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The Relationship Among Suture Complexity, Shell Form, and Stratigraphic Formation In Ammonites Of The Western Interior Seaway

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THE RELATIONSHIP AMONG SUTURE COMPLEXITY, SHELL FORM,
AND STRATIGRAPHIC FORMATION IN AMMONITES OF THE
WESTERN INTERIOR SEAWAY

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

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GRADUATE COMMITTEE APPROVAL

The graduate committee of Darrah Jorgensen approves this thesis as meeting partial fulfillment of the requirements for the Degree of Master of Science.

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ABSTRACT

Throughout ammonite evolution, shell suture patterns grew increasingly more complex, but the purpose of these sutures has long been debated. One hypothesis is that suture complexity is related to the structural integrity of the shell under pressure. To test this hypothesis, suture complexity was compared to shell form and stratigraphic formation to determine if there were significant differences in suture complexity, as a proxy for structural integrity, among shell forms or stratigraphic formations. Highly complex sutures might have allowed for the tightly coiled form of many ammonites, an advantage compared to less coiled forms because the pressure is distributed over more points on the shell. If this is the case, coiled forms should have more complex suture patterns. Suture pattern complexities of coiled, straight, and heteromorphic ammonite shell forms from the Pierre, Carlile, Greenhorn, Graneros, and Mowry shales were quantified using box-counting fractal analysis. Results indicate there is a significant difference in the median suture complexity among the defined shell forms ($H = 27.9$, $df = 2$, $p < 0.001$). A Kruskal-Wallis multiple comparisons test confirms there is a significant difference in median suture complexity between coiled and heteromorphic shell forms ($p < 0.03$), and a significant difference in median suture complexity between heteromorphic and straight shell forms ($p < 0.03$). However, there is no significant difference in median suture complexity between coiled and straight shell forms ($p > 0.03$). The most complex suture patterns are typically found in tightly coiled shells, possibly adding structural support as the coiled form evolved. Most of the straight shell forms examined in this

project evolved from coiled forms and perhaps retained highly complex sutures to protect against hydrostatic pressure. On the other hand, heteromorphic shell forms may have significantly reduced their suture complexity to loosen the coil of their shell. However, these forms did not require suture patterns as complex as the straight shell forms because the partially coiled shell would have provided more protection against hydrostatic pressure than the straight shell. Results also show no significant difference in median suture complexities among formations ($H = 5.24$, $df = 4$, $p = 0.264$), suggesting that there is no significant change in median suture complexity over time.

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INTRODUCTION

The clade Ammonoidea encompasses a group of extinct molluscan cephalopods that thrived in the Late Cretaceous Western Interior Seaway. Ammonoidea includes the ammonites and their relatives – the goniatites and ceratites. This clade is closely related to living nautiloids. However, ammonites have more complex septa than nautiloids (Dzik, 1984). Septa are shallow, concave walls that divide the ammonoid shell into chambers. Ammonite septa contain folds that radiate outward from the center of the shell and become more tightly folded as they merge with the shell's exterior wall (Monks and Palmer, 2002). The pattern in which the septa join with the shell wall forms the shell's suture pattern (Li et al., 2011). Suture patterns have changed through time, and so are used for taxonomic identification (Westermann, 1996; Wippich and Lehmann, 2004).

The function of sutures in ammonite shells has been widely debated among researchers, and several hypotheses have been proposed. The most widely accepted hypotheses consider complex sutures as a component in resisting stress caused by hydrostatic pressure (Daniel et al., 1997; Boletzky, 1999; Olóriz et al., 2002). Complex sutures may have evolved as a mechanism not only to resist hydrostatic pressure, but also to aid the formation of the different shell forms by supporting the coiled phragmocone (Pérez-Claro et al., 1997).

Jacobs (1990) suggests that different suture patterns in *Baculites* – a straight-shelled ammonite – were caused by differences in the environments in which the organisms lived. Complex suture patterns in *Baculites* might have provided increased

structural support against compressional forces when the organisms were adjusting to changing water pressures as they moved vertically in the water column. The complex suture patterns allowed for a thickening of the shell, which would have acted as buttresses by giving the shell the ability to resist shattering from pressure.

Pérez-Claro et al. (1997) analyzed suture patterns and whorls resulting from coiling, and suggested that sutures increased shell tensile strength rather than compressional strength. The authors concluded that complex sutures help strengthen the shell and increase its structural integrity as it bends.

Other research indicates that complex sutures give no functional advantage to the organism (Boyajian and Lutz, 1992). Olóriz et al. (2002) reexamined the functional significance of septa by analyzing the suture complexity of ammonoids colonizing deep habitats in the Late Jurassic and found no trend among suture complexities and the whorl, coiling, or shell shape.

Previous research has only examined complexity in a single shell form. The relationship among suture complexity, shell form, and stratigraphic formation has not previously been examined. Western Interior Seaway ammonites exhibited a wide range of straight, coiled, and heteromorphic (semi-coiled) shell forms. The ancestral ammonite shell form is a long, straight shell such as the orthocone (Figure 1). Most ammonites, however, had coiled shells, which evolved in the Devonian from the ancestral straight-shell form (Monks and Palmer, 2002). Some

ammonite lineages – such as *Baculites* – secondarily evolved a straight shell from coiled shells.

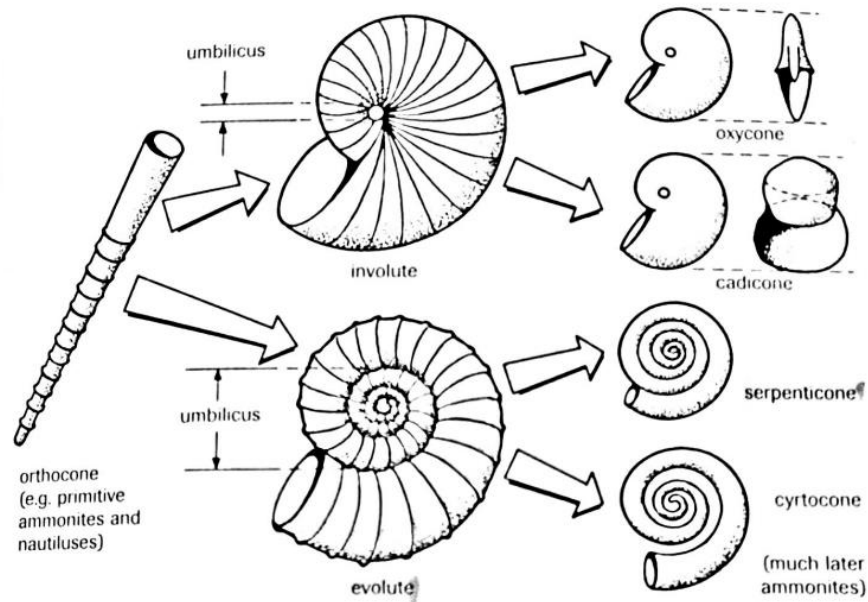


Figure 1: **Evolution of Ammonite Shells from Basal Straight Form.** The ancestral straight shell form (orthocone) evolved into the coiled shell form, splitting into two varieties. These forms split again into a variety of forms, with the evolute shell secondarily uncoiling. Figure from Monks and Palmer, 2002.

While Ammonitida exhibits several types of suture patterns (Figure 2), ammonitic sutures are prevalent in the shells of ammonites found in Western Interior Seaway deposits. Ammonitic sutures typically have rounded lobes and saddles that are subdivided or fluted (Figure 2). This suture pattern is found in both straight and coiled shell forms, though it is not clear if and how suture patterns relate to shell form. The primary purpose of this study is to examine the relationship between suture complexity and shell form in

Cretaceous ammonites. The suture patterns of coiled, straight, and heteromorphic ammonite shell forms from five shales of the Western Interior Seaway were quantified using box-counting fractal analysis to determine if there is a significant difference in suture complexity through the Cretaceous among shell forms. In this study, suture complexity is used as a proxy for structural integrity. If complex suture patterns provide increased shell strength (*sensu* Pérez-Claro et al., 1997), then coiled ammonites should have more complex suture patterns due to the increased complexity of the shell's shape.

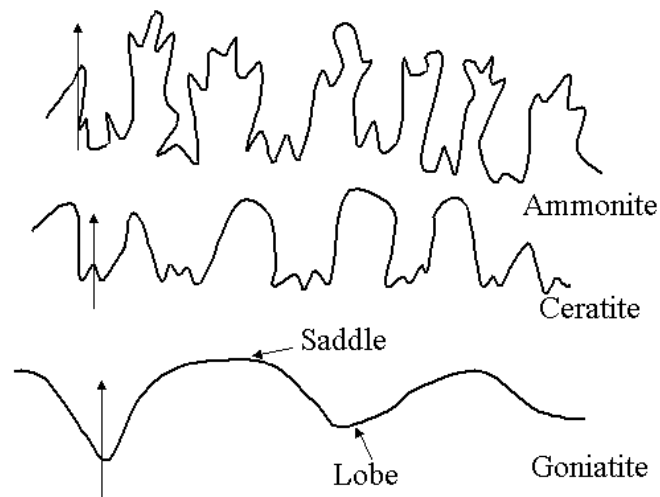


Figure 2: **Varieties of Suture Complexities found in Ammonoidea:** The three common types of suture patterns in Ammonoidea. The most complex fluting is found within ammonitic sutures. Figure from Pérez-Claro et al., 1997.

Quantifying Complexity

It is necessary that researchers use a consistent method for defining complexity during a study, but determining the best method of defining suture pattern complexity has been debated among researchers as often as suture function itself (Jacobs, 1990; Daniel et al, 1997; Allen, 2006). This is significant because utilizing different complexity measures could affect the results of the study. Historically, there have been three methods used to define suture pattern complexity: the Fourier method, GIS, and fractal analysis.

Fourier waveform analysis is primarily used to represent complex shapes as components of sine waves. A Short-time Fourier transform (STFT) divides a long-time signal into shorter segments of equal length and applies a Fourier transform separately on each shorter segment (Allen, 1977). The STFT is usually plotted as a function of time. The Fourier method determines whether components close together are separate, or if there is a change in frequencies. On ammonites, a STFT examines the suture line to find variance, and creates a function that best fits the smoothed reproduction of each suture pattern (Allen, 2006).

One of the limitations of the Fourier method is that it uses a fixed resolution or window width, and the width of the window is related to how the signal is represented. A wide window gives greater frequency resolution, but poor time resolution. A narrower window gives greater time resolution, but poor frequency resolution. Maximizing one will minimize the other, lowering the power of the analysis.

Manship (2004) developed a method that uses ArcGIS™ to create templates to aid in identification of unknown ammonite specimens by mapping the suture complexity of ammonites. In her study, suture complexity showed little variability among suture forms and among species. Yacobucci and Manship (2011) employed similar methods using GIS to quantify the suture complexity by determining distances between points on the suture. The templates were compared to unknown specimens to identify them (Yacobucci and Manship, 2011).

GIS methods are accurate in the placement of points and user-friendly. However, there is subjectivity in the method, as the points are placed manually, possibly leading to error in point positioning. Despite its utility in identifying specimens based on suture pattern, the GIS method cannot quantify suture complexity.

Several types of fractal analyses have been performed to quantify ammonite suture complexity. Lutz and Boyajian (1995) calculated the fractal dimensions of several ammonoid genera. A fractal dimension is a ratio providing an index of complexity by comparing how details in a pattern change with scale. This technique is useful for quantifying complicated geometric forms in which the details at small scales are more important than the overall form at larger scales. These fractal forms are defined as self-similar and irregular (Vicsek, 1992). Because ammonitic suture patterns are self-similar and bend irregularly, with the irregularity of the suture changing based on how it is oriented when measured, the complexity of these patterns can be quantified well using fractal analysis.

Institutional abbreviations – **DMNS**, Denver Museum of Nature and Science, Denver, Colorado, U.S.A.; **FHSM**, Fort Hays State University Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; **KUIP**, Invertebrate Paleontology, University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, Kansas, U.S.A.; **SDSM**, South Dakota School of Mines and Technology Museum of Geology, Rapid City, South Dakota, U.S.A.; **UCM**, University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.; **USGS**, United States Geological Society Core Research Center, Denver, Colorado, U.S.A.; **UT**, University of Texas Non-Vertebrate Paleontology Lab, Austin, Texas, U.S.A.; and **YPMIP**, Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

MATERIALS & METHODS

Study Area and Materials

The Western Interior Seaway was a shallow inland sea that extended from the Arctic Ocean to the Gulf of Mexico during the latter half of the Cretaceous (113 mya – 66 mya). North America was separated into two landmasses: Appalachia in the east and Laramidia in the west. During maximum transgression, the seaway was approximately 970 km wide and 3200 km long, but was probably never more than approximately 200 m deep (Sageman and Arthur, 1994).

Many marine paleoenvironments from the Cretaceous are preserved in the shale and limestone deposits across the Great Plains Region. Ammonites from Western Interior Seaway shales were included in this study due to the large number of specimens and the high quality of suture preservation present in these stratigraphic formations. Formations studied include the Mowry Shale, Graneros Shale, Greenhorn Shale, Carlile Shale, and Pierre Shale. This study was limited to organisms with ammonitic sutures, as ammonoids with goniatic and ceratitic sutures were not present in the time periods examined. Ammonoids with straight ($n = 127$), coiled ($n = 210$), and heteromorphic ($n = 51$) shell forms were used to examine the relationship between suture pattern and shell form, and suture pattern and stratigraphic formation.

The Graneros Shale Formation was deposited in the middle Albian and Cenomanian Age of the Cretaceous Period (113.0 mya – 93.9 mya). This formation represents the first episode of offshore marine sedimentation in the central part of the

Western Interior Seaway during the early transgression of the Greenhorn Marine Cycle (Kauffman, 1985). It is approximately 10 m thick in Kansas and as thick as 60 m in Colorado. It consists of a bluish-gray, non-calcareous shale with few beds of sandstone and sandy shale (Fox, 1962; Figure 3). The ammonite specimens from the Graneros Shale included in this study are from Colorado (n = 7), Kansas (n = 15), Texas (n = 2), and South Dakota (n = 1), and represent coiled (n = 25) and heteromorphic (n = 1) shell forms (Appendix A).

The Mowry Shale is a geologic formation that was deposited in the Cenomanian Age of the Cretaceous Period (100.5 mya – 93.9 mya). It is approximately 50 m thick and consists of highly siliceous, hard gray shales with numerous interbedded thin bentonite beds (Nixon, 1973). The Mowry Shale Formation is most abundant in Wyoming and Colorado, reaching into the western-most parts of Nebraska and South Dakota (Figure 3). Its stratigraphic position is equivalent to the middle of the Graneros Formation of Kansas and Colorado (Figure 3). The ammonite specimens from the Mowry Shale that were included in this study are from Montana (n = 7), Texas (n = 12), and Wyoming (n = 10), and represent coiled (n = 28) and straight (n = 1) shell forms (Appendix B).

The Greenhorn Formation consists of four alternating members of shale and limestone. Only ammonite specimens from the shale members – the Hartland and Pfeifer Shales – were included in this study. The Greenhorn Formation can be found in eastern Colorado and Wyoming, northeastern New Mexico, southwestern Montana, and extending east as far as Kansas, Nebraska, and South Dakota (Wilmarth, 1935).

The Hartland Shale Member of the Greenhorn Formation was deposited in the late Cenomanian Age of the Cretaceous Period (100.5 mya – 93.9 mya) as one of the Greenhorn's lower members (Figure 3). It is approximately 25 m thick and consists of calcareous shale with an upper part of thin, chalky limestone beds and a lower part of chalky shale with thin crystalline limestone (Fox, 1962). The ammonite specimens from the Hartland Shale that were included in this study are from Kansas (n = 1), Montana (n = 2), South Dakota (n = 10), and Wyoming (n = 4), and represent coiled (n = 15) and straight (n = 2) shell forms (Appendix C).

The Pfeifer Shale Member of the Greenhorn Formation was deposited in the early Turonian Age of the Cretaceous Period (93.9 mya – 92.3 mya). It is approximately 5 m thick in Kansas and consists primarily of chalky shale (Fox, 1962; Figure 3). The ammonite specimens from the Pfeifer Shale included in this study are from Colorado (n = 1), South Dakota (n = 1), Kansas (n = 1), Oklahoma (n = 1), and Wyoming (n = 2), and represent coiled (n = 5) and straight (n = 1) shell forms (Appendix C).

The Carlile Shale was deposited in the middle to late Turonian Age of the Cretaceous Period (93.9 mya – 90.5 mya). It is approximately 90 m thick and consists of non-calcareous shale to less sandy, very calcareous shale (Fox, 1962; Figure 3). This Formation is found in western Kansas, southeastern Colorado, and New Mexico. The ammonite specimens from the Carlile Shale included in this study are from Colorado (n = 2), Kansas (n = 35), Montana (n = 8), New Mexico (n = 2), South Dakota (n = 26), Texas

(n = 1), and Wyoming (n = 11), and represent coiled (n = 37), straight (n = 23), and heteromorphic (n = 24) shell forms (Appendix D).

The Pierre Shale Formation was deposited during the Campanian Age of the Cretaceous Period (83.6 mya – 72.1 mya). It is approximately 210 m thick at the type locality and overlies the Niobrara Formation (Bertog, 2010; Figure 3). It consists of dark-gray fossiliferous shale with gypsum veins and iron oxide concretions. Its dark color indicates a high organic carbon content, implying a low oxygen environment during deposition and lack of decay on the ocean floor. The Pierre Shale was deposited when the Great Plains were under the deepest portion of the Western Interior Seaway (Schultz et al., 1980). The ammonite specimens from the Pierre Shale included in this study are from Colorado (n = 70), Kansas (n = 23), Montana (n = 24), New Mexico (n = 2), South Dakota (n = 72), Utah (n = 2), and Wyoming (n = 65), and represent coiled (n = 110), straight (n = 122), and heteromorphic (n = 26) shell forms (Appendix E).

Era	System	Series	Geologic Formations	
Mesozoic	Cretaceous	Upper	Pierre Shale	
			Niobrara Formation	
			Carlile Shale	
			Greenhorn Formation	Pfeifer Shale Mbr
				Jetmore Chalk Mbr
				Hartland Shale Mbr
		Lincoln LS Mbr		
		Lower	Mowry Shale	Graneros Sh
			Dakota Sandstone	
			Thermopolis Shale	Newcastle SS
				Kiowa Sh
				Skull Creek Sh
			Cloverly Formation	Cheyenne SS

Figure 3: **Western Interior Seaway Stratigraphic Column:** Stratigraphic column of the Western Interior Seaway ranging north to South Dakota, south to Texas, west to Wyoming and east to Kansas. The light lines (bottom right) show stratigraphic formations that are coeval but from different geographic regions. The red text indicates the formations sampled for this study.

Because ammonite suture patterns change through ontogeny, only mature specimens were used for this analysis. Signs of maturity are (1) slowed growth, showing crowded and overlapping sutures; (2) weakening or disappearance of the sculptural elements in the body chamber; (3) modification of the ornamentation near the peristome; (4) modification of the body chamber through a change in coiling; and (5) development of lappets and rostra in the peristome (Sarti, 1999). Of these, septal crowding is the most widely recognized and cited indication of maturity in ammonoids (Kennedy and Cobban, 1976; Gygi, 1990; Gygi, 1999; Sarti, 1999; Gygi, 2001; Monks and Palmer, 2002; Klug et al., 2015). Septal crowding affects the distance of at least the last two septa and occurs when the distance (typically measured by angles) between septa has decreased (Klug et al., 2015). Mature specimens were chosen based on this decreased distance between septa.

Defining Suture Complexity

Specimens were photographed using a Canon PowerShot 180, 20-megapixel camera. The specimens were photographed at macro level to ensure the suture patterns would be visible. Extraneous features – such as nacre, ribbing, and ornamentation – were removed using the ImageJ photo manipulation software, as these features can cause the analysis to shift focus away from the suture patterns.

A photograph of each specimen was analyzed to determine suture complexity using the FracLac fractal analysis extension for ImageJ. As sutures typically appear as a

different color than the shell, FracLac automatically converts the image to binary, which allows the computer to look at the difference in color as data. FracLac defaults for grid design and scaling method were used. The suture complexity of each specimen was quantified using Box-Counting Fractal Analysis (D_b). The program samples the image several times using Koch's Curve to increase the number of grid cells, and the results from these samplings are averaged providing the fractal dimension for the specimen. The fractal dimension – a ratio providing a statistical index of complexity comparing how details in a pattern change with scale – is calculated using $D_b = \frac{\log(N_a) - \log(b)}{\log\left(\frac{1}{s_a}\right) - \log\left(\frac{1}{s_b}\right)}$, where N is the number of grid cells in which the suture pattern is present and 1/s is the grid cell size (Kennedy and Cobban, 1976; Figure 4). This fractal dimension is the quantified suture complexity.

Statistical Analysis

Data were separated into three categories within each stratigraphic formation based on shell form: coiled, straight, and heteromorphic. Although coiled and heteromorphic forms were represented by multiple taxa, the straight-shelled forms analyzed were predominately *Baculites*. While *Baculites* are phylogenetically heteromorphs, they are considered a straight-shell form for this analysis because they are the only heteromorph that have completely uncoiled and reverted to the basal straight form.

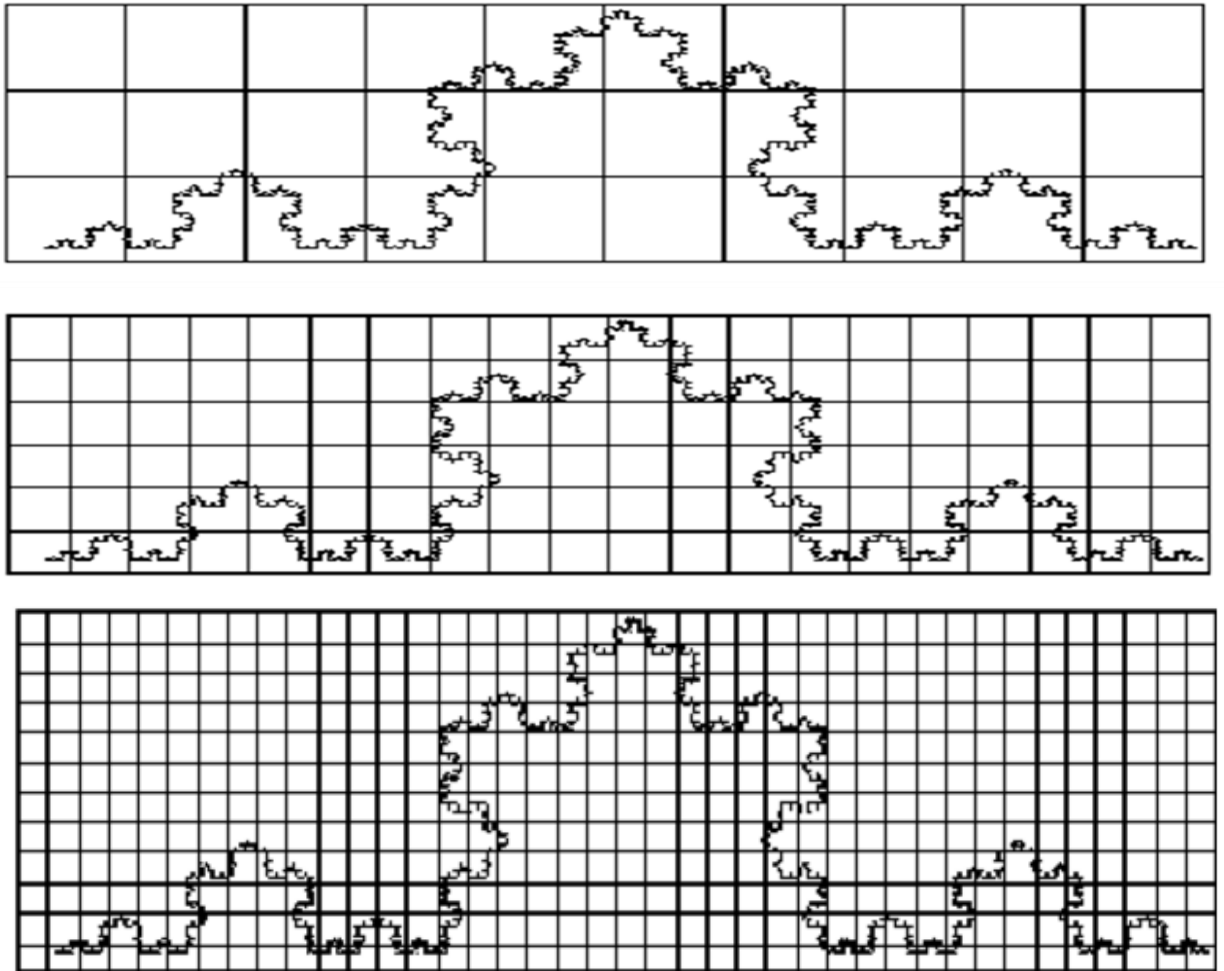


Figure 4: **Box-Counting of Fractal Pattern using Koch's Curve:** The counts where the fractal appears (N) in these images are 18, 41, and 105 grid cells respectively. The three grid size ratios were 1: $\frac{1}{2}$: $\frac{1}{4}$. The complexity of a fractal is quantified by $D_b = \frac{\log(N_a) - \log(N_b)}{\log(\frac{1}{s_a}) - \log(\frac{1}{s_b})}$. After placing the counts and ratios into the equation and averaging the three results, the fractal dimension for the above image was found to be 1.27 ± 0.002 . Figure from Wahl (1994).

Specimens from each stratigraphic formation were also separated into Mowry, Graneros, Greenhorn, Carlile, and Pierre shales regardless of shell form. The Hartland and Pfeifer Members of the Greenhorn Formation were combined due to small sample size. To eliminate confounding variables, shell forms that were significantly different from each other were removed from the stratigraphic formation analysis.

A Kruskal-Wallis test was used to determine if there were significant differences in median suture complexities among the three shell forms or among the stratigraphic formations (Glantz, 2005). The Kruskal-Wallis test can only indicate if a significant difference exists, but not among which categories. Therefore, if a significant result was indicated by the Kruskal-Wallis test, a Kruskal-Wallis multiple comparison test was used to further delineate differences. The non-parametric Kruskal-Wallis test was chosen over the parametric analysis of variance (ANOVA) because the fractal dimension data did not meet assumptions required for the ANOVA and data transformations were not able to correct for non-normality.

Before performing Kruskal-Wallis tests, the data had to be subset to ensure relatively equal sample sizes from each shell form and each stratigraphic formation. When multiple statistical tests are performed, the Type I statistical error rate (the rate at which the test falsely rejects a null hypothesis) increases. This inflation in the Type I error rate – the Bonferroni Inequality – can be corrected by lowering the significance level of each test. Therefore, the significance level for the Kruskal-Wallis tests

performed for this study was lowered ($\alpha = 0.03$) using a Bonferroni correction. All statistical tests were completed using the statistical program R (ver. 3.2.3).

RESULTS

Results from the Kruskal-Wallis statistical test indicate there is a significant difference in median suture complexity among the shell forms ($H = 27.9$, $df = 2$, $p < 0.001$). A Kruskal-Wallis multiple comparisons test indicates that median coiled shell sutures are significantly more complex than median heteromorphic shell sutures ($p < 0.03$). Median straight shell sutures are more complex than median heteromorphic shell sutures ($p < 0.03$). However, there is no significant difference in median suture complexity between straight and coiled shell forms ($p > 0.03$; Figure 5, Table 1).

Table 1: Median Suture Complexity of Shell Forms for Ammonite Specimens

	Coiled	Straight	Heteromorph
Complexity	1.762	1.755	1.719

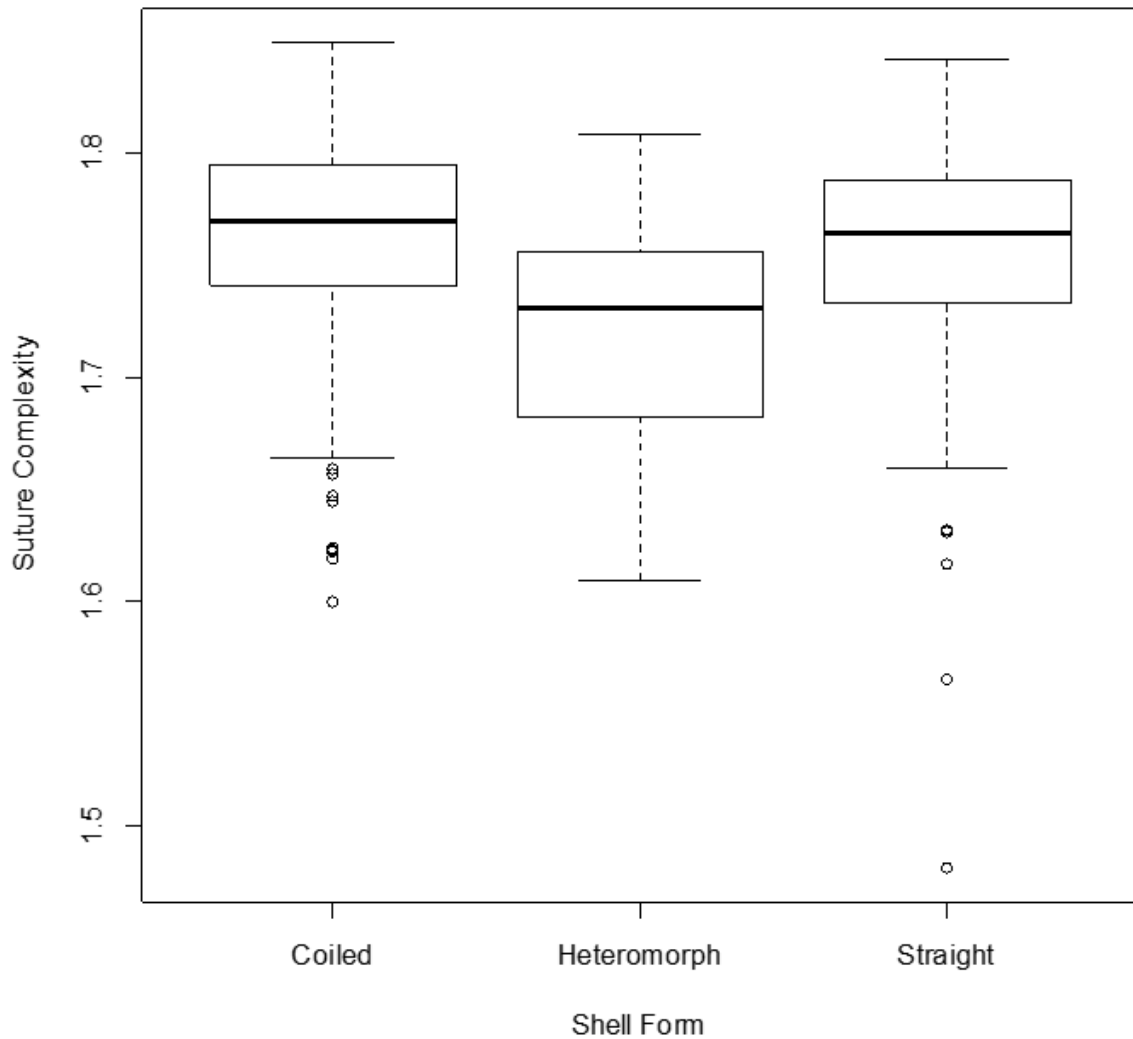


Figure 5: **Suture Complexity of Ammonite Shell Forms from the Western Interior Seaway:** In this figure, the solid, black bars indicate the median suture complexity for each shell form.

A Kruskal-Wallis statistical test was also completed to determine if there was a significant difference among median suture complexities of ammonite specimens from

the Mowry Shale (n = 28), Graneros Shale (n = 23), Greenhorn Shale members (n = 20), Carlile Shale (n = 34), and Pierre Shale (n = 35). Results indicate there is no significant difference in median suture complexity among stratigraphic formations (H = 5.24, df = 4, p = 0.264; Figure 6, Table 2).

Table 2: Median Suture Complexity of Ammonite Specimens from Shale Formations

	Mowry	Graneros	Greenhorn	Carlile	Pierre
Complexity	1.752	1.741	1.755	1.736	1.760

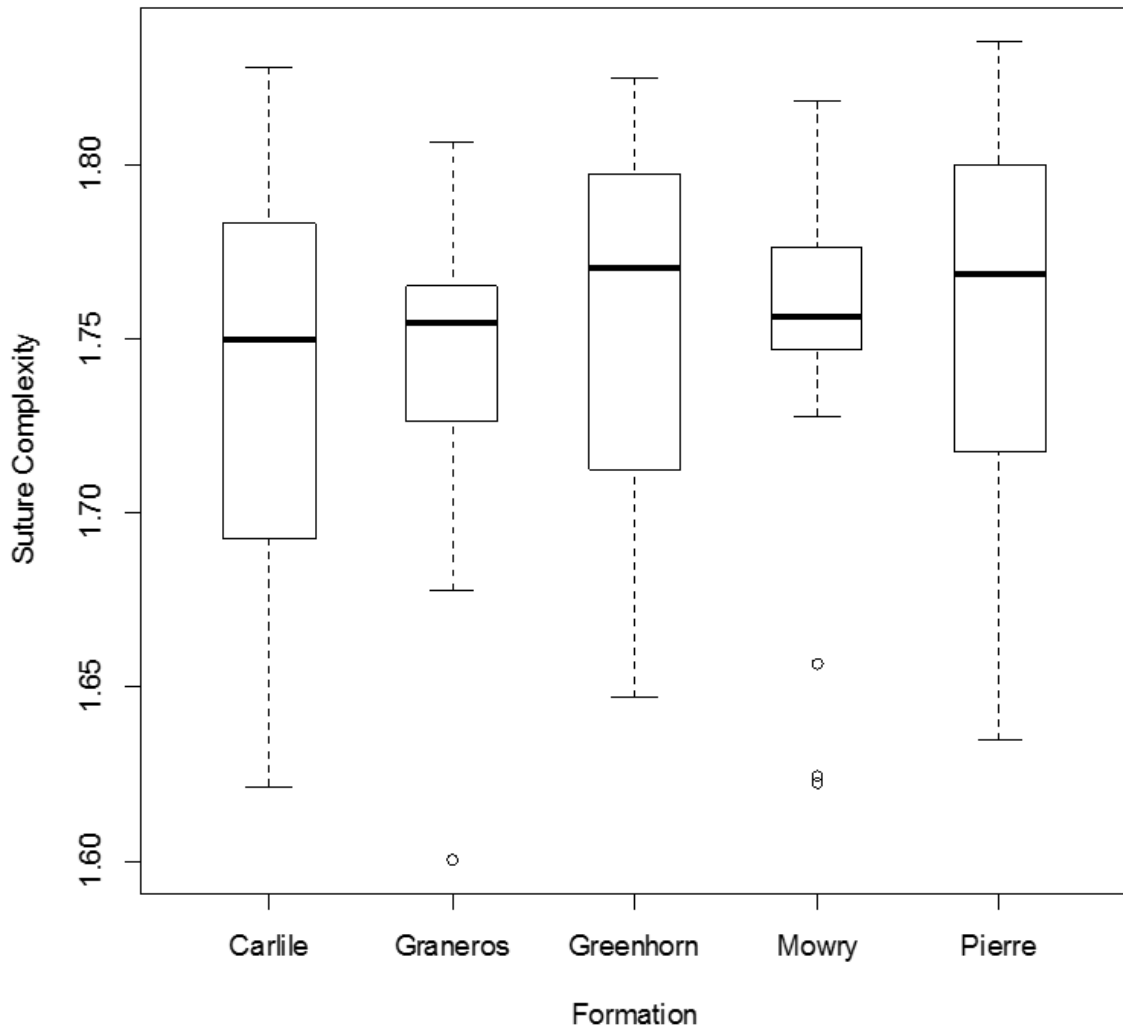


Figure 6: Suture Complexity of Ammonites from Western Interior Seaway Shales: In this figure, the solid, black bars indicate the median suture complexity for each formation.

DISCUSSION

While ammonite suture patterns have been studied for many decades, suture complexity has not been compared among shell forms. The results of this study indicate that there are significant differences in suture pattern complexity among the shell forms, and that complex suture patterns might have aided the coiling process and provided increased protection against hydrostatic pressure.

Coiled shells were found to have the most complex suture patterns of the three shell forms examined (though not significantly different from straight shells). This lends support to the hypothesis that complex suture patterns evolved to support the shell as it coiled (Jacobs, 1990). A complex suture pattern would allow more surface area for septa attachment between the septal joints, providing interlocking strength and allowing a tighter coil (Drew and Pelligrino, 2002; Miura et al., 2009).

Heteromorphic and secondarily straight forms, such as *Baculites*, evolved from the coiled shell form, uncoiling their shells over evolutionary time (Mikhailova and Baraboshkin, 2009). Like coiled forms, heteromorphic forms still had a partially rounded shell to distribute the force of hydrostatic pressure (Lu et al., 1998). Results from this study find heteromorphic and *Baculites* shells to have less complex suture patterns than their coiled relatives. Assuming complex sutures are necessary to aid tight coiling (as hypothesized above), heteromorphic ammonites would not have needed to retain highly complex sutures. This could explain the reduction in suture complexity of heteromorphic forms as lineages underwent the uncoiling process through their evolutionary history. It is

unknown why heteromorphic ammonites uncoiled their shells or whether suture patterns became less complex before the shell started this uncoiling process, but those questions are outside the focus of this project.

Unexpectedly, *Baculites* had more complex sutures than heteromorphic forms, though not significantly different from coiled forms. This indicates that *Baculites* retained complexity similar to their coiled ancestors. A straight shell is not able to spread force as effectively as coiled forms, and is, therefore, more susceptible to damage from hydrostatic pressure (Li et al., 2011). Complex suture patterns that were important to the coiling process in coiled forms might have been exapted to protect the straight shell against hydrostatic pressure, acting in a similar manner to corrugated metal (Boletzky, 1999). This exaptation could explain why suture complexity is not significantly different between coiled and straight-shelled forms.

Additionally, it has been suggested that suture patterns of *Baculites* were adapted to form ribbing that further protected the organism from hydrostatic pressure (Jacobs, 1990). The ribbing might have acted as a keel, pressing out as pressure pushed in on the shell. Susceptibility to hydrostatic pressure could also explain why there are relatively few genera in the Baculitidae clade compared to the diverse clades found among the coiled shell forms such as Collignoniceratidae. The straight-shelled forms were not as successful as the coiled and, therefore, did not diversify like their coiled counterparts.

Ammonites are hypothesized to have hunted at the lower edge of the photic zone (Pasche and May, 2001). Some ammonites are thought to have fed at great depths with a

wide range of vertical mobility, but most were probably vertical migrants in the mesopelagic zone, like extant nautiloids (Westermann, 1996). For each 10 m of water below the surface, the water pressure increases by approximately 0.987 atm (Saunders, 1981). Therefore, organisms must adjust to changing pressures as they move vertically in the water column. If ammonites were vertical migrants, they might have evolved more complex shell sutures, compared to earlier ceratitic and goniatic clades, to protect their shell from intense changes in hydrostatic pressure.

Attributing depths in the water column for ammonites has proven difficult due to the large range of habitats utilized by their closest living relatives (Nesis, 1987). It has been hypothesized that different ammonite forms had different niches, which led to the development of the three forms (Jacobs, 1990). The straight-shelled forms perhaps lived in the middle of the water column or near shoals (Westermann, 1996), heteromorphic ammonites perhaps lived in shallower waters at depths of 30-100 m (Pasche and May, 2001), and the coiled shell forms might have lived in deeper environments, like nautiloids today (Nesis, 1987). If the different forms of ammonites had different niches, the suture patterns might have evolved to an optimal complexity for the shell form's particular niche. However, more research will need to be completed to support or reject these hypotheses.

This study also analyzed whether there is a relationship between ammonite suture complexity and stratigraphic formation from the Western Interior Seaway. The lack of a significant difference in suture complexity among formations could be explained by the

shales included in this study representing similar depositional conditions. These similar conditions could contribute to differences in suture complexity among the stratigraphic formations being difficult to detect (Table 2). Western Interior Seaway shales were probably deposited in stratified, deep, still water off-shore from beach sands (Chamley, 1991). The black color of these shales implies that they formed in oxygen-deficient environments at the water-sediment interface. If more oxygen had been present, the organic matter would have fully decayed, not leaving the dark coloring. This oxygen-poor environment also allowed for sulfide minerals such as pyrite to form, which covered portions of the preserved specimens (Holland, 1979).

Even if organisms lived in a range of environments above the depositional zone, organisms from all environments in the water column would have fossilized within the same depositional zone. Therefore, each formation represents a mixing of environments that existed in the water column above its depositional zone. This mixing could lead to an averaging that could result in the lack of significant differences found among ammonites from different formations.

CONCLUSION

Ammonites of the Western Interior Seaway exhibit significantly different shell suture complexities among coiled, heteromorphic, and straight forms. The most complex suture patterns were found in tightly-coiled shells, possibly adding structural support to the coil. Heteromorphic shell forms have significantly less complex sutures than those of straight and coiled shell forms. Heteromorphic shell forms might have significantly reduced their suture complexity to loosen the coil of their shell. These forms might not have required suture patterns as complex as the straight shell forms because their partially coiled shells would have provided similar protection against hydrostatic pressure to the coiled form. Most of the straight-shelled forms examined in this study evolved from coiled forms and might have exapted highly complex sutures to protect against hydrostatic pressure. This could explain why they have more complex sutures than heteromorphic forms.

Ammonite suture complexity did not show a significant difference among stratigraphic formations. The formations studied represent similar depositional conditions, which could potentially explain this lack of significant difference.

Future work will include studying a wider range of stratigraphic formations and comparing goniatic and ceratitic suture patterns to ammonitic suture patterns to determine if there is a progression of complexity among differing shell forms. Other goals of future research are to distinguish niche partitioning in the ammonitic shell forms and examine taxonomic bias of suture preservation.

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APPENDIX A

Graneros Shale Complexity Data

Museum #	Identification	State	County	Member	Shell Form	Complexity
USGS_2288	<i>Acanthoceras</i>	Colorado	Pueblo		Coiled	1.7987
UT_10708	<i>Scaphites hippocrepis</i>	Texas			Heteromorph	1.6984
UT_11128	<i>Acanthoceras</i>	Texas			Coiled	1.7857
KUIP_150282	<i>Plesioacanthoceras amphibolum</i>	Colorado	Pubelo		Coiled	1.7602
KUIP_282251	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.6003
KUIP_286262	<i>Acanthoceras amphibolum</i>	Kansas	Wilson		Coiled	1.6847
KUIP_286263	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.779
KUIP_286321	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7387
KUIP_286338	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7137
KUIP_286340	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7579
KUIP_287411	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7547
KUIP_287650	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7451
KUIP_288066	<i>Acanthoceras amphibolum</i>	Kansas	Wilson		Coiled	1.6777
KUIP_288067	<i>Acanthoceras amphibolum</i>	Kansas	Wilson		Coiled	1.7033
KUIP_288085	<i>Acanthoceras amphibolum</i>	Kansas	Wilson		Coiled	1.7609
KUIP_288089	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7676
KUIP_288098	<i>Acanthoceras amphibolum</i>	Kansas	Ellsworth		Coiled	1.7465
USGS_D4428	<i>Plesioacanthoceras</i>	Colorado	Pueblo		Coiled	1.7642
USGS_D5126	<i>Plesioacanthoceras amphibulum</i>	Colorado	Pueblo		Coiled	1.6909
USGS_D5708	<i>Acanthoceras</i>	Colorado	Pueblo		Coiled	1.8069
USGS_D5711	<i>Acanthoceras</i>	Colorado	Pueblo		Coiled	1.7493
USGS_D5718	<i>Acanthoceras</i>	Colorado	Pueblo		Coiled	1.7794
USGS_D6587	<i>Acanthoceras muldoonense</i>	Colorado	Pueblo		Coiled	1.7663
USGS_D7367	<i>Acanthoceras</i>	South Dakota	Fall River	Thatcher	Coiled	1.7387

APPENDIX B

Mowry Shale Complexity Data

Museum #	Identification	State	County	Shell Form	Complexity
USGS_224	<i>Metengonoceras</i>	Texas		Coiled	1.7543
USGS_339	<i>Neogastropolites</i>	Wyoming	Big Horn	Coiled	1.7503
FHSMIP_664	<i>Metengonoceras</i>	Montana		Coiled	1.7899
USGS_2169	<i>Epengonoceras dumbli</i>	Texas	Grayson	Coiled	1.7755
USGS_2170	<i>Metengonoceras</i>	Texas		Coiled	1.7413
USGS_2176	<i>Metengonoceras</i>	Texas		Coiled	1.7497
USGS_2177	<i>Metengonoceras</i>	Texas		Coiled	1.7279
USGS_4140	<i>Metengonoceras</i>	Texas		Coiled	1.7759
USGS_7320	<i>Metengonoceras</i>	Texas		Coiled	1.7595
USGS_9933	<i>Metengonoceras dumbli</i>	Texas	Grayson	Coiled	1.7507
UT_10423	<i>Baculites</i>	Texas	Travis	Straight	1.7445
USGS_22614	<i>Metengonoceras</i>	Texas		Coiled	1.6244
USGS_23042	<i>Metengonoceras</i>	Wyoming	Wheatland	Coiled	1.7562
USGS_24065-1	<i>Metengonoceras</i>	Montana	Petroleum	Coiled	1.7441
USGS_24065-2	<i>Neogastropolites muelleri</i>	Montana	Petroleum	Coiled	1.757
USGS_24065-3	<i>Neogastropolites muelleri</i>	Montana	Petroleum	Coiled	1.7894
USGS_24417	<i>Metengonoceras</i>	Texas		Coiled	1.7715
USGS_24555	<i>Metengonoceras</i>	Wyoming	Park	Coiled	1.7832
USGS_24565	<i>Metengonoceras</i>	Wyoming	Park	Coiled	1.7953
USGS_24567	<i>Metengonoceras</i>	Wyoming	Park	Coiled	1.8186
USGS_24568	<i>Metengonoceras</i>	Wyoming	Park	Coiled	1.7764
USGS_26589	<i>Ergonoceras</i>	Montana	Judith Basin	Coiled	1.7498
UCM_29766	<i>Metengonoceras</i>	Wyoming	Big Horn	Coiled	1.7748
UT_30675	<i>Gastropolites</i>	Montana		Coiled	1.7391
YPMIP_527510	<i>Neogastropolites</i>	Montana	Carbon	Coiled	1.6567
USGS_D13229	<i>Metengonoceras</i>	Wyoming	Big Horn	Coiled	1.6226
USGS_D1738	<i>Neogastropolites</i>	Wyoming	Hot Springs	Coiled	1.7765
USGS_D9496	<i>Epengonoceras</i>	Texas	Fannin	Coiled	1.7522

APPENDIX C

Greenhorn Complexity Data

Museum #	Identification	State	County	Member	Shell Form	Complexity
FHSMIP_531	<i>Baculites</i>	Kansas	Smith	Hartland	Straight	1.7955
UT_4269	Ammonitida	Oklahoma	Cimarron	Pfeifer	Coiled	1.7157
USGS_12610	<i>Thomasites</i>	Colorado	Larimer	Pfeifer	Coiled	1.7298
USGS_12658	<i>Metoriceras</i>	Wyoming		Pfeifer	Coiled	1.7951
USGS_22817	<i>Proplacenticerias pseudoplacenta</i>	Wyoming	Natrona	Hartland	Coiled	1.81
USGS_22871	<i>Acanthoceras wyomingensis</i>	Montana		Hartland	Coiled	1.7981
USGS_23153	<i>Pachydiscus</i>	Wyoming	Natrona	Hartland	Coiled	1.8253
SDSM_43554	<i>Metoicoceras gilinanum</i>	South Dakota		Hartland	Coiled	1.7768
SDSM_112541	Ammonitida	South Dakota		Hartland	Coiled	1.796
YPMIP_850126	Ammonitida	South Dakota	Butte	Hartland	Coiled	1.7971
YPMIP_850127	Ammonitida	South Dakota	Butte	Hartland	Coiled	1.8061
YPMIP_850128	Ammonitida	South Dakota	Butte	Hartland	Coiled	1.7091
YPMIP_850129	Ammonitida	South Dakota	Butte	Hartland	Coiled	1.7414
YPMIP_850132	Ammonitida	South Dakota	Butte	Hartland	Coiled	1.647
YPMIP_850133	Metoicoceras	South Dakota	Butte	Hartland	Coiled	1.6645
USGS_33-8	<i>Acanthoeras wyomingensis</i>	Montana		Hartland	Coiled	1.8021
USGS_D10512	<i>Calycoceras obrieni</i>	South Dakota	Lawrence	Hartland	Coiled	1.6906
USGS_D11560	<i>Dunveganoceras</i>	Wyoming	Weston	Pfeifer	Coiled	1.7637
USGS_D12917	<i>Proplacenticerias</i>	South Dakota	Pennington	Pfeifer	Coiled	1.7444
USGS_D13182	<i>Calycoceras</i>	South Dakota	Butte	Hartland	Coiled	1.7839
USGS_D624	<i>Baculites</i>	Kansas		Pfeifer	Straight	1.7822
USGS_D783	<i>Baculites</i>	Wyoming	Natrona	Hartland	Straight	1.7829
USGS_D9805	<i>Borrisiakoceras</i>	Wyoming		Hartland	Coiled	1.7055

APPENDIX D

Carlile Shale Complexity Data

Museum #	Identification	State	County	Member	Shell Form	Complexity
FHSMIP_666	<i>Baculites</i>	Kansas	Smith		Straight	1.8043
FHSMIP_832	Ammonitida	Kansas	Osborne	Blue Hill	Coiled	1.7881
FHSMIP_901	<i>Proplacentceras pseudoplacenta</i>	Kansas	Trego	Blue Hill	Coiled	1.8188
UT_968	<i>Baculites</i>	Montana	Hot Springs		Straight	1.6847
UT_970	<i>Baculites</i>	Montana	Hot Springs		Straight	1.6926
UT_978	<i>Baculites</i>	Montana	Hot Springs		Straight	1.7808
USGS_1202	<i>Baculites</i>	Kansas	Logan		Straight	1.7657
USGS_1396	<i>Baculites</i>	Kansas	Logan		Straight	1.7959
USGS_1411	<i>Baculites</i>	Kansas	Logan		Straight	1.6312
USGS_1477	<i>Baculites</i>	Kansas	Logan		Straight	1.704
SDSM_1507	<i>Prionocyclus wyomingensis</i>	South Dakota	Fall River		Coiled	1.7654
USGS_1571	<i>Baculites</i>	Kansas	Logan		Straight	1.8051
UT_1635	<i>Baculites</i>	New Mexico	Union		Straight	1.6317
UT_1672	<i>Priontropis woolgari</i>	South Dakota	Fall River		Coiled	1.6698
USGS_2967-1	<i>Prionocyclus wyomingensis</i>	South Dakota	Meade		Coiled	1.7649
USGS_2967-2	<i>Baculites</i>	South Dakota	Meade		Straight	1.7251
DMNS_4049	<i>Prionocyclus macombi</i>	South Dakota	Fall River		Coiled	1.7964
DMNS_4129	<i>Baculites yokoyami</i>	South Dakota	Butte		Straight	1.7086
DMNS_4157	<i>Scaphites whitfieldi</i>	South Dakota	Fall River		Heteromorph	1.6096
DMNS_7856	<i>Baculites crickmayi</i>	South Dakota	Fall River		Straight	1.8038
UT_10571	<i>Desmoscaphites</i>	Montana	Big Horn		Heteromorph	1.7991
UT_10703	<i>Desmoscaphites</i>	Montana	Big Horn		Heteromorph	1.6945
UT_11129	<i>Scaphites venericosus depressus</i>	Montana	Big Horn		Heteromorph	1.795
USGS_12642	<i>Puzosia</i>	South Dakota			Coiled	1.7841
USGS_14696	Ammonitida	Kansas	Osborne	Blue Hill	Coiled	1.7203
UCM_18386	<i>Prionocyclus hyatti</i>	Kansas	Osborne		Coiled	1.7505
USGS_21187	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7922
USGS_21192-1	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.6239

USGS_21192-2	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7851
USGS_21194-1	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7
USGS_21194-2	<i>Prionocyclus wyomingensis</i>	South Dakota	Butte		Coiled	1.768
USGS_21197	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7343
USGS_21199	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7704
USGS_21424	Ammonitida	Wyoming	Crook		Coiled	1.7287
USGS_21838	<i>Prionocyclus hyatti</i>	South Dakota	Meade		Coiled	1.7557
USGS_21838	<i>Scaphites arcadiensis</i>	Wyoming			Heteromorph	1.7581
USGS_22871	Ammonitida	South Dakota	Fall River		Coiled	1.7807
USGS_23474	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.7635
KUIP_32027	<i>Scaphites calilensis</i>	Kansas	Mitchell		Heteromorph	1.7751
KUIP_32031	<i>Scaphites pygaeus</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6873
KUIP_32033	<i>Scaphites pygmaeus</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6397
UT_36374	<i>Prionocyclus hyatti</i>	Kansas	Ellis	Blue Hill	Coiled	1.7821
UT_36375	<i>Prionocyclus novimexicanus</i>	South Dakota	Fall River		Coiled	1.7893
UT_36383	<i>Prionocyclus novimexicanus</i>	South Dakota	Fall River		Coiled	1.767
UT_36865	<i>Baculites</i>	Colorado	Pitkin		Straight	1.7141
UT_38294	<i>Baculites</i>	Montana	Hot Springs		Straight	1.7644
UT_41543	Ammonitida	Colorado	Montezuma		Coiled	1.7912
KUIP_58911	<i>Proplacenticeras pseudoplacenta</i>	Kansas	Bloomington	Blue Hill	Coiled	1.7931
KUIP_58912	<i>Proplacenticeras pseudoplacenta</i>	Kansas	Ellis	Blue Hill	Coiled	1.7794
UT_63025	<i>Prionocyclus novimexicanus</i>	Wyoming	Big Horn		Coiled	1.7534
KUIP_65849	<i>Prionocyclus hyatti</i>	Kansas	Mitchell	Blue Hill	Coiled	1.7076
KUIP_108769	<i>Scaphites arcadiensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6667
KUIP_108770	<i>Scaphites kansiensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7262
KUIP_108774	<i>Scaphites calilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6716
KUIP_108776	<i>Scaphites calilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7504
KUIP_108778	<i>Scaphites calilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7466
KUIP_108780	<i>Scaphites carlilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6754
KUIP_108806	<i>Scaphites inflexus</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7305
KUIP_108807	<i>Scaphites hattini</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7174
KUIP_108809	<i>Scaphites hattini</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7856

SDSM_112533	<i>Baculites rugosus</i>	Wyoming			Straight	1.7852
SDSM_112534	<i>Placenticerus meeki</i>	Wyoming			Coiled	1.7809
SDSM_112535	<i>Baculites grandis</i>	Wyoming			Straight	1.828
SDSM_112536	<i>Baculites</i>	Wyoming			Straight	1.795
SDSM_112537	<i>Baculites</i>	Wyoming			Straight	1.8204
SDSM_112538	<i>Baculites</i>	Wyoming			Straight	1.8112
SDSM_112539	<i>Baculites</i>	Wyoming			Straight	1.7831
SDSM_112540	<i>Prionocyclus novimexicanus</i>	Wyoming			Coiled	1.7985
KUIP_143749	<i>Scaphites carlilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.6214
KUIP_143756	<i>Prionocyclus hyatti</i>	Kansas	Osborne	Blue Hill	Coiled	1.7729
KUIP_143759	<i>Prionocyclus hyatti</i>	Kansas	Osborne	Blue Hill	Coiled	1.7724
KUIP_148278	<i>Placenticerus pseudoplacenta</i>	Kansas	Osborne	Blue Hill	Coiled	1.7913
KUIP_286636	<i>Scaphites carlilensis</i>	Kansas	Ellis	Blue Hill	Heteromorph	1.7456
KUIP_286656	<i>Scaphites carlilensis</i>	Kansas	Ellis	Blue Hill	Heteromorph	1.7422
KUIP_312957	<i>Scaphites carlilensis</i>	Kansas	Mitchell	Blue Hill	Heteromorph	1.7414
KUIP_312965	<i>Scaphites carlilensis</i>	Kansas	Osborne	Blue Hill	Heteromorph	1.6799
KUIP_312971	<i>Scaphites carlilensis</i>	Kansas	Osborne	Blue Hill	Heteromorph	1.6899
USGS_D10154	<i>Baculites</i>	Texas	Fannin		Straight	1.5473
USGS_D11410	<i>Coilopoceras springeri</i>	New Mexico	Coffee		Coiled	1.7895
USGS_D2387	<i>Prionocyclus</i>	South Dakota	Butte		Coiled	1.6592
USGS_D3743	Ammonitida	South Dakota			Coiled	1.7094
DMNS_EPI.33630	<i>Collignonicerus woolgari</i>	South Dakota	Fall River		Coiled	1.7331
DMNS_EPI.33635	<i>Scaphites nigricollensis</i>	South Dakota	Butte		Heteromorph	1.7829
USGS_UN2	<i>Baculites</i>	South Dakota	Butte		Straight	1.6905

APPENDIX E

Pierre Shale Complexity Data

Museum #	Identification	State	County	Member	Shell Form	Complexity
KUIP_55	Ammonitida	Wyoming	Upton		Coiled	1.7759
KUIP_67	Ammonitida	Wyoming	Upton		Coiled	1.7633
KUIP_70	<i>Baculites</i>	Wyoming	Upton		Straight	1.7596
KUIP_91	<i>Baculites</i>	Wyoming	Upton		Straight	1.77
KUIP_92	<i>Baculites</i>	Wyoming	Upton		Straight	1.7723
KUIP_93	<i>Baculites</i>	Wyoming	Upton		Straight	1.7904
KUIP_206	<i>Baculites</i>	Wyoming	Upton		Straight	1.6592
KUIP_221	Ammonitida	Wyoming	Upton		Coiled	1.7972
KUIP_222	Ammonitida	Wyoming	Upton		Coiled	1.7482
KUIP_268	<i>Baculites</i>	Wyoming	Upton		Straight	1.76
KUIP_269	<i>Baculites</i>	Wyoming	Upton		Straight	1.7612
KUIP_273	<i>Baculites</i>	Wyoming	Upton		Straight	1.6167
KUIP_275	<i>Baculites</i>	Wyoming	Upton		Straight	1.7889
KUIP_276	<i>Baculites</i>	Wyoming	Upton		Straight	1.7533
KUIP_292	<i>Baculites</i>	Wyoming	Upton		Straight	1.8049
SDSM_304	<i>Sphenodiscus lenticularis</i>	South Dakota			Coiled	1.8215
KUIP_313	Ammonitida	Wyoming	Upton		Coiled	1.7983
KUIP_320	<i>Baculites</i>	Wyoming	Upton		Straight	1.7544
KUIP_334	<i>Baculites</i>	Wyoming	Upton		Straight	1.7546
KUIP_340	<i>Baculites</i>	Wyoming	Upton		Straight	1.7919
KUIP_341	<i>Baculites</i>	Wyoming	Upton		Straight	1.7891
KUIP_347	<i>Baculites</i>	Wyoming	Upton		Straight	1.7601
KUIP_359	Ammonitida	Wyoming	Upton		Coiled	1.6232
KUIP_366	<i>Baculites</i>	Wyoming	Upton		Straight	1.814
KUIP_371	<i>Baculites</i>	Wyoming	Upton		Straight	1.6966
SDSM_392	<i>Placenticeras meeki</i>	South Dakota			Coiled	1.8175
SDSM_396	<i>Baculites compressus</i>	South Dakota			Straight	1.721
KUIP_396	<i>Baculites</i>	Wyoming	Upton		Straight	1.8422
FHSMIP_413	<i>Baculites</i>	South Dakota			Straight	1.789
UCM_551	Ammonitida	Colorado	Grand		Coiled	1.7887

FHSMIP_577	<i>Placenticeras</i>	South Dakota	Pennington		Coiled	1.8192
SDSM_862	<i>Hoploscaphites nodosus</i>	South Dakota			Coiled	1.7364
FHSMIP_1076	<i>Baculites</i>	Kansas	Wallace	Lake Creek	Straight	1.6609
FHSMIP_1267	<i>Baculites grandis</i>	South Dakota	Meade		Straight	1.7997
SDSM_1577	<i>Baculites compressus</i>	South Dakota			Straight	1.7205
SDSM_1721	<i>Anapachydiscus complexus</i>	South Dakota			Coiled	1.7989
UCM_2034	<i>Heteroceras nebrascense</i>	Colorado	Larimer		Heteromorph	1.6885
SDSM_2070	Ammonitida	South Dakota			Coiled	1.8346
SDSM_2228	<i>Baculites</i>	South Dakota			Straight	1.684
SDSM_2250	<i>Baculites</i>	South Dakota			Straight	1.7471
UCM_2585	<i>Baculites ovatus</i>	Wyoming	Albany		Straight	1.7421
SDSM_2938	<i>Didymoceras cheyennese</i>	South Dakota			Heteromorph	1.7747
SDSM_2948	<i>Baculites</i>	South Dakota			Straight	1.8062
UCM_2966	<i>Baculites ovatus</i>	Colorado	Larimer		Straight	1.7405
SDSM_2968	<i>Placenticeras</i>	South Dakota	Pennington		Coiled	1.6942
SDSM_2987	<i>Baculites</i>	South Dakota	Hunter		Straight	1.8179
SDSM_3014	<i>Baculites</i>	South Dakota			Straight	1.7773
SDSM_3083	<i>Placenticeras pseudocostatum</i>	South Dakota	Butte		Coiled	1.8333
SDSM_3084	Ammonitida	South Dakota	Butte		Coiled	1.7793
UCM_3107	<i>Baculites ovatus</i>	Colorado	Pueblo		Straight	1.7609
SDSM_3283	<i>Placenticeras</i>	South Dakota	Butte		Coiled	1.8188
UCM_3853	<i>Baculites ovatus</i>	Wyoming	Natrona		Straight	1.7761
DMNS_4042	<i>Placenticeras intercalare</i>	Colorado	Pueblo		Coiled	1.8121
DMNS_4044	<i>Placenticeras meeki</i>	Wyoming	Niobrara		Coiled	1.8208
DMNS_4045	<i>Placenticeras meeki</i>	Wyoming	Niobrara		Coiled	1.7773
DMNS_4047	<i>Placenticeras meeki</i>	Wyoming	Niobrara		Coiled	1.8151
DMNS_4056	<i>Menuites portlocki</i>	Wyoming	Niobrara		Coiled	1.7945
DMNS_4068	<i>Hoploscaphites</i>	Wyoming	Niobrara		Coiled	1.7958
DMNS_4073	<i>Discoscaphites</i>	Wyoming	Niobrara		Coiled	1.6894
DMNS_4128	<i>Baculites gilberti</i>	Wyoming	Niobrara		Straight	1.7122
DMNS_4131	<i>Baculites gregoryensis</i>	Colorado	Pueblo		Straight	1.718
DMNS_4136	<i>Baculites</i>	Wyoming	Niobrara		Straight	1.7736
DMNS_4137	<i>Baculites reesidei</i>	Wyoming	Niobrara		Straight	1.8393

DMNS_4138	<i>Baculites compressus</i>	South Dakota	Pennington		Straight	1.7875
DMNS_4139	<i>Baculites perplexus</i>	Wyoming	Niobrara		Straight	1.7573
DMNS_4140	<i>Baculites scotti</i>	Wyoming	Niobrara		Straight	1.7683
DMNS_4143	<i>Baculites eliasi</i>	Wyoming	Niobrara		Straight	1.7727
DMNS_4147	<i>Baculites</i>	Montana	Carter		Straight	1.7955
DMNS_4152	<i>Baculites baculus</i>	South Dakota	Pennington		Straight	1.6803
DMNS_4154	<i>Baculites grandis</i>	Colorado	El Paso		Straight	1.7079
UCM_4850	<i>Baculites anceps</i>	Wyoming	Big Horn		Straight	1.7505
DMNS_5633	<i>Jeletzkytes nodosus</i>	Colorado	Larimer		Coiled	1.7736
DMNS_7858	<i>Baculites rugosus</i>	South Dakota	Pennington		Straight	1.7588
DMNS_7867	<i>Baculites reesidei</i>	South Dakota	Meade		Straight	1.7803
DMNS_7871	<i>Baculites grandis</i>	South Dakota	Pennington		Straight	1.7854
UCM_8508	<i>Baculites compressus</i>	Colorado	Elbet		Straight	1.7943
DMNS_8718	<i>Baculites</i>	Colorado	Pueblo		Straight	1.6959
USGS_9161	<i>Didymoceras jorgenseni</i>	South Dakota	Fall River		Heteromorph	1.7867
UCM_9393	<i>Heteroceras tortum</i>	Wyoming	Weston		Heteromorph	1.7536
UCM_9395	<i>Baculites ovatus</i>	Wyoming	Weston		Straight	1.8153
UCM_9396	<i>Baculites compressus</i>	Wyoming	Weston		Straight	1.778
UCM_9798	<i>Baculites compressus</i>	Colorado	Lincoln		Straight	1.754
SDSM_10150	<i>Placenticeras meeki</i>	South Dakota			Coiled	1.7506
SDSM_10169	<i>Baculites</i>	South Dakota			Straight	1.7454
USGS_11725	Ammonitida	Utah	Kane		Coiled	1.75
UCM_13280	<i>Placenticeras</i>	Wyoming	Albany		Coiled	1.7621
UCM_15923	<i>Placenticeras whitfieldi</i>	South Dakota	Pennington		Coiled	1.7787
UCM_16878	<i>Placenticeras whitfieldi</i>	South Dakota	Pennington		Coiled	1.8042
DMNS_16889	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8012
DMNS_16890	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8225
DMNS_16898	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8179
DMNS_16899	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.795
DMNS_16925	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8316
DMNS_16926	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8047
DMNS_16928	<i>Placenticeras costatum</i>	Colorado	Grand		Coiled	1.8225

UCM_17316	<i>Baculites ovatus</i>	Wyoming	Weston		Straight	1.7638
UCM_17385	<i>Scaphites nodasus</i>	Wyoming	Weston		Heteromorph	1.7631
UCM_18483	<i>Scaphites</i>	Wyoming	Weston		Heteromorph	1.7048
UCM_18501	<i>Baculites compressus</i>	Wyoming	Weston		Straight	1.7882
UCM_19831	<i>Baculites</i>	Wyoming	Niobrara		Straight	1.7168
DMNS_19915	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.7798
DMNS_19916	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.8235
DMNS_19919	<i>Jeletzkytes</i>	Colorado	Jefferson		Coiled	1.8129
DMNS_19925	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.8003
DMNS_19928	<i>Jeletzkytes</i>	Colorado	Jefferson		Coiled	1.7739
DMNS_19937	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.7657
DMNS_19941	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.7672
DMNS_19945	<i>Jeletzkytes</i>	Colorado	Jefferson		Coiled	1.7255
USGS_21422	<i>Baculites sweetgrassensis</i>	Montana	Toole		Straight	1.7331
USGS_22339	<i>Metioceras whitei</i>	Utah	Kane		Coiled	1.7166
DMNS_22877	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.767
DMNS_22920	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.7544
USGS_23056	<i>Didymoceras cheyennensis</i>	Colorado	El Paso		Heteromorph	1.7332
UCM_30222	<i>Baculites</i>	Colorado	Grand		Straight	1.7643
UCM_30392	<i>Anapachydiscus</i>	Colorado	Pueblo		Coiled	1.798
UCM_30394	<i>Baculites scotti</i>	Colorado	Pueblo		Straight	1.7856
DMNS_30421	<i>Exiteloceras jenneyi</i>	Colorado	Larimer		Heteromorph	1.8084
DMNS_30425	<i>Baculites cuneatus</i>	Colorado	Larimer		Straight	1.7739
DMNS_30431	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.7028
DMNS_30433	<i>Baculites grandis</i>	Colorado	Jefferson		Straight	1.8065
UCM_31618	<i>Baculites</i>	Colorado	Lincoln		Straight	1.7551
UCM_32490	<i>Placenticeras intercalare</i>	Colorado	Paso		Coiled	1.7913
UCM_32492	<i>Placenticeras intercalare</i>	Colorado	Paso		Coiled	1.7932
UCM_32742	<i>Placenticeras meeki</i>	Colorado	Grand		Coiled	1.7676
KUIP_33986	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.6449
KUIP_33990	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7342
KUIP_33991	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7625
KUIP_33993	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7575

KUIP_34013	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7221
KUIP_34015	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.6729
KUIP_34023	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.75
KUIP_34066	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7036
KUIP_47172	<i>Baculites</i>	Kansas	Wallace	Lake Creek	Straight	1.7759
KUIP_47186	<i>Baculites reesidei</i>	Kansas	Wallace	Salt Grass Shale	Straight	1.734
KUIP_50108	<i>Baculites</i>	Kansas	Wallace		Straight	1.7849
KUIP_50121	<i>Baculites</i>	Kansas	Logan	Sharon Springs	Straight	1.7418
KUIP_50143	<i>Baculites</i>	Kansas		Salt Grass Shale	Straight	1.743
KUIP_50163	<i>Baculites</i>	Kansas	Cheyenne	Beecher Island	Straight	1.7848
KUIP_50164	<i>Baculites corrugatus</i>	Kansas	Wallace		Straight	1.8069
KUIP_50657	<i>Baculites</i>	Kansas		Beecher Island	Straight	1.5656
KUIP_50658	<i>Baculites</i>	Kansas		Beecher Island	Straight	1.4813
KUIP_50666	<i>Baculites</i>	Colorado			Straight	1.7664
KUIP_50678	<i>Baculites</i>	Colorado			Straight	1.719
KUIP_50679	<i>Baculites</i>	Colorado			Straight	1.7334
KUIP_50685	<i>Baculites ovatus</i>	Colorado			Straight	1.753
UT_53349	<i>Placenticeras meeki</i>	South Dakota	Pennington		Coiled	1.6961
KUIP_59646	<i>Baculites reesidei</i>	Kansas	Wallace		Straight	1.7904
KUIP_59647	<i>Baculites reesidei</i>	Kansas	Wallace		Straight	1.7233
KUIP_59661	<i>Baculites pseudovatus</i>	Kansas	Wallace		Straight	1.7798
KUIP_59662	<i>Baculites reesodei</i>	Kansas	Wallace		Straight	1.7523
KUIP_59665	<i>Baculites grandis</i>	Kansas	Wallace		Straight	1.7609
KUIP_59666	<i>Baculites clinobatus</i>	Kansas	Wallace		Straight	1.7638
KUIP_59667	<i>Baculites grandis</i>	Kansas	Wallace	Beecher Island	Straight	1.7139
KUIP_59669	<i>Baculites pseudovatus</i>	Kansas	Wallace		Straight	1.6623
SDSM_64515	<i>Baculites</i>	South Dakota			Straight	1.8001
SDSM_64531	<i>Baculites</i>	South Dakota			Straight	1.7463
SDSM_68515	<i>Baculites</i>	South Dakota			Straight	1.7811
USGS_88060	<i>Baculites</i>	Colorado	Grand		Straight	1.807
SDSM_109273	<i>Pachydiscus</i>	South Dakota		Red Bird	Coiled	1.8183
SDSM_109276	<i>Placenticeras meeki</i>	South Dakota			Coiled	1.7824

SDSM_109485	<i>Baculites</i>	South Dakota	Pennington		Straight	1.7793
SDSM_110491	<i>Baculites</i>	South Dakota			Straight	1.7372
SDSM_112053	<i>Prionocyclus</i>	South Dakota			Coiled	1.7669
SDSM_112530	<i>Placenticerus meeki</i>	South Dakota	Butte		Coiled	1.8159
SDSM_112531	<i>Placenticerus meeki</i>	South Dakota	Butte		Coiled	1.7186
SDSM_112532	<i>Baculites</i>	South Dakota	Pennington		Straight	1.7401
SDSM_112542	<i>Pachydiscus</i>	South Dakota			Coiled	1.7721
SDSM_112600	<i>Baculites</i>	South Dakota			Straight	1.8295
SDSM_112601	<i>Baculites</i>	South Dakota			Straight	1.7227
SDSM_112602	<i>Baculites</i>	South Dakota			Straight	1.7877
SDSM_112603	<i>Baculites</i>	South Dakota			Straight	1.8091
SDSM_112604	<i>Baculites</i>	South Dakota			Straight	1.7344
SDSM_112605	<i>Baculites</i>	South Dakota			Straight	1.717
SDSM_112606	<i>Baculites</i>	South Dakota			Straight	1.7897
SDSM_112607	<i>Baculites</i>	South Dakota			Straight	1.7859
SDSM_113009	<i>Placenticerus</i>	South Dakota			Coiled	1.7941
SDSM_113010	<i>Placenticerus meeki</i>	South Dakota			Coiled	1.7865
SDSM_113011	<i>Placenticerus</i>	South Dakota			Coiled	1.8408
SDSM_113013	<i>Placenticerus meeki</i>	South Dakota			Coiled	1.7892
SDSM_113014	<i>Placenticerus meeki</i>	South Dakota			Coiled	1.8495
SDSM_113015	<i>Placenticerus meeki</i>	South Dakota			Coiled	1.8166
KUIP_148165	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7693
KUIP_148277	<i>Placenticerus meeki</i>	Kansas	Wallace	Weskan	Coiled	1.7935
KUIP_148280	<i>Placenticerus meeki</i>	Kansas	Wallace	Lake Creek	Coiled	1.7919
KUIP_148283	<i>Placenticerus meeki</i>	Kansas	Wallace	Lake Creek	Coiled	1.8019
KUIP_148425	<i>Baculites</i>	Colorado	Yuma	Beecher Island	Straight	1.6888
KUIP_150260	<i>Hoploscaphites nodosus</i>	Montana	Dawson		Coiled	1.7684
KUIP_150359	<i>Baculites</i>	South Dakota			Straight	1.7789
KUIP_151185	<i>Placenticerus</i>	Kansas	Wallace	Weskan	Coiled	1.6871
KUIP_297480	<i>Placenticerus meeki</i>	Kansas	Wallace	Weskan	Coiled	1.7218
USGS_D13490	<i>Didymoceras nebrascenses</i>	South Dakota	Fall River		Heteromorph	1.7896
USGS_D1352	<i>Baculites compressus</i>	Colorado	Grand		Straight	1.7077
USGS_D1409	<i>Didymoceras</i>	Colorado	Pueblo		Heteromorph	1.6254

USGS_D1411	<i>Didymoceras</i>	Colorado	Pueblo		Heteromorph	1.6349
USGS_D1422	<i>Didymoceras nebrascenses</i>	South Dakota	Fall River		Heteromorph	1.7342
USGS_D1467	<i>Baculites</i>	Colorado	Larimer		Straight	1.7614
USGS_D221	<i>Didymoceras cheyennensis</i>	Colorado	El Paso		Heteromorph	1.7031
USGS_D2629	<i>Didymoceras nebrascenses</i>	South Dakota	Fall River		Heteromorph	1.7042
USGS_D2719	<i>Baculites reesidei</i>	Colorado	Larimer		Straight	1.7682
USGS_D2821	<i>Baculites reesidei</i>	Colorado	Larimer		Straight	1.7911
USGS_D368	<i>Baculites</i>	Colorado	Larimer		Straight	1.7418
USGS_D409-1	<i>Didymoceras tortum</i>	South Dakota	Buffalo		Heteromorph	1.6441
USGS_D409-2	<i>Didymoceras cochleatum</i>	South Dakota	Buffalo		Heteromorph	1.6824
USGS_D409-3	<i>Didymoceras platycostatum</i>	South Dakota	Buffalo		Heteromorph	1.6835
USGS_D409-4	<i>Didymoceras mortoni</i>	South Dakota	Buffalo		Heteromorph	1.7565
USGS_D5033	<i>Baculites</i>	Colorado	Larimer		Straight	1.8014
USGS_D5416	<i>Baculites compressus</i>	Colorado	Grand		Straight	1.7864
USGS_D5974	<i>Baculites scotti</i>	Colorado	Grand		Straight	1.695
USGS_D8771	<i>Didymoceras cheyennensis</i>	Colorado	El Paso		Heteromorph	1.6728
USGS_D904	<i>Didymoceras</i>	Colorado	Pueblo		Heteromorph	1.7348
DMNS_EPI.16893	<i>Placentoceras costatum</i>	Colorado	Grand		Coiled	1.7893
DMNS_EPI.33138	<i>Placentoceras cummingsi</i>	New Mexico	Rattlesnake	Colorado	Coiled	1.8147
DMNS_EPI.33140	<i>Pseudaspidoceras pseudonodosoides</i>	New Mexico	Rattlesnake	Colorado	Coiled	1.8268
DMNS_EPI.33384	<i>Jeletzkytes criptonodosus</i>	Wyoming	Niobrara		Coiled	1.8289
DMNS_EPI.33387	<i>Menuites oralensis</i>	Wyoming	Niobrara		Coiled	1.8134
DMNS_EPI.33390	<i>Jeletzkytes criptonodosus</i>	Wyoming	Niobrara		Coiled	1.7006
DMNS_EPI.33391	<i>Jeletzkytes plenus</i>	Wyoming	Niobrara		Coiled	1.7615
DMNS_EPI.33396	<i>Jeletzkytes plenus</i>	Wyoming	Niobrara		Coiled	1.7687
DMNS_EPI.33411	<i>Placentoceras meeki</i>	Wyoming	Niobrara		Coiled	1.7576
DMNS_EPI.33413	<i>Placentoceras intercalare</i>	Wyoming	Niobrara		Coiled	1.7599
DMNS_EPI.33417	<i>Jeletzkytes criptonodosus</i>	Wyoming	Weston		Coiled	1.7701
DMNS_EPI.33421	<i>Jeletzkytes criptonodosus</i>	Wyoming	Niobrara		Coiled	1.6471
DMNS_EPI.33426	<i>Hoploscaphites</i>	Wyoming	Niobrara		Coiled	1.6196
DMNS_EPI.33427	<i>Hoploscaphites</i>	Wyoming	Niobrara		Coiled	1.8242

DMNS_EPI.33433	<i>Menuites portlocki complexus</i>	Wyoming	Niobrara		Coiled	1.7989
DMNS_EPI.33439	<i>Menuites oralensis</i>	Wyoming	Niobrara		Coiled	1.8215
DMNS_EPI.33618	<i>Jeletzkytes brevis</i>	South Dakota	Pennington		Coiled	1.7156
DMNS_EPI.33628	<i>Scaphites carlensis</i>	South Dakota	Butte		Heteromorph	1.771
DMNS_EPI.33631	<i>Menuites oralensis</i>	South Dakota	Fall River		Coiled	1.7375
DMNS_EPI.33636	<i>Prionocyclus</i>	South Dakota	Fall River		Coiled	1.7331
DMNS_EPI.33637	<i>Jeletzkytes nodosus</i>	South Dakota	Pennington		Coiled	1.7131
DMNS_EPI.33638	<i>Jeletzkytes</i>	South Dakota	Pennington		Coiled	1.7632
DMNS_EPI.36401	<i>Placenticerus meeki</i>	Colorado	Fremont		Coiled	1.6814
DMNS_EPI.36403	<i>Exiteloceras jenneyi</i>	Colorado	Pueblo		Heteromorph	1.7531
DMNS_EPI.36406	<i>Didymoceras stevensoni</i>	Colorado	Larimer		Heteromorph	1.6372
DMNS_EPI.36411	<i>Placenticerus meeki</i>	Colorado	Larimer		Coiled	1.8258
DMNS_EPI.36426	<i>Placenticerus meeki</i>	Colorado	Pueblo		Coiled	1.7734
DMNS_EPI.36427	<i>Metoicoceras</i>	Colorado	Pueblo		Coiled	1.7714
DMNS_EPI.36429	<i>Menuites oralensis</i>	Colorado	Pueblo		Coiled	1.7842
DMNS_EPI.36439	<i>Rhaeboceras halli</i>	Colorado	Larimer		Coiled	1.8007
DMNS_EPI.36443	<i>Placenticerus costatum</i>	Colorado	Boulder		Coiled	1.8356
DMNS_EPI.36448	<i>Placenticerus placenta</i>	Colorado	Jefferson		Coiled	1.7732
DMNS_EPI.36452	<i>Scaphites tetonensis</i>	Montana	Chouteau	Colorado	Heteromorph	1.7237
DMNS_EPI.36458	<i>Jeletzkytes quadrangularis</i>	Montana	Dawson		Coiled	1.8111
DMNS_EPI.36460	<i>Jeletzkytes crassus</i>	Montana	Dawson		Coiled	1.7585
DMNS_EPI.36462	<i>Jeletzkytes crassus</i>	Montana	Dawson		Coiled	1.7119
DMNS_EPI.36465	<i>Jeletzkytes plenus</i>	Montana	Dawson		Coiled	1.7275
DMNS_EPI.36466	<i>Jeletzkytes brevis</i>	Montana	Dawson		Coiled	1.7795
DMNS_EPI.36468	<i>Jeletzkytes nodosus</i>	Montana	Dawson		Coiled	1.7368
DMNS_EPI.36471	<i>Placenticerus intercolari</i>	Montana	Carter		Coiled	1.7583
DMNS_EPI.36475	<i>Scaphites preventricosus</i>	Montana	Toole	Colorado	Heteromorph	1.7734
DMNS_EPI.36478	<i>Clioscapites novimexicanus</i>	Montana	Toole	Colorado	Coiled	1.7867
DMNS_EPI.36490	<i>Baculites compressus</i>	Wyoming	Niobrara		Straight	1.7119
DMNS_EPI.36769	<i>Baculites eliasi</i>	Wyoming	Niobrara		Straight	1.7632
DMNS_EPI.36782	<i>Baculites</i>	Montana	Carter		Straight	1.7478

DMNS_EPI.36786	<i>Baculites</i>	Montana	Carter		Straight	1.6247
DMNS_EPI.4181	<i>Baculites eliasi</i>	Wyoming	Niobrara		Straight	1.7694
DMNS_EPI.547	<i>Scaphites plenus</i>	South Dakota			Heteromorph	1.7538