specimens indicates a change to waters with a different isotopic composition – potentially migration to a more nektobenthic habitat in cooler waters. Oxygen isotope values remain highly variable (> 3‰ within individual specimens) throughout adulthood, indicating either a high degree of seasonality in the WIS or the migration of *S. lobatus* through different environments (vertically or laterally within the water column). Values of $\delta^{13}C$ show no pattern and are variable throughout ontogeny in all specimens, either a result of differential incorporation of metabolic carbon through the lifetime of the animal or reflecting changes to the dissolved inorganic carbon pool in shallow water environments. Distribution within the Fox Hills Formation indicates a consistent pattern in which smaller specimens of *S. lobatus* are more commonly preserved in the offshore silts of the Little Eagle lithofacies of the Trail City Member, and larger specimens are more commonly preserved in the nearshore, time-equivalent Irish Creek lithofacies and the overlying sandy lithofacies of the Timber Lake Member. These data are consistent with the hypothesis that adult *Sphenodiscus* were adapted to inhabit shallow water environments.

## Introduction

The richly fossiliferous Upper Cretaceous marine strata of the U.S. Western Interior (Figure 1) preserve an excellent record of ammonoid cephalopods (ammonites), which forms the basis of an unparalleled biostratigraphic scheme for the region developed by William (Bill) Cobban and colleagues over more than 50 years (Cobban et al., 2006). Despite their abundance as fossils, the life history and ecology of ammonites is an area of ongoing debate due to the exceptional rarity of soft tissue preservation in the fossil record and uncertainty about their closest extant relatives, hampering comparison to modern cephalopods (e.g., Jacobs and Landman, 1993). Today, many cephalopods exhibit changes in their preferred habitat through ontogeny (Rexfort and Mutterlose, 2006; Price et al., 2009; Lukeneder et al., 2010); as mobile organisms they can migrate through the water column and experience different environmental conditions over short timescales (Linzmeier et al., 2016; Linzmeier, 2019). Studies of shell morphology and hydrodynamics, as well as facies associations, have traditionally provided important clues into ammonite ecology. Modern *Nautilus* shells are also commonly subject to post-mortem drift and this phenomenon could have affected some (but not all) ammonites (Chamberlain and Ward, 1981; Wani et al., 2005; Yacobucci, 2018), suggesting that where shells are found as fossils may not match the environment in which the animals lived.

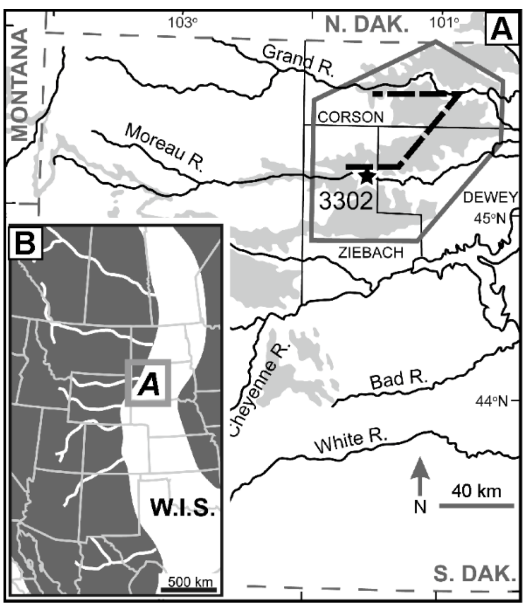


Figure 1: (A) Location map showing the distribution of outcrops of the Fox Hills Formation in South Dakota, North Dakota, Montana, and Wyoming (grey shading). The 'type area' (Waage, 1968) in Corson, Dewey, and Ziebach counties (South Dakota) from where most samples in the Yale Peabody Museum (YPM) and Timber Lake and Area Museum (TLM) collections used in this study are derived is indicated by the grey polygon. Dashed black line is roughly equivalent to the cross-section in Figure 3. American Museum of Natural History (AMNH) locality #3302, the single locality in the Elk Butte Member of the Pierre Shale is also marked. (B) Inset shows paleogeography of the Western Interior Seaway

(WIS) during the late Maastrichtian *Hoploscaphites birkelundae* range zone (Cobban et al., 1994); grey box shows extent of A.

One of the most common ammonite taxa in Maastrichtian (72 – 66 Ma) deposits of the US Western Interior is the oxyconic genus *Sphenodiscus* (Meek, 1871) (Figure 2). Compressed oxyconic morphotypes like *Sphenodiscus* are frequently found in strata deposited in proximal marine settings, sometimes above wave-base, and often with no other ammonite fossils present (Waage, 1968; Batt, 1989; Wani, 2006; Ifrim and Stinnesbeck, 2010). Hydrodynamic studies show that they are suited to relatively rapid movement through the water column, with their streamlined shape ideal for active swimming, and they may have had the ability to stabilize their shells in high energy conditions characteristic of very shallow waters (Jacobs and Chamberlain, 1996; Wani, 2006; Hebdon et al., 2020).

Stable oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotope analysis of shell carbonate is a promising method for unraveling the ecology of ammonites like *Sphenodiscus* and enables direct comparison to modern cephalopod taxa (e.g., Lukeneder et al., 2010; 2015; Moriya et al., 2015). Like most mollusks, ammonites probably exhibited continuous growth, and secreted their shells in oxygen isotopic equilibrium with seawater. Examining isotopic ratios through ontogeny can therefore provide important clues as to habitat, life history, and even metabolism during their lifetime (e.g., Sessa et al., 2015; Landman et al., 2018; Rowe et al., 2020). Comparison between different groups can also provide clues as to differential habitat among ammonite groups. For example, Sessa et al. (2015) studied the isotopic composition of shell material from three ammonite genera (*Discoscaphites*, *Eubaculites*, and *Sphenodiscus*) from the Maastrichtian Owl Creek Formation in Mississippi and compared these to benthic bivalves and benthic and planktic foraminifera. They suggest that baculitids and scaphitids lived close to the bottom, but that *Sphenodiscus* inhabited a different environment to the other ammonite genera for at least part of their lives based on overlapping values with both planktic and benthic taxa.

In this study, we reconstruct the life history and habitat of *Sphenodiscus* from the Pierre Shale and Fox Hills Formation of the US Western Interior. To do this, we examine the isotopic composition of well-preserved shell material taken from multiple *Sphenodiscus* specimens, and pair isotopic analyses with a study of fossil distribution across different (paleo)environments.

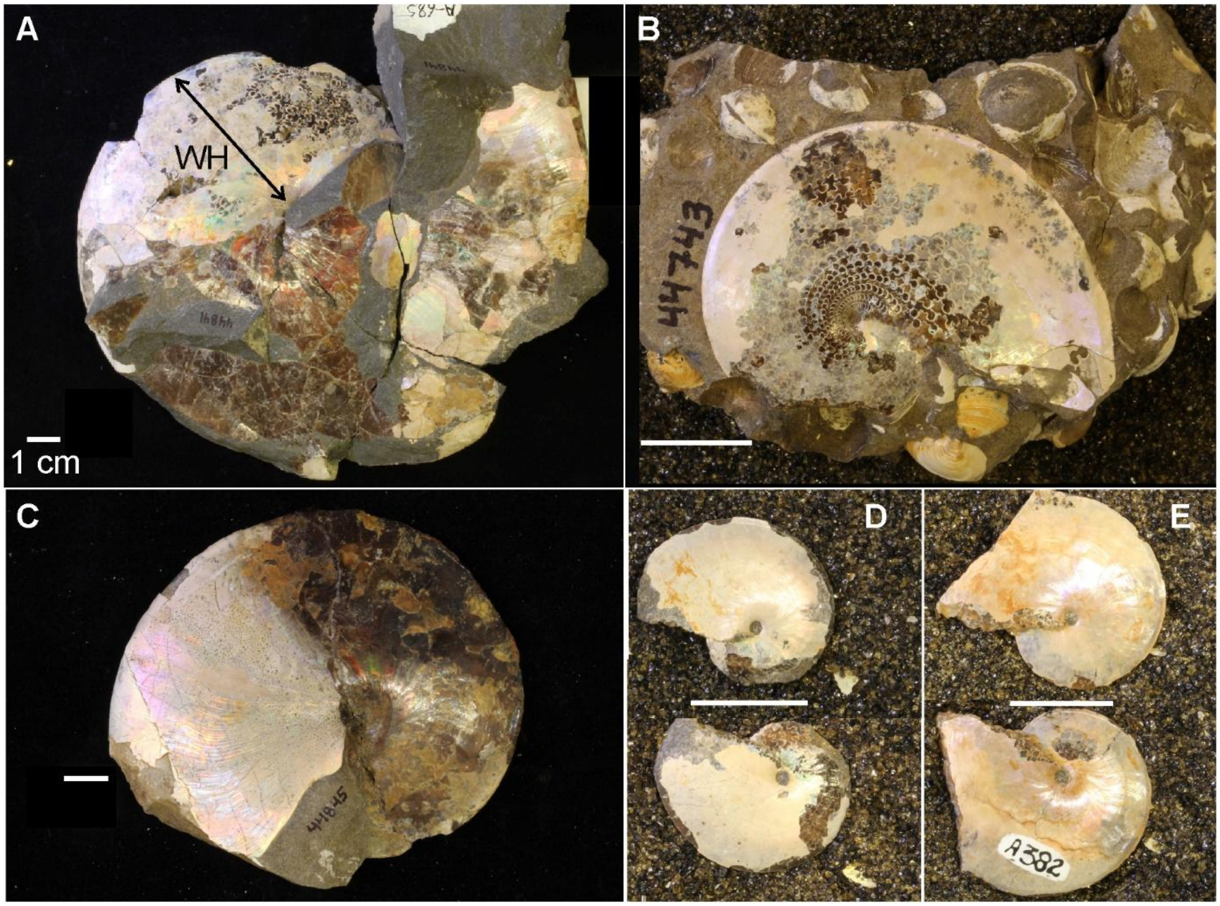


Figure 2: Examples of specimens of *Sphenodiscus lobatus* from the Fox Hills Formation sampled in this study from the Invertebrate Paleontology collections of the Yale Peabody Museum, all showing preservation of iridescent aragonitic shell material. A: YPM IP 044841, Trail City Member (*Protocardia*-*Oxytoma* Assemblage Zone). B: YPM IP 044743, Trail City Member (*Limopsis*-*Gervillia* Assemblage Zone). C: YPM IP 044845, Timber Lake Member (*Sphenodiscus* layer). D: YPM IP 044712, Trail City Member (*Limopsis*-*Gervillia* Assemblage Zone). E: YPM IP 044707, Trail City Member (*Limopsis*-*Gervillia* Assemblage Zone). Whorl height (WH) indicated on panel A. All scale bars = 1 cm. All photos taken by M. Prangley (Yale Peabody Museum - 2016).

**Taxonomic background**

The taxonomy of Late Cretaceous sphenodiscid ammonites is still in flux, complicated by wide-ranging intraspecific and potentially ecophenotypic variability in important features such as morphology of the suture line (Kennedy et al., 1997; Landman et al., 2004; Ifrim and Stinnesbeck, 2010). Using the currently most accepted taxonomy, based on the presence or absence of rows of nodes on the flanks (Cobban and Kennedy, 1995), two species are recognized in the US Western Interior from the Maastrichtian stage; *Sphenodiscus pleurisepta* (Conrad, 1857) occurs in the *Hoploscaphites birkelundae* Zone of the Pierre Shale in Meade and Pennington counties, South Dakota, the Fox Hills Formation in Niobrara County, Wyoming (Kennedy et al., 1996), and in the upper part of the Pierre Shale and Fox Hills Formation in Weld County, Colorado (Landman and Cobban, 2003). *Sphenodiscus lobatus* (Tuomey, 1856) (Figure 2) (considered synonymous with *Sphenodiscus lenticularis* (Owen, 1852) and *Sphenodiscus splendens* (Hyatt, 1903) by Cobban and Kennedy (1995) and Kennedy et al. (1996)), occurs in the *Hoploscaphites nicolletii* and *Hoploscaphites nebrascensis* zones of the Pierre Shale and Fox Hills Formation in north-central South Dakota (Landman and Waage, 1993; Kennedy et al., 1996), and in the *Hoploscaphites nebrascensis* Zone of the Pierre Shale in southeastern South Dakota and northeastern Nebraska (Kennedy et al., 1998).

**Geological Setting**

We analyzed specimens of *Sphenodiscus lobatus* from the Pierre Shale and Fox Hills Formation of north-central South Dakota - considered the 'type area' of the Fox Hills Formation (Waage, 1968) (Figure 1; Figure 3, Table 1). These strata were deposited during the final regression of the Late Cretaceous Western Interior Seaway (WIS) (Slattery et al., 2015). They record a transition from offshore marine conditions (represented by shales of the Elk Butte Member of the Pierre Shale) through a range of deep sub-tidal to littoral environments affected by the progradation of a large submarine sand bar (siltstones and sandstones of the Trail City, Timber Lake, and Iron Lightning members of the Fox Hills Formation), to terrestrial delta plain and coal swamp deposits (the Hell Creek Formation) (Waage, 1968; Landman and Waage, 1993). It is important to note that even in the most offshore settings, water depths in the WIS were probably ≤ 100 m (Gill et al., 1966).

Specimens used in this study were derived from fossiliferous concretion horizons, which in the Trail City and Timber Lake members of the Fox Hills Formation are classified as assemblage zones (AZ's) named after their dominant fauna (Waage, 1968; Witts et al., 2020). A single fossiliferous concretion horizon is also present in the upper Elk Butte Member of the Pierre Shale in Ziebach County SD (American Museum of Natural History (AMNH) locality #3302) (Figure 3), characterized by unusually large specimens of the ammonite genera *Hoploscaphites* and *Discoscaphites* (Landman and Waage, 1993; Witts et al., 2020). Concretion horizons in the Fox Hills Formation have been interpreted to represent marine communities affected by recurrent mass mortality events, although the precise mechanism behind these events is unknown (Waage, 1964). Changes in oxygen levels, turbidity, or salinity caused by periods of rapid freshwater influx are all considered likely. The excellent preservation of fossils and occurrence of delicate elements such as in-situ ammonite jaws (aptychi) in the concretions have been used to argue for rapid burial and minimal post-mortem transport of these fossils (Landman and Waage, 1993).

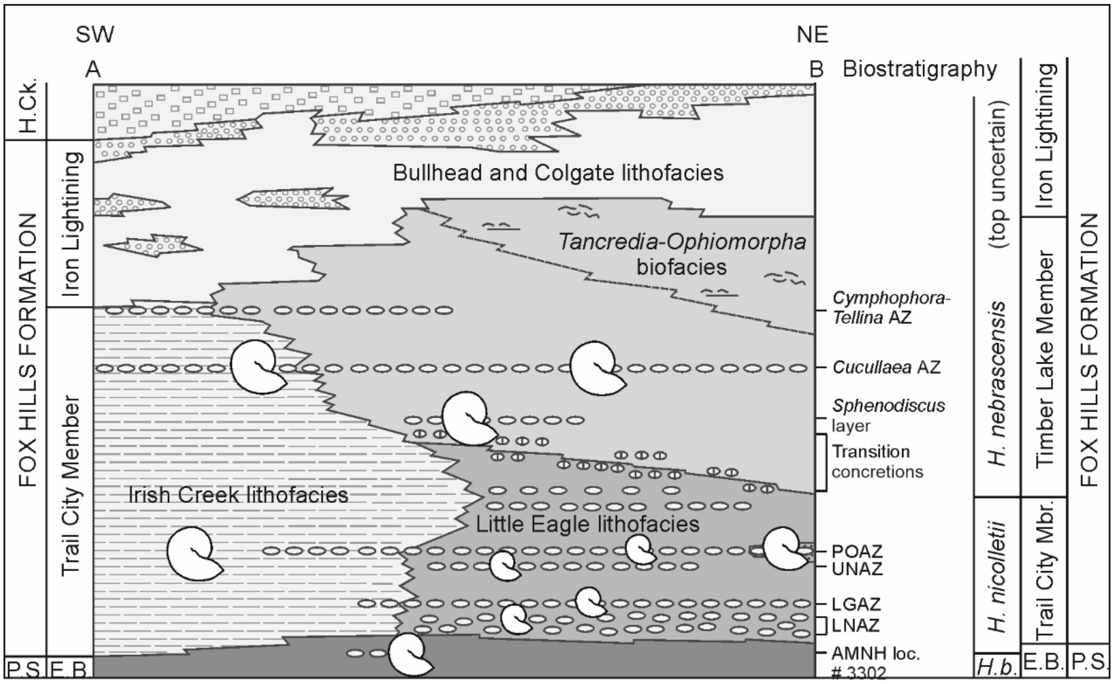


Figure 3: Schematic cross-section and overview of the Fox Hills Formation along a southwest to northeast transect (A-B) in the 'type area' of South Dakota (Figure 1) with different facies highlighted. Lithostratigraphy and ammonoid biostratigraphy of the uppermost Pierre Shale (P.S.) (Elk Butte Member = E.B.), Fox Hills Formation (Trail City, Timber Lake, and Iron Lightning members), and relationship with the overlying Hell Creek Formation (H. Ck.) also illustrated. LNAZ = Lower *nicolletii* Assemblage Zone. LGAZ = *Limopsis-Gervillia* Assemblage Zone. UNAZ = Upper *nicolletii* Assemblage Zone. POAZ = *Protocardia-Oxytoma Assemblage Zone*. *H. nicolletii* = *Hoploscaphites nicolletii*. *H.b.* = *Hoploscaphites birkelundae*. Size of ammonoid symbols qualitatively represents the relative size of *Sphenodiscus lobatus* specimens found at different stratigraphic horizons. Figure is modified from Waage (1968), Witts et al. (2020). Readers are referred to these papers, as well as Waage (1964) and Landman and Waage (1993), for detailed lithological descriptions of each facies within the Fox Hills Formation.

## Methodology

Samples analyzed in this study are held in the Invertebrate Paleontology collections of the Yale Peabody Museum of Natural History (YPM IP) (New Haven, CT) (Figure 2) and the Timber Lake and Area Museum (TLM) (Timber Lake, SD). Sampling of shell material was conducted using a small scalpel cleaned in deionized water, and samples were taken from the mid-flanks of the outer shell where possible. We sampled a total of 13 specimens, sometimes taking multiple samples from the same specimen (Table 1). Shell pieces were divided into two, with one piece used for isotopic analysis and one for preservation assessment. The whorl height (WH) was measured on the specimens at the point of sampling. Given the accretionary growth of ammonites, plotting isotopic data against WH can act as a proxy for assessing ontogenetic changes (e.g., Lukeneder et al., 2010; Lukeneder, 2015), even in fragmentary specimens. We also compiled published isotopic data from this species and geological setting available in the published literature (Cochran et al., 2003; Dennis et al., 2013; Zakharov et al., 2014).

Isotopic analyses were conducted at the University of Santa Cruz Stable Isotope Laboratory using standard techniques. Prior to analysis, 40-60 micrograms of solid sample were vacuum-roasted for one hour at 65°C. Samples were analyzed for $\delta^{18}O$ and $\delta^{13}C$ via acid digestion using an individual vial acid drop ThemoScientific Kiel IV carbonate device interfaced to a ThermoScientific MAT-253 dual-inlet isotope ratio mass spectrometer (IRMS). Samples were reacted at 75°C in orthophosphoric acid (specific gravity = 1.92 g/cm3) to generate carbon dioxide and water. Non-condensable gases were pumped away, and the $CO_2$ analyte was then cryogenically separated from water, finishing with the introduction of pure $CO_2$ into the IRMS via the dual inlet. Raw data were corrected against samples of calibrated in-house granular Carrara Marble standard reference material and granular NBS-18 limestone international standard reference material. The in-house Carrara Marble was extensively calibrated against NIST Standard Reference Materials (NBS-19, NBS-18, and LSVEC) and further calibrated in intercomparison studies with international laboratories. Raw data were also corrected for offset from the international standard PDB (PeeDee Belemnite) for $\delta^{18}O$ and $\delta^{13}C$ and corrected for instrument specific source ionization effects. Two aliquots of powdered Atlantis II calcium carbonate were run "as-a-sample" to monitor quality control and long-term performance. Precision of Atlantis II at UCSC SIL is 0.05‰ for both $\delta^{18}O$ and $\delta^{13}C$.

We converted values of $\delta^{18}O$ to seawater temperature using the equation of Grossman and Ku (1986) for aragonite, as modified by Hudson and Anderson (1989), with δ water values in terms of VSMOW:

$$T(^{\circ}C) = 19.7 - 4.34(\delta_{aragonite} - \delta_{water})$$

Most studies have assumed the $\delta^{18}O_{water}$ value of the WIS was -1‰, often considered a canonical value for an 'ice-free' Cretaceous Earth (Shackleton and Kennett 1975), and that salinity in the seaway was normal. These assumptions have been challenged based on studies of strontium (Cochran et al., 2003) and carbonate clumped isotopes (Dennis et al., 2013; Petersen et al., 2016), which suggest spatial and temporal variation in $\delta^{18}O_{water}$ values and salinity are possible in the shallow environment of the WIS (see discussion below).

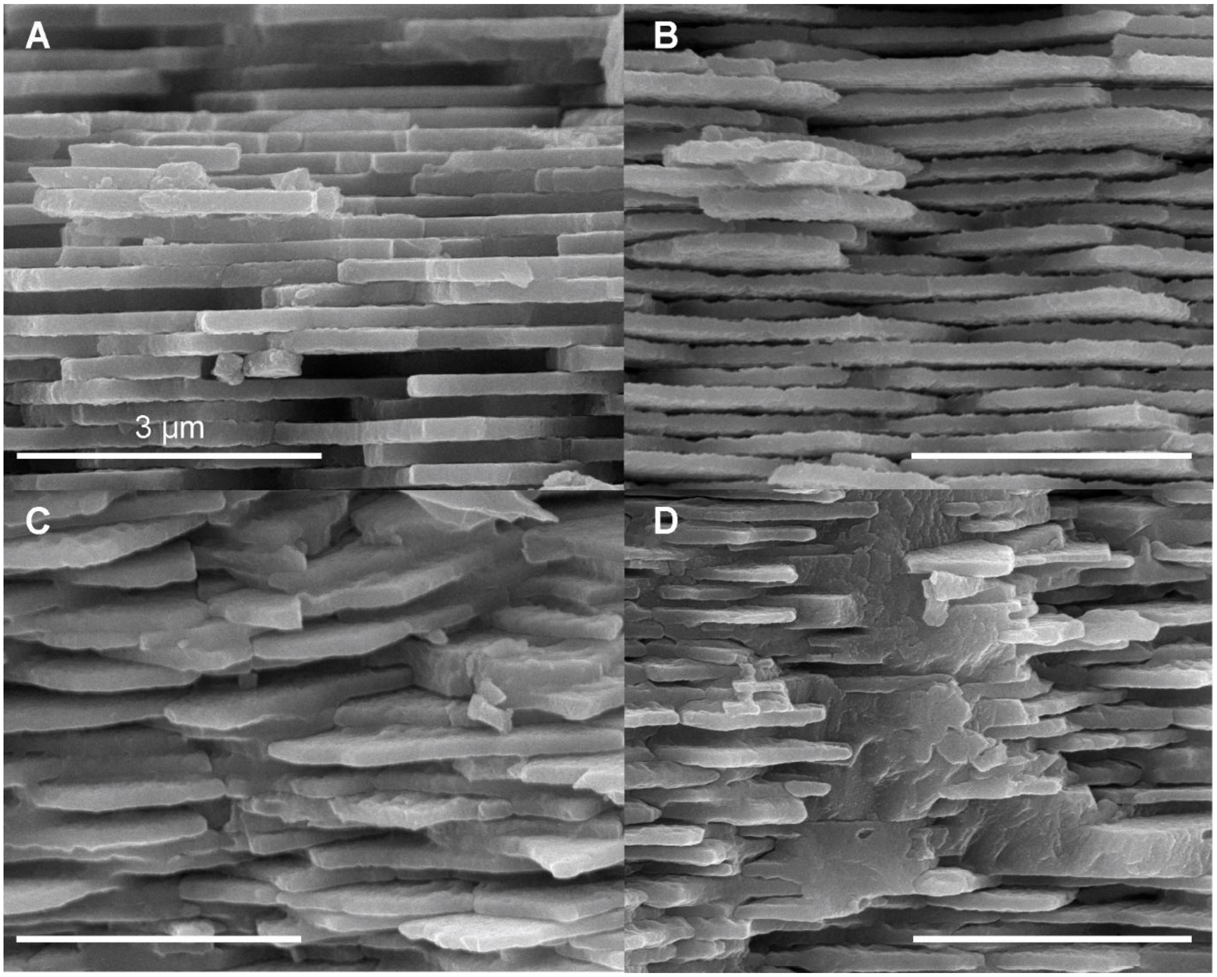


Figure 4: SEM images showing the range of preservation quality of nacreous microstructure from *Sphenodiscus lobatus* specimens using the Preservation Index (PI) scale of Cochran et al. (2010). A: YPM IP 044707, PI = 4. B: YPM IP 044845, PI = 3.5. C: YPM IP 044712, PI = 3. D: YPM IP 044718, PI = 2.5. Only specimens with PI ≥ 3 were used for isotopic analysis. All scale bars = 3 μm.

One shell piece from each pair was mounted on a stub, gold-coated, and examined using a Scanning Electron Microscope at the Museum Imaging Facility at the American Museum of Natural History (AMNH) to assess preservation quality. Prior work has shown that the state of preservation of nacreous shell microstructure of aragonitic ammonite shells is a predictor of the integrity of their oxygen and carbon isotope signatures, using the Preservation Index (PI) scale (Cochran et al., 2010) (Figure 4). Pristine shells are coded as ‘excellent’ (PI = 5), which is visually equivalent to modern, un-fossilized aragonitic shell. As preservation quality degrades, the nacreous tablets fuse together, eventually becoming virtually indistinguishable (PI = 1, ‘poor’ preservation). We only analyzed samples with PI ≥ 3 in our study to assure that the shell material preserved the original isotope signature (Cochran et al., 2010).

### Results

SEM examination revealed that the microstructural preservation of shell samples from *Sphenodiscus lobatus* ranged from 'fair' (Preservation Index = 2.5) to 'very good/excellent' (Preservation Index = 4.5) using the scale developed by Cochran et al. (2010) (Figure 4). Most samples we examined (n = 26/29) had a PI >3 and were therefore suitable for isotopic analysis.

Isotopic data range from -4.50‰ to 0.05‰ ($\delta^{18}O$) and from -9.56‰ to -0.97‰ ($\delta^{13}C$) (Table 1). A cross-plot (Figure 5) revealed no significant overall trend between $\delta^{18}O$ and $\delta^{13}C$ ($r^2 = 2 \times 10^{-7}$). When plotted ontogenetically using WH at the position of sampling (Figure 6A; Figure 7A) and coded by stratigraphy (Figure 6B; Figure 7B), however, several consistent patterns are evident. Samples from small specimens and early whorls of *Sphenodiscus lobatus,* representing early ontogeny (WH < 40 mm), exhibit depleted $\delta^{18}O$ values (average = -3.7‰) (Figure 6A). The $\delta^{18}O$ values of larger specimens and later whorls (WH > 40 mm, presumably representing later ontogeny) are higher (average = -1.9‰). Samples from these later ontogenetic stages also show substantial $\delta^{18}O$ variability – up to 3‰ within an individual specimen. $\delta^{13}C$ values show no trend with ontogeny or stratigraphic position (Figure 7) but cover a very wide range.

Using the equation of Grossman and Ku (1986) and assuming a Cretaceous 'ice-free world' $\delta^{18}O_{seawater}$ value of -1‰, the measured $\delta^{18}O$ values convert to water temperatures of between 16 and 35°C. When plotted ontogenetically, temperatures range between 28 and 35°C for *Sphenodiscus lobatus* in early ontogeny (< 40 mm WH). The positive shift in $\delta^{18}O$ values seen in all specimens with WH > 40 mm corresponds to cooler estimated temperatures between 16 and 28°C (Figure 6A).

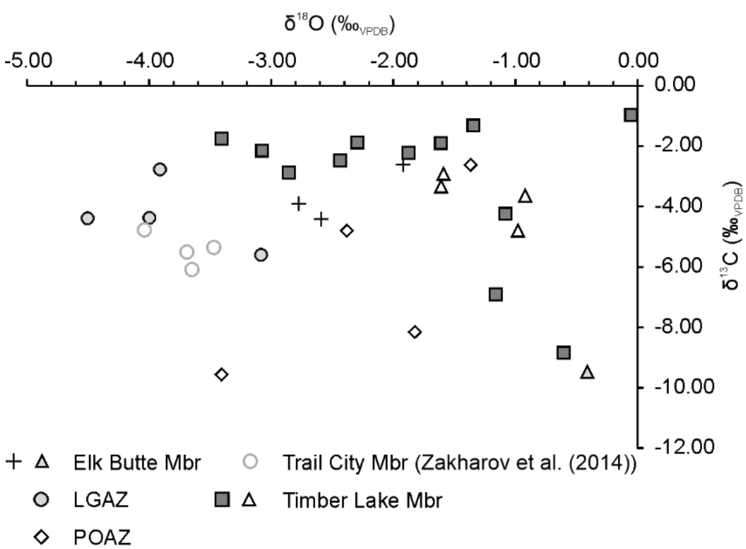


Figure 5: Cross-plot of $\delta^{18}O$ and $\delta^{13}C$ values for specimens of *Sphenodiscus lobatus*. No significant correlation between these variables indicates a low possibility for diagenetic alteration of shell material. Plot includes material from the Elk

Butte Member of the Pierre Shale and Timber Lake Member from Cochran et al. (2003) and Dennis et al. (2013) (triangles) not included in Figure 6 because of lack of whorl height data.

## Discussion

### *Isotopic data and habitat*

The lack of any relationship between $\delta^{18}O$ and $\delta^{13}C$ values that might be expected from diagenetic alteration (such as a positive correlation with decreasing microstructural preservation – documented for older WIS ammonites by Cochran et al. (2010)) and the good microstructural preservation of shell material suggests that isotopic values can be interpreted as primary environmental or ecological signals. Calculated temperature estimates are also broadly in line with those reported for samples from Campanian and Maastrichtian strata in other studies from the WIS (e.g., Wright, 1987; Fatheree et al., 1998; Cochran et al., 2003; Dennis et al., 2013; Landman et al., 2018; Ellis and Tobin, 2019; Witts et al., 2020).

The pattern of depleted $\delta^{18}O$ values in small specimens/early ontogeny occur both in our data and those from prior investigations which included *Sphenodiscus* samples from the Pierre Shale and Fox Hills Formation (Cochran et al., 2003; Dennis et al., 2013; Zakharov et al., 2014). Similar values also occur irrespective of stratigraphic horizon (Figure 6B; Figure 7B). Depleted $\delta^{18}O$ values are seen in early ontogeny of *Sphenodiscus lobatus* from both the Trail City Member (n = 8 samples) and a single sample from the Timber Lake Member. More enriched $\delta^{18}O$ values are seen in larger specimens/later ontogeny in samples from both the Trail City (*Protocardia-Oxytoma* Assemblage Zone - POAZ) and Timber Lake members, as well as the offshore Elk Butte Member of the Pierre Shale. This suggests that the change in isotopic values represents an ecological signal in this species of ammonite, specifically a consistent shift in habitat during its life history.

The most parsimonious interpretation of depleted oxygen isotope values in early ontogeny of *Sphenodiscus lobatus* (Figure 6A) is that they indicate a warm, perhaps surface water, environment for this ammonite during this stage of its life history. There is currently no accurate measurement for growth rate in ammonites, so it is not possible to constrain the length of time individuals may have spent in this environment. In the WIS, Linzmeier et al. (2018) also recorded light $\delta^{18}O$ values in earliest ontogeny of *Hoploscaphites* specimens from the Fox Hills Formation using SIMS analysis, which they interpreted as a planktic phase in surface waters immediately following hatching in these ammonites. Currently accepted growth estimates suggest ammonites exhibited rapid growth like modern coleoids (Ellis and Tobin, 2019). As such, early whorls < 40 mm WH in *Sphenodiscus lobatus* may only represent a year or so of growth.

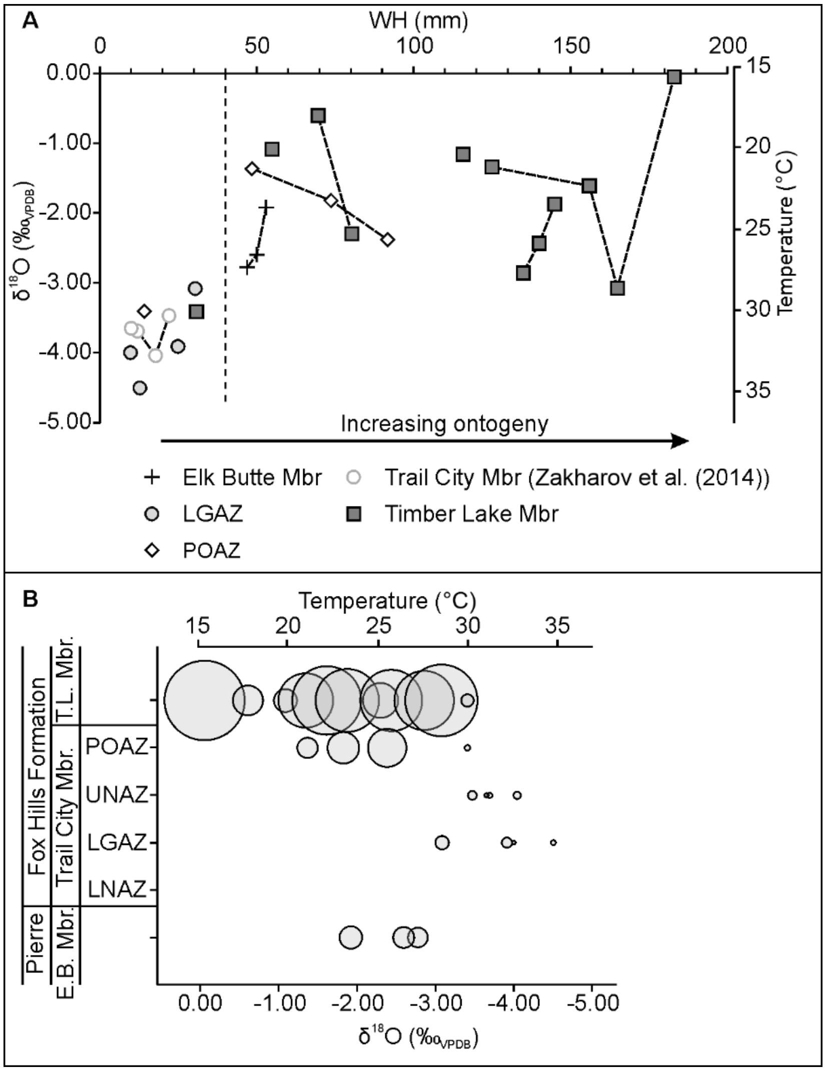


Figure 6: (A) $\delta^{18}O$, temperature from specimens of *Sphenodiscus lobatus* plotted against whorl height (WH) as a proxy for ontogeny. Vertical dashed line indicates a WH of 40 mm to highlight overall shift in values in larger specimens. Dashed lines connecting data points indicate multiple samples derived from a single specimen. (B) $\delta^{18}O$, temperature data plotted stratigraphically as a 'bubble plot'. Size of the bubbles illustrates relative WH at the position of sampling, so smaller bubbles = early whorls and early ontogeny relative to larger bubbles which represent later whorls and later ontogeny. Note samples from early whorls (small bubbles) with depleted isotope data in Trail City Member assemblage zones. Both plots include data from this study and from Zakharov et al. (2014) from the Trail City Member. Precision for $\delta^{18}O$ measurements is 0.05‰.

Temperatures approaching 35°C are unrealistically high given that modern cephalopods cannot tolerate waters in excess of 30°C (Vidal et al., 2014), and may partly reflect variation between water masses in the shallow WIS (Cochran et al., 2003; Dennis et al., 2013; Petersen et al., 2016). Extensive freshwater input into the seaway could have led to the formation of locally brackish shallow and surface waters due to density differences, therefore leading to lowered $\delta^{18}O_{seawater}$ composition and an overestimation of temperatures using the assumed value of -1‰ in these settings. Similarly, depleted isotope values from oxycone ammonites (*Placenticeras*) and some juvenile heteromorphs (*Baculites*) in older WIS strata have been related to this phenomenon and a presumed surface water habitat in a 'brackish water cap' with reduced salinity (Tsujita and Westermann, 1998; Landman et al., 2018; Rowe et al., 2020). Regardless of the presence of stratification, salinities throughout the water column were probably not lower than 20 psu, as this is also generally considered the tolerance limit for modern cephalopods (Vidal et al., 2014).

The consistent change in $\delta^{18}O$ values at a WH of 40 mm (Figure 6A) appears to represent a change in the habitat of *Sphenodiscus lobatus* at this stage of its life history. By comparison to limited isotopic data from benthic bivalves (Cochran et al., 2003; Dennis et al., 2013; Petersen et al., 2016; Linzmeier et al., 2018) and nektobenthic scaphitid ammonites (Witts et al., 2020), this is perhaps best interpreted as migration to a nektobenthic habitat with overall cooler temperatures. Similar ontogenetic migrations from warmer to cooler environments are seen in other ammonite taxa (e.g., Jurassic *Cadoceras* (Lukeneder et al., 2010)), as well as modern shallow water cephalopods like *Sepia* (Rexfort and Mutterlose, 2006).

The wide range of oxygen isotope values in later ontogeny could reflect several processes:

1) Temperature gradients and seasonality of environmental conditions in the shallow waters of the WIS may have been substantial. In a recent compilation of data from modern epeiric seaways, Judd et al. (2020) demonstrated that these settings show higher average temperatures and greater seasonal variability than the open ocean at a similar latitude. Dennis et al. (2013) observed a range of temperatures calculated from carbonate clumped isotope measurements on single samples from shells of a bivalve and gastropods collected from the Timber Lake Member. A similar range of $\delta^{18}O$ and temperature values were also recorded in benthic mollusks and fish otoliths from the Timber Lake and Iron Lightning members (Carpenter et al., 2003). More detailed reconstruction of the variation of $\delta^{18}O$ from two sessile benthic bivalves taken from a single concretion at the contact between the Trail City and Timber Lake members (Linzmeier et al., 2018) convert to a comparable range, almost 8°C if temperature is the primary driver of change in $\delta^{18}O$. As noted above, it has been suggested that variable $\delta^{18}O$ values in the shallow WIS are also driven by changes in salinity, which alter $\delta^{18}O_{seawater}$ (Petersen et al., 2016), even in benthic environments (Wright et al., 1987). Such changes could have occurred over short timescales due to freshwater input during storms or seasonal monsoon conditions (Fricke et al., 2010). However, existing studies using mollusks to develop these models lack a rigorous assessment of microstructural and elemental preservation (Cochran et al., 2010) and should be treated with caution.

2) Adult *Sphenodiscus lobatus* may have migrated vertically and laterally, passing through environments with differing temperature or $\delta^{18}O_{seawater}$ values. Shell hydrodynamic studies suggest compressed oxycone

morphotypes were ideal for rapid movement in the water column and may have been capable of stabilizing themselves in high energy conditions (Wani, 2006). Modern cephalopods are primarily mobile organisms, and while *Nautilus* is probably a poor analog, it exhibits daily migration along a depth gradient that is captured in high-resolution isotopic data (Lukeneder, 2015; Linzmeier et al., 2016; Linzmeier, 2019). Similar migrations are also recorded in oceanic cuttlefish and squid (Rexfort and Mutterlose, 2006; Stewart et al., 2013). Due to the relatively shallow bathymetry of the WIS, lateral migration between environments is considered likely to produce greater variation in $\delta^{18}O$ than vertical migration.

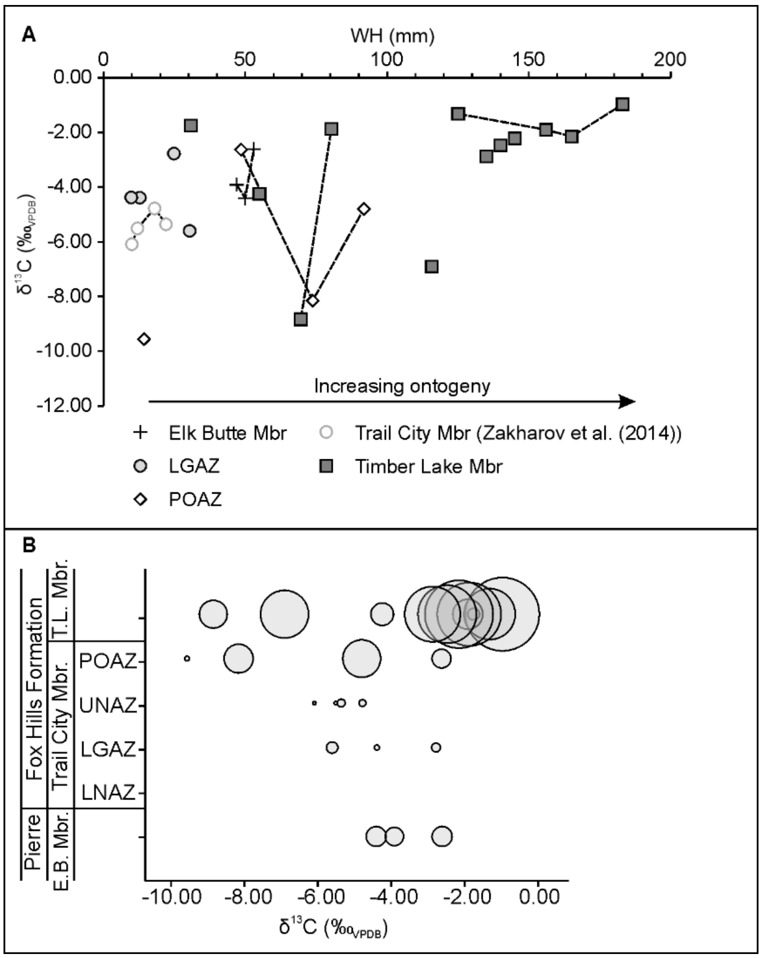


Figure 7: (A) $\delta^{13}C$ data from specimens of *Sphenodiscus lobatus* plotted against whorl height (WH) as a proxy for ontogeny. Dashed lines connecting data points indicate multiple samples derived from a single specimen. (B) $\delta^{13}C$ data plotted stratigraphically as a 'bubble plot'. Like Figure 6, size of the bubbles illustrates relative WH at the position of sampling. Both plots include data from this study and from Zakharov et al. (2014) from the Trail City Member. Precision for $\delta^{13}C$ measurements is 0.05‰.

Variable carbon isotope data from *Sphenodiscus lobatus* (Figure 7) are more difficult to explain as a primary environmental signal because the carbon isotope composition of cephalopod shell material can be affected by the differential incorporation of isotopically light metabolic carbon into the shell through ontogeny (i.e., a 'vital effect') (e.g., McConnaughey et al., 1997; Rexfort and Mutterlose, 2006; Tobin and Ward, 2015). Landman et al. (2018) used the approach of McConnaughey et al. (1997) to calculate the various carbon inputs into shells of the ammonite genus *Baculites* in the WIS, and we extrapolate their method to data herein. If the $\delta^{13}C$ of WIS seawater DIC is +2‰, $\delta^{13}C$ of metabolic carbon is -20‰ (close to values from modern cephalopods (Crocker et al., 1985), then the shell $\delta^{13}C$ values ranging from ~ -2 to -6‰ in *Sphenodiscus* represent 30 to 50% metabolic carbon. Landman et al. (2018) estimated 30% metabolic carbon for Campanian WIS *Baculites*. $\delta^{13}C$ values in large specimens (Timber Lake Member) seem to converge to about -2‰, suggesting that the fraction of metabolic carbon in the shell might decrease through ontogeny as growth slows. Alternatively, if the low $\delta^{18}O$ values of the *Sphenodiscus* samples partially represent a nearshore environment affected by less than fully marine salinity and warmer temperatures, then the $\delta^{13}C$ of the DIC may be lower than surface water of the open WIS. This would decrease the fraction of metabolic carbon necessary to produce the observed $\delta^{13}C$ values.

*Stratigraphic distributions, taphonomy, and habitat*

Stratigraphic distribution patterns of *Sphenodiscus* in the Fox Hills Formation were studied qualitatively by Waage (1968) who noted that smaller specimens are more commonly found in the fossiliferous assemblage zones in the Little Eagle lithofacies of the Trail City Member. These marine siltstones were deposited in an offshore environment flanking a large submarine sand bar, distal to nearshore, delta-front, and estuarine deposits represented by the Irish Creek lithofacies and Iron Lightning Member (Figure 3). Waage (1968) suggested the environment represented by the Trail City Member functioned as an offshore 'nursery' for juvenile *Sphenodiscus* during slack periods in the growth of the sand bar (Figure 8). Perhaps inhabiting these environments (paired with a surface water habitat) provided some advantage to juvenile sphenodiscids such as a refuge from predators (Takeda et al., 2016) or lack of competition with adults of the same species. Larger, sometimes complete *Sphenodiscus lobatus* – representing mature forms up to and greater than 50 cm in total diameter (Waage, 1968) – are more common in the concretionary horizons of the overlying sandy facies of the Timber Lake Member (the *Sphenodiscus* layer and *Cucullaea* AZ) representing the shallower margins of the sand bar, and as isolated specimens in the more nearshore Irish Creek lithofacies, laterally equivalent to both the Trail City and Timber Lake members to the east (Figure 3; Figure 8).

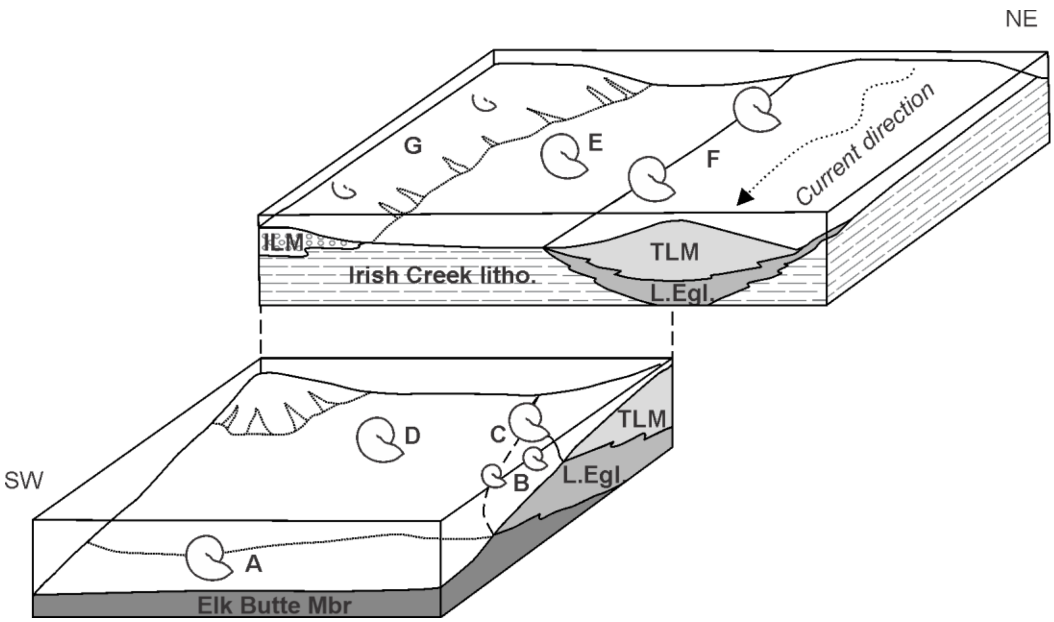


Figure 8: Reconstruction of the environments represented by the upper Pierre Shale and Fox Hills Formation in north-central South Dakota, illustrating the possible life history of *Sphenodiscus lobatus* reconstructed from isotopic data and fossil distributions. This reconstruction is time composite, and therefore schematic. Large, adult specimens of *Sphenodiscus lobatus* are sporadically present in offshore environments below wave base, represented by the shales of the Elk Butte Member of the Pierre Shale (A). This ammonite is more common in the shallower water facies of the Trail City Member of the Fox Hills Formation (B, C, D). Here, small specimens probably representing juveniles live in a warm, surface water habitat with occasional salinity variations, and are commonly preserved in offshore silts off the down current end of a prograding submarine sand bar (Little Eagle lithofacies = L.Egl. (B)). Larger adult specimens migrate to a more nektobenthic habitat and are most frequently found in areas where coarser, sandy sediments record the initial encroachment of the Timber Lake Member (TLM) sand bar (e.g., POAZ) (C). Large adults also live in laterally equivalent, more proximal environments (Irish Creek lithofacies) (D, E) and are common around the sandy, shallow submerged margins of the Timber Lake sand bar, where their compressed oxycone shells potentially provided an adaptive advantage to higher energy conditions (F). Occasionally they exhibit post-mortem drift and fragments end up in deltaic and even flood plain sediments (Iron Lightning Member, ILM and Hell Creek Formation) closer to the coast (G). Adult, nektobenthic *Sphenodiscus lobatus* probably migrated laterally between these different environments (A, C-F), potentially exhibiting a final migration into shallower water settings for breeding during latest ontogeny.

Larger specimens first become common in the uppermost Trail City assemblage zone (POAZ) coincident with an overall increase in grain size at this level, representing an influx of sandy sediment preceding the arrival of the Timber Lake Member sand body into the Fox Hills ‘type area’ (Waage, 1968). This is consistent with the findings of Batt (1989) and others that large oxycone ammonite morphotypes are often found in sandy sediments representing proximal marine environments, with their compressed shell morphology probably providing a hydrodynamic adaptation to these settings (see also Wani, 2006; Ifrim and Stinnesbeck, 2010). A small, but statistically significant increase in shell compression is also seen in specimens of the scaphitid ammonite *Hoploscaphites nicolletii* from POAZ compared to the underlying Trail City Member AZ's, which probably represents an ecophenotypic response to the higher energy environment of deposition (Witts et al., 2020). Consistent with our variable isotopic data from later ontogeny, large *Sphenodiscus* were not restricted to these environments, as the presence of examples with WH > 40 mm in the offshore Elk Butte Member of the Pierre Shale demonstrates (AMNH loc. #3302 in this study and localities in Kennedy et al. (1998)).

It is important to consider that final stratigraphic distributions may not always represent the primary habitat of ammonites. In comparison to modern cephalopods like *Sepia*, occurrences of large adult specimens in shallow settings could be due to migration to these environments to spawn in latest ontogeny before death (e.g., Rexfort and Mutterlose, 2006; Bloor et al., 2013). A similar migration into shallow (estuarine) environments for spawning by the fish *Vorhisia vulpes* was suggested by Carpenter et al. (2003), based on occurrences and isotopic data from otoliths in the Iron Lightning Member. Otolith $\delta^{18}O$ and $\delta^{13}C$ does not record the environmental signal of these very shallow-water environments in latest ontogeny, suggesting growth had ceased by the time of migration to estuarine settings. It is important to note that we did not sample latest ontogeny (i.e., closest to the aperture) in any of the largest specimens examined, so our isotopic data do not provide information about the final stages of the life history of *Sphenodiscus lobatus*.

It is also possible that oxycone ammonite shells could have undergone short-term post-mortem drift, before sinking in shallow water environments. Fragmentary specimens of *Sphenodiscus lobatus* have been recorded as high in the section as the basal Hell Creek Formation (Hartman and Kirkland, 2002), which may represent examples of this phenomenon (Figure 8). In fact, most *Sphenodiscus* specimens from the Fox Hills Formation are incomplete. Even specimens preserving at least part of the body chamber tend to show breakages parallel and adoral to the last septum or crushed and fragmented body chambers. This suggests that most specimens suffered some degree of transport, even along the seafloor. Wani (2006) noted that oxyconic shells can become mobile in relatively slow currents. Post-mortem drift is generally considered less likely for small ammonites, which based on experiments with different size modern *Nautilus*, probably sank relatively rapidly in the environment in which they lived (Wani et al., 2005). Small, early ontogenetic specimens from the Trail City Member therefore accurately reflect their original habitat, which based on isotopic data was probably high in the water column. Small sphenodiscids in these settings would have had very fragile body chambers that could be easily crushed or distorted following arrival on the seafloor.

The presence of in-situ aptychi (jaws) and delicate 'hook-like' structures in other common ammonites of different (heteromorph) morphotypes from the Fox Hills Formation (i.e., *Hoploscaphites*, *Discoscaphites*), indicate that they did not exhibit long-term or long-distance post-mortem drift or transport (Landman and Waage, 1993). Complete, apparently undamaged scaphitids are common in the Trail City Member AZ's, while fragmentary or broken specimens increase in abundance in the shallow settings of the Timber Lake Member (Waage, 1964; Landman and Waage, 1993). This accords with reconstructions of the life history of scaphitids as slow-moving, nektobenthic planktivores, which did not undergo substantial lateral migration between environments (Cochran et al., 2003; Landman et al., 2012). Further work is needed to ascertain whether *Sphenodiscus* shows similar taphonomic patterns through the section. Differential taphonomy paired with isotopic data could act as an additional proxy for ecological and habitat differences between different ammonite groups in the WIS.

**Conclusions**

Our analyses of the isotopic composition of well-preserved shell material of *Sphenodiscus lobatus* from the Maastrichtian Pierre Shale and Fox Hills Formations suggest this ammonite species exhibited a change in its habitat through ontogeny. Early whorls, presumably representing juvenile growth stages, consistently indicate higher temperatures and may point to a surface water environment, perhaps in waters with lowered salinities affected by freshwater input. Stratigraphic distributions indicate small specimens representing this stage of life history were more common in the offshore Little Eagle lithofacies of the Trail City Member. Data from later ontogeny suggest a change to a more nektobenthic habitat with cooler temperatures; this transition occurring consistently in multiple specimens from different stratigraphic horizons at a whorl height of around 40 mm. A wide range of variability in oxygen isotopes points to the likelihood for a high degree of seasonality in water column conditions, and/or active swimming with vertical and lateral migration of *S. lobatus* through different environmental conditions. The latter of which is consistent with the streamlined, oxyconic morphology of this ammonite, and stratigraphic distributions of this species. Occurrences of large specimens in more proximal settings (Irish Creek lithofacies) or those with coarser sediments (POAZ, Timber Lake Member) are consistent with the idea that adult *Sphenodiscus* was adapted to live in very shallow, presumably higher-energy environments. It is also possible that this ammonite migrated into shallower water environments in latest ontogeny for spawning before death. In contrast to oxygen isotopes, we suggest depleted carbon isotope values show less of a primary environmental signal, and instead record a "vital effect" related to metabolic carbon input, potentially slowing in later ontogeny.

These preliminary data provide an impetus for future high-resolution sclerochronological and taphonomic study of *Sphenodiscus lobatus*. Our results also emphasize the need for the generation of additional stratigraphically constrained isotopic data from co-occurring benthic, nektobenthic, and planktonic organisms to better estimate ammonite ecology and life history in these settings. Such an approach is needed in epeiric seaways such as the WIS to gain a better understanding of water column structure, and the degree of seasonality during the deposition of the complex shallow marine environments such as those represented by the Fox Hills Formation.

**Acknowledgements**

We are grateful to Susan Butts, Jessica Utrup and M. Prangley (Yale Peabody Museum, New Haven CT), and Kathy Nelson (Timber Lake and Area Museum, SD) for collections assistance, photography, and permission to sample specimens held in their care. Thanks to Colin Carney and Dyke Andreasen (UCSC-SIL) for assistance with stable isotope analysis. Mariah Slovacek, and Anastasia Rashkova (AMNH) are thanked for help with sampling and SEM analysis. The manuscript benefited from helpful reviews and comments by Benjamin Linzmeier, Peter Harries, Neal Larson, and Joshua Slattery. This research was funded by a Lerner-Gray Postdoctoral Research Fellowship at the Richard Gilder Graduate School and AMNH, a Postdoctoral Fellowship at UNM, and the René M. Vandervelde Scholarship of the Association of Applied Paleontological Sciences awarded to James Witts. Additional funding from the Newell Fund (AMNH) is gratefully acknowledged.

**References**

BATT, R. J. 1989. Ammonite shell morphotype distributions in the Western Interior Greenhorn Sea and some paleoecological implications. *PALAIOS*, **4**, 32–42.

BLOOR, I. S. M., WEARMOUTH, V. J., COTTERELL, S. P., MCHUGH, M. J., HUMPHRIES, N. E., JACKSON, E. L., ATTRILL, M. J. and SIMS, D. W. 2013. Movements and behaviour of European common cuttlefish *Sepia officinalis* in English Channel inshore waters: First results from acoustic telemetry. *Journal of Experimental Marine Biology and Ecology*, **448**, 19–27.

CARPENTER, S. J., ERICKSON, J. M. and HOLLAND, F. D. 2003. Migration of a Late Cretaceous fish. *Nature*, **423**, 70–74.

CHAMBERLAIN, J.A., WARD, P.D., and WEAVER, S.J. 1981. Post-mortem ascent of *Nautilus* shells: implications for cephalopod paleobiogeography. *Paleobiology,* **7**, 494–509.

COBBAN, W.A., MEREWEATHER, E.A., FOUCH, T.D., and OBRADOVICH, J.D. 1994. Some Cretaceous Shorelines in the Western Interior of the United States. *In* CAPUTO, M.V., PETERSON, J.A., AND FRANCZYK, K.J. Eds., Mesozoic Systems of the Rocky Mountain region, USA: SEPM Rocky Mountain Section, Denver, 393-425.

COBBAN, W.A., and KENNEDY, W.J. 1995. Maastrichtian ammonites chiefly from the Prairie Bluff Chalk in Alabama and Mississippi. *Paleontological Society Memoir* **44**, 1–40.

COBBAN, W. A., WALASZCZYK, I., OBRADOVICH, J. D. and MCKINNEY, K. C. 2006. A USGS Zonal Table for the Upper Cretaceous Middle Cenomanian−Maastrichtian of the Western Interior of the United States Based on Ammonites, Inoceramids, and Radiometric Ages. *U.S. Geological Survey Open-File Report*, **1250**, 46.

COCHRAN, J. K., LANDMAN, N. H., TUREKIAN, K. K., MICHARD, A. and SCHRAG, D. P. 2003. Paleoceanography of the Late Cretaceous (Maastrichtian) Western Interior Seaway of North America: evidence from Sr and O isotopes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **191**, 45–64.

COCHRAN, J.K., KALLENBERG, K., LANDMAN, N.H., HARRIES, P.J., WEINREB, D., TUREKIAN, K.K., BECK, A.J., and COBBAN, W.A. 2010. Effect of diagenesis on the Sr, O, and C isotope composition of late Cretaceous mollusks from the Western Interior Seaway of North America, *American Journal of Science,* **310**, 69–88.

CONRAD, T.A. 1857. Description of Cretaceous and Tertiary fossils. *In* W.H. Emory (editor), Report on the United States and Mexican Boundary Survey. *United States 34th Congress, 1st Session, Senate Ex Document 108 and House Ex Document 135* **1 (2)**, 141–174.

CROCKER, K. C., DENIRO, M. J. and WARD, P. D. 1985. Stable isotopic investigations of early development in extant and fossil chambered cephalopods I. Oxygen isotopic composition of eggwater and carbon isotopic composition of siphuncle organic matter in *Nautilus*. *Geochimica et Cosmochimica Acta*, **49**, 2527–2532.

DENNIS, K. J., COCHRAN, J. K., LANDMAN, N. H. and SCHRAG, D. P. 2013. The climate of the Late Cretaceous: New insights from the application of the carbonate clumped isotope thermometer to Western Interior Seaway macrofossil. *Earth and Planetary Science Letters*, **362**, 51–65.

ELLIS, N.M., TOBIN, T.S. 2019. Evidence for seasonal variation in $\delta^{13}C$ and $\delta^{18}O$ profiles of *Baculites* and implications for growth rate. *Palaeontology* **62**, 583–598.

FATHEREE, J.W., HARRIES, P.J., QUINN, T.M. 1998. Oxygen and carbon isotopic “dissection” of *Baculites compressus* (Mollusca: Cephalopoda) from the Pierre Shale (Upper Campanian) of South Dakota: implications for paleoenvironmental reconstruction. *PALAIOS* **13**, 376–385.

FRICKE, H.C., FOREMAN, B.Z., and SEWALL, J.O. 2010. Integrated climate model-oxygen isotope evidence for a North American monsoon during the Late Cretaceous. *Earth and Planetary Science Letters* **289**, 11–21.

GILL, J.R., COBBAN, W.A., and KIER, P.M. 1966, The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming, with a section on a new echinoid from the Cretaceous Pierre Shale of eastern Wyoming. *U.S. Geological Survey Professional Paper* **393**, p. 73.

GROSSMAN, E.L. and KU, T-L. 1986, Oxygen and carbon isotope fractionation in biogenic aragonite: Temperature Effects. *Chemical Geology: Isotope Geoscience section,* **59**, 59–74.

HARTMANN, J.H., and KIRKLAND, J.I., 2002, Brackish and marine mollusks of the Hell Creek Formation of North Dakota: Evidence for a persisting Cretaceous seaway. *In:* Hartmann, J.H., Johnson, K.R., and Nichols, D.J., eds., The Hell Creek Formation of the northern Great Plains: An integrated continental record of the end of the Cretaceous. *Boulder, Colorado, Geological Society of America Special Paper* **361,** p. 271–296.

HEBDON, N., RITTERBUSH, K. and CHOI, Y. 2020. Computational fluid dynamics modeling of fossil ammonoid shells. *Palaeontologia Electronica*.

HUDSON, J.D., and ANDERSON, T.F. 1989. Ocean temperatures and isotopic compositions through time. *Earth and Environmental Transactions of the Royal Society of Edinburgh: Earth Sciences,* **80**, 183–192.

HYATT, A. 1903. Pseudoceratites of the Cretaceous. *Monographs of the United States Geological Survey* Vol XLIV, 351 p.

IFRIM, C. and STINNESBECK, W. 2010. Migration pathways of the late Campanian and Maastrichtian shallow facies ammonite *Sphenodiscus* in North America. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **292**, 96–102.

JACOBS, D. K. and LANDMAN, N. H. 1993. *Nautilus* – a poor model for the function and behavior of ammonoids? *Lethaia* **26**, 101–111.

JACOBS, D. K. and CHAMBERLAIN, J. A. 1996. Buoyancy and Hydrodynamics in Ammonoids. *In* LANDMAN, N. H., TANABE, K. and DAVIS, R. A. (eds.) *Ammonoid Paleobiology*, Springer US, Boston, MA, 169–224 pp.

JUDD, E.J., BHATTACHARYA, T., and IVANY, L.C. 2020. A dynamical framework for interpreting ancient sea surface temperatures. *Geophysical Research Letters,* **47**, e2020GL089044.

KENNEDY, W. J., LANDMAN, N. H. and COBBAN, W. A. 1996. The Maastrichtian ammonites *Coahuilites sheltoni* Böse, 1928, and *Sphenodiscus pleurisepta* (Conrad, 1857), from the uppermost Pierre shale and basal Fox Hills formation of Colorado and Wyoming. *American Museum Novitates*, **3186**, 14 pp.

KENNEDY, W.J., COBBAN, W.A., and LANDMAN, N.H. 1997. Maastrichtian ammonites from the Severn Formation of Maryland. *American Museum Novitates*, **3210**, 30 pp.

KENNEDY, W. J., LANDMAN, N. H., CHRISTENSEN, W. K., COBBAN, W. A. and HANCOCK, J. M. 1998. Marine connections in North America during the late Maastrichtian: palaeogeographic and palaeobiogeographic significance of *Jeletzkytes nebrascensis* Zone cephalopod fauna from the Elk Butte Member of the Pierre Shale, SE South Dakota and NE Nebraska. *Cretaceous Research*, **19**, 745–775.

LANDMAN, N. H. and WAAGE, K. M. 1993. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota and Wyoming. *Bulletin of the AMNH*, **215**, 257.

LANDMAN, N.H., and COBBAN, W. A. 2003. Ammonites from the upper part of the Pierre Shale and Fox Hills Formation of Colorado. *American Museum Novitates*, **3388**, 45.

LANDMAN, N.H., JOHNSON, R.O., and EDWARDS, L.E. 2004. Cephalopods from the Cretaceous/Tertiary boundary interval on the Atlantic Coastal Plain, with a description of the highest ammonite zones in North America. Part 1. Maryland and North Carolina. *American Museum Novitates*, **3454**, 64 pp.

LANDMAN, N.H., COBBAN, W. A, and LARSON, N. L. 2012, Mode of life and habitat of scaphitid ammonites. *Geobios*, **45**, 87–98.

LANDMAN, N.H., COCHRAN, J.K., SLOVACEK, M., LARSON, N.L., GARB, M.P., BREZINA, J. and WITTS, J.D. 2018. Isotope sclerochronology of ammonites (*Baculites compressus*) from methane seep and non-seep sites in the Late Cretaceous Western Interior Seaway, USA: Implications for ammonite habitat and mode of life. *American Journal of Science* **318**, 603–639.

LINZMEIER, B. J., KOZDON, R., PETERS, S. E. and VALLEY, J. W. 2016. Oxygen Isotope Variability within *Nautilus* Shell Growth Bands. *PLOS ONE*, **11**, e0153890.

LINZMEIER, B.J., LANDMAN, N. H., PETERS, S. E., KOZDON, R., KITAJIMA, K. and VALLEY, J. W. 2018, Ion microprobe–measured stable isotope evidence for ammonite habitat and life mode during early ontogeny. *Paleobiology*, **44**, 684–708.

LINZMEIER, B.J., 2019. Refining the interpretation of oxygen isotope variability in free-swimming organisms. *Swiss Journal of Paleontology,* **138**, 109–121.

LUKENEDER, A., HARZHAUSER, M., MÜLLEGGER, S. and PILLER, W. E. 2010. Ontogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($\delta^{18}O$, $\delta^{13}C$). *Earth and Planetary Science Letters*, **296**, 103–114.

LUKENEDER, A. 2015. Ammonoid habitats and life history. In: Klug, C., Korn, D., DeBaets, K., Kruta, I., Mapes, R.H. (eds). *Ammonoid Paleobiology: From anatomy to ecology*. Springer Netherlands; 2015, pp. 689–791.

MCCONNAUGHEY, T. A., BURDETT, J., WHELAN, J. F. and PAULL, C. K. 1997. Carbon isotopes in biological carbonates: Respiration and photosynthesis. *Geochimica et Cosmochimica Acta*, **61**, 611–622.

MEEK, F.B. 1871. Preliminary paleontological report, consisting of lists of fossils, with descriptions of some new types etc. Preliminary Report of the United States Geological Survey of Wyoming (Hayden). **4**, 287–318.

MORIYA, K. 2015. Isotope signature of Ammonoid Shells. In: Klug, C., Korn, D., DeBaets, K., Kruta, I., Mapes, R.H. (eds). *Ammonoid Paleobiology: From anatomy to ecology*. Springer Netherlands; 2015, 793–836.

OWEN, D.D. 1852. Report of a geological survey of Wisconsin, Iowa, and Minnesota and incidentally of a portion of Nebraska Territory. Philadelphia: Lippincott.

PETERSEN, S. V., TABOR, C. R., LOHMANN, K. C., POULSEN, C. J., MEYER, K. W., CARPENTER, S. J., ERICKSON, J. M., MATSUNAGA, K. K. S., SMITH, S. Y. and SHELDON, N. D. 2016. Temperature and salinity of the Late Cretaceous Western Interior Seaway. *Geology*, **44**, 903–906.

PRICE, G.D., TWITCHETT, R.J., SMALE, C., and MARKS, V. 2009. Isotopic analysis of the life history of the enigmatic squid *Spirula spirula* with implications for the study of fossil cephalopods. *PALAIOS* **24**, 273–279.

REXFORT, A., MUTTERLOSE, J. 2006. Stable isotope records from *Sepia officinalis* – a key to understanding the ecology of belemnites? *Earth and Planetary Science Letters* **247**, 212–221.

ROWE, A. J., LANDMAN, N. H., COCHRAN, J. K., WITTS, J. D. and GARB, M. P. 2020. Late Cretaceous Methane Seeps as Habitats for Newly Hatched Ammonites. *PALAIOS*, **35**, 151–163.

SESSA, J.A., LARINA, E., KNOLL, K., GARB, M., COCHRAN, J.K., HUBER, B.T., MACLEOD, K.G., and LANDMAN, N.H., 2015. Ammonite habitat revealed via isotopic composition and comparisons with co-occurring benthic and planktonic organisms. *Proceedings of the National Academy of Science* **112**, 15562–15567.

SLATTERY, J.S., COBBAN, W.A., MCKINNEY, K.C., HARRIES, P.J., SANDNESS, A.L. 2015. Early Cretaceous to Paleocene paleogeography of the Western Interior Seaway: the interaction of eustasy and tectonism. *In* Bingle-Davis, M. (Ed.), *Field Guide, Cretaceous Conference: Evolution and Revolution*: Casper, Wyoming, Wyoming Geological Association, 22–60.

STEWART, J. S., FIELD, J. C., MARKAIDA, U. and GILLY, W. F. 2013. Behavioral ecology of jumbo squid (*Dosidicus gigas*) in relation to oxygen minimum zones. *Deep Sea Research Part II: Topical Studies in Oceanography*, **95**, 197–208.

TAKEDA, Y., TANABE, K., SASAKI, T., and LANDMAN, N.H. 2016. Durophagous predation on Scaphitid ammonites in the Late Cretaceous Western Interior Seaway of North America. *Lethaia* **49**, 28–42.

TSUJITA, C. J. and E.G. WESTERMANN, G. 1998. Ammonoid habitats and habits in the Western Interior Seaway: a case study from the Upper Cretaceous Bearpaw Formation of southern Alberta, Canada. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **144**, 135–160.

TUOMEY, M. 1856. Description of some new fossils from the Cretaceous rocks of the southern States. *Proceedings of the Academy of Natural Sciences of Philadelphia,* **7**, 167–172.

VIDAL, E.A.G., VILLANUEVA, R., ANDRADE, J.P., GLEADALL, I.G., IGLESIAS, J., KOUETA, N., ROSAS, C., SEGAWA, S., GRASSE, B., FRANCO-SANTOS, R.M., ALBERTIN, C.B., CAAMAL-MONSREAL, C., CHIMAL, M.E., EDSINGER-GONZALES, E., GALLARDO, P., LE PABIC, C., PASCUAL, C., ROUMBEDAKIS, K., WOOD, J., 2014. Cephalopod culture: current status on main biological models and research priorities. *Advances in Marine Biology* 67: 1–98.

WAAGE, K.M. 1964. Origin of repeated fossiliferous concretion layers in the Fox Hills Formation. *Kansas Geological Survey Bulletin* **168**, 541–563.

WAAGE, K.M., 1968. The Type Fox Hills Formation: Cretaceous (Maestrichtian), South Dakota. Part 1. Stratigraphy and palaeoenvironments. *Yale University Peabody Museum of Natural History Bulletin* **97**, 1–175.

WANI, R., KASE, T., SHIGETA, Y., DE OCAMPO, R. 2005. New look at ammonoid taphonomy, based on field experiments with modern chambered nautilus. *Geology* **33**, 849–852.

WANI, R. 2006. The peculiar taphonomy of the streamlined late Campanian ammonite *Metaplacenticeras subtilistriatum* from northern Hokkaido, Japan. *Cretaceous Research* **27**, 863–871.

WITTS, J. D., LANDMAN, N. H., HOPKINS, M. J. and MYERS, C. E. 2020. Evolutionary stasis, ecophenotypy and environmental controls on ammonite morphology in the Late Cretaceous (Maastrichtian) Western Interior Seaway, USA. *Palaeontology* 63: 791–806.

WRIGHT, E.K. 1987. Stratification and paleocirculation of the Late Cretaceous Western Interior Seaway of North America. *Geological Society of America Bulletin* **99**, 480–490.

YACOBUCCI, M. M. 2018. Postmortem transport in fossil and modern shelled cephalopods. *PeerJ*, **6**, e5909.

ZAKHAROV, Y. D., TANABE, K., SAFRONOV, P. P., POPOV, A. M., & SMYSHLYAEVA, O. P. 2014. New data on microstructure and isotopic composition of some cephalopods from the Upper Cretaceous of North America and Europe: Significance for oxygen isotope palaeotemperature measurements. *In* B. Berning & A. Lukeneder (Eds.), *Recent and fossil cephalopods* (pp. 113– 132). Denisia 32, zugleich Kataloge des Oberösterreichischen Landesmuseums Neue Serie 157, Linz, Austria: Oberösterreichisches Landesmuseum Linz.

Table 1: Specimens of *Sphenodiscus lobatus* analyzed in this study. YPM = Yale Peabody Museum, TLM = Timber Lake and Area Museum. Stratigraphic information, whorl height of the shell at position of sample (WH), preservation index (PI) ranking of shell sample, and $\delta^{13}C$, $\delta^{18}O$, and temperature data calculated using the equation of Grossman and Ku (1986). Note letters (e.g., 'YPM XXXA, B etc.) or underscored numbers (_1 etc.) following sample number denote multiple samples from the same specimen at different whorl heights.

| Sample # | Formation | Member | Zone | WH at position of sample | PI | $\delta^{13}C$ | $\delta^{18}O$ | Temperature (°C) |
|---|---|---|---|---|---|---|---|---|
| TLM Spheno 3_1 | Pierre Shale | Elk Butte | | 47 | 4 | -3.91 | -2.77 | 27.4 |
| TLM Spheno 3_2 | Pierre Shale | Elk Butte | | 50 | 3.5 | -4.41 | -2.59 | 26.6 |
| TLM Spheno 3_3 | Pierre Shale | Elk Butte | | 53 | 3 | -2.61 | -1.92 | 23.7 |
| YPM 44705 | Fox Hills | Trail City | LGAZ | 30.4 | 3 | -5.61 | -3.08 | 28.7 |
| YPM 44707 | Fox Hills | Trail City | LGAZ | 12.8 | 4 | -4.39 | -4.50 | 34.9 |
| YPM 44712 | Fox Hills | Trail City | LGAZ | 9.8 | 3 | -4.38 | -4.00 | 32.7 |
| YPM 44743 | Fox Hills | Trail City | LGAZ | 24.9 | 3.5 | -2.78 | -3.91 | 32.3 |
| YPM 44813 | Fox Hills | Trail City | POAZ | 14.2 | 3 | -9.56 | -3.41 | 30.2 |
| YPM 44841A | Fox Hills | Trail City | POAZ | 91.8 | 3 | -4.80 | -2.38 | 25.7 |
| YPM 44841B | Fox Hills | Trail City | POAZ | 73.7 | 4 | -8.15 | -1.82 | 23.3 |
| YPM 44841C | Fox Hills | Trail City | POAZ | 48.5 | 3 | -2.63 | -1.37 | 21.3 |
| YPM 44845 | Fox Hills | Timber Lake | *Sphenodiscus* layer | 55 | 3.5 | -4.24 | -1.08 | 20 |
| YPM 44864 | Fox Hills | Timber Lake | *Sphenodiscus* layer | 30.8 | 3.5 | -1.76 | -3.41 | 30.2 |
| YPM 44915A | Fox Hills | Timber Lake | *Sphenodiscus* layer | 145 | 3.5 | -2.23 | -1.87 | 23.5 |
| YPM 44915B | Fox Hills | Timber Lake | *Sphenodiscus* layer | 140 | 4 | -2.48 | -2.43 | 25.9 |
| YPM 44915C | Fox Hills | Timber Lake | *Sphenodiscus* layer | 135 | 4 | -2.88 | -2.86 | 27.8 |
| YPM 44951A | Fox Hills | Timber Lake | *Sphenodiscus* layer | 125 | 3 | -1.32 | -1.34 | 21.2 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| YPM 44951C | Fox Hills | Timber Lake | *Sphenodiscus* layer | 156 | 3 | -1.90 | -1.61 | 22.3 |
| YPM 44951D | Fox Hills | Timber Lake | *Sphenodiscus* layer | 165 | 3 | -2.15 | -3.07 | 28.7 |
| YPM 44951E | Fox Hills | Timber Lake | *Sphenodiscus* layer | 183 | 3.5 | -0.97 | -0.05 | 15.6 |
| TLM Spheno1-1 | Fox Hills | Timber Lake | *Sphenodiscus* layer | 80.36 | 4 | -1.88 | -2.30 | 25.3 |
| TLM Spheno1-2 | Fox Hills | Timber Lake | *Sphenodiscus* layer | 69.57 | 3 | -8.84 | -0.61 | 18 |
| TLM Spheno 2-1 | Fox Hills | Timber Lake | *Sphenodiscus* layer | 115.77 | 4 | -6.90 | -1.16 | 20.4 |