The Biogeography and Macroevolutionary Trends of Late Paleozoic Cephalopods in the North American Midcontinent Sea: Understanding the response of pelagic organisms to changing climate during the Late Paleozoic Ice Age

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Abstract:

Geographic range is an important macroevolutionary parameter that is frequently considered in paleontological studies. Species distribution and geographic range size are determined by a variety of biotic and abiotic factors that are well known to affect the differential birth and death of species. Thus, considering how species distributions and geographic range sizes fluctuate over time can provide important insight into evolutionary dynamics across the geologic time scale. In this study, I examine how geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and Early Permian in the North American Midcontinent Sea in an important pelagic clade, the Cephalopoda, using Geographic Information Systems (GIS). This period is particularly interesting for biogeographic and evolutionary analysis because it is characterized by repetitive glacial cycles, a global transition from an icehouse to greenhouse climate during the Late Paleozoic Ice Age and sluggish macroevolutionary dynamics, i.e. low speciation and extinction rates, that have been repeatedly documented in studies of other marine invertebrate taxa from both Gondwana and Pangea.

The analyses presented herein indicate that cephalopod species diversity fluctuated throughout the Pennsylvanian and Early Permian matching the findings of other studies that examined diversity components of the Late Paleozoic marine invertebrate fauna. However, contrary to studies that focused on benthic taxa, my analyses found that: mean geographic range size of cephalopod species did not change significantly through time, despite numerous climate oscillations throughout this period; and further, geographic range size did not correlate with macroevolutionary rates. This result suggests that pelagic organisms may have a different response to climate change than benthic organisms and thus additional consideration of this issue is needed. Finally, these analyses indicate that, in the case of cephalopods, macroevolutionary

patterns during the Late Paleozoic were more ‘dynamic’ than previously characterized. Thus, the macroevolutionary patterns recovered may depend on the taxon analyzed.

Author’s Disclaimer:

All taxonomic actions in this work are hereby disclaimed for nomenclatural purposes, as recommended in Article 8 of the International Code of Zoological Nomenclature (ICZN, 1999).

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Chapter 1

Chapter 1: The Biogeography and Macroevolutionary Trends of Late Paleozoic Cephalopods in the North American Midcontinent Sea

Introduction:

Geographic range is an important macroevolutionary parameter (Lieberman, 2000, 2003, 2008, 2012) that is frequently considered in paleontological studies (Jablonski, 1986; Rode & Lieberman, 2004; Hendricks et al., 2008). Species distribution and geographic range size are determined by a variety of biotic and abiotic factors (Brown et al., 1996; Lieberman, 2000; Peterson, 2011; Saupe et al., 2015; Beard, 2016) that are well known to affect the differential birth and death of species (Lieberman & Vrba, 1995; Simões et al., 2016). Thus, considering how species distributions and geographic range sizes fluctuate over time can provide important insight into evolutionary dynamics across the geologic time scale. In this study, I examine how geographic range size, and rates of speciation and extinction changed throughout the Pennsylvanian and Early Permian in the North American Midcontinent Sea in an important clade of pelagic invertebrates, the Cephalopoda. This period is particularly interesting for biogeographic and evolutionary analysis because it is characterized by repetitive glaciation cycles, a global transition from an icehouse to greenhouse climate during the Late Paleozoic Ice Age (LPIA) (Montanez & Poulsen, 2013), and sluggish macroevolutionary dynamics, i.e. low speciation and extinction rates, that have been repeatedly documented in studies of other marine invertebrate taxa from both Gondwana and Pangea (Sepkoski, 1998; Stanley & Powell, 2003; Bonelli & Patzkowsky, 2011).

The Late Paleozoic Ice Age (LPIA) was the longest lived glacial period of the Phanerozoic and represents one of the only well documented transitions in Earth history from an icehouse to greenhouse climate (Montanez & Poulsen, 2013). Our understanding of the LPIA has emerged through recent work on the stratigraphy, isotope ecology, and sedimentology of the Paleozoic (Mii et al., 1999; Heckel, 2008; Dimichele et al., 2009; Montanez & Poulsen, 2013). Current understanding suggests that in Gondwana there were three glacial successions: Glacial I was characterized by glaciation throughout the Late Devonian to Early Mississippian; Glacial II by glaciation throughout the Late Mississippian to Middle Pennsylvanian; and Glacial III by glaciation throughout the Late Pennsylvanian to Early Permian (Isbell, 2003; Montanez & Poulsen, 2013). Glacial I and Glacial II would have been characterized by moderate glaciations on a regional scale throughout portions of Gondwana and Pangea, while Glacial III would have been characterized by more extreme glaciations (Fielding et al., 2008; Montanez & Poulsen, 2013) reaching to the 35˚ latitudinal band in both the northern and southern hemispheres (Powell, 2007). In this study, I will focus on the time interval that includes the glacial and interglacial periods of Glacial II and Glacial III of the Midcontinent Region of the United States (Pennsylvanian -Early Permian) due to the extensive literature available on the cephalopod fossil record and the abundance of specimens available in museum collections.

In many ways, there may be an important parallel between modern day climate and the climate of the LPIA. Researchers argue that the linkage of the LPIA and the Quaternary Ice Age glaciations to Milankovitch Cycles with characteristically low CO_2 concentrations and bi-polar modes of global glaciation are unique similarities between these ice ages that are not shared with any other ice age in Earth's history (Raymond & Metz, 2004). The transition from an icehouse to greenhouse climate over the Late Paleozoic to Early Permian may be considered analogous to the modern climate transition that began at the end of the Quaternary Ice Age and has been accelerating due to human activity (Stanley & Powell, 2003; Raymond & Metz, 2004; Heckel, 2008; Montanez & Poulsen, 2013). The similarities between the LPIA and the Quaternary Ice

Ages suggest that elucidating patterns in the former might provide an important historical ‘baseline’ for the biotic response to climate transitions. In this way, it will be possible to better understand the causation of sluggish rates of evolution during protracted intervals of glaciation and anticipate biogeographic responses during icehouse-greenhouse climate transitions. This could ultimately provide greater insight into the ecological and evolutionary responses of paleo-communities to glacial cycling (Dietl & Flessa, 2011).

There have been a variety of hypotheses proposed for the distinctively sluggish macro-evolutionary dynamics of the LPIA. Some studies contend that this pattern is a result of environmental changes linked to glacial cycling while others point to tectonic activity driving the slow ecologic restructuring and sluggish macroevolutionary dynamics throughout the LPIA (Fielding et al., 2008; Dimichele et al., 2009; Falcon-Lang & DiMichele, 2010; Cecil et al., 2014). To date, many of the studies focusing on the macroevolutionary dynamics of the LPIA have concentrated on benthic marine invertebrates and did not explicitly investigate evolutionary patterns in pelagic marine invertebrates despite the diversity and abundance of these organisms within the Late Paleozoic marine ecosystems. Given the significant role that geographic factors play in speciation (Mayr, 1942; Eldredge & Gould, 1972; Brooks & McLennan, 1991; Lieberman, 2000; Chaimanee et al., 2012), we might expect that pelagic organisms, because of their innate ability to swim or passively travel with current, might show different patterns relative to taxa that were benthic (at least as adults). Thus, it is important to establish the specific response of pelagic organisms such as nautiloids and ammonoids to see how they may differ relative to their benthic counterparts.

Background:

Geologic Setting of the LPIA in the Midcontinent Region of North America:

The Pennsylvanian Midcontinent of North America is subdivided into five stages: Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian (Kansas Geological Survey, 2005). The Permian is subdivided into three stages: Wolfcampian, Leonardian, and Guadalupian (Kansas Geological Suvery, 2010). My thesis focuses on fossil specimens from the entirety of the Pennsylvanian and from the Wolfcampian of the Permian due to their availability in the collections at the Biodiversity Institute, University of Kansas, and other institutions. During this period, most of the landmasses on Earth were agglomerated into the supercontinent Pangea. Pangea formed through the collision of Laurentia and Gondwana and was surrounded by the Panthalassic and Tethyan Seas and punctuated by several inland seas in the tropical zone (Tabor & Poulsen, 2007). Throughout the Late Carboniferous, the Midcontinent region of the United States was positioned in western Pangea and covered by a tropical epi-continental sea; bordered by the Rocky Mountain orogeny to the west/north-west and the Appalachian Mountain belt to the south/south east (Algeo & Heckel, 2008). During this period, tectonic plate activity, glacial cycles, and carbon cycling would have greatly influenced the climate of the Midcontinent Sea (Montanez, 2007; Tabor & Poulsen, 2007; Algeo & Heckel, 2008).

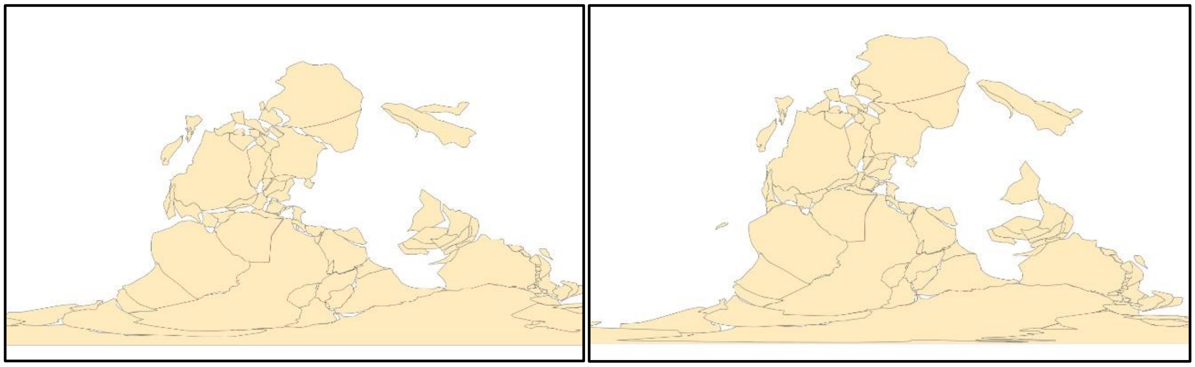


Figure 1: Continental configuration during the Morrowan (315 million years ago) and the Wolfcampian (285 million years ago) stages of the Late Paleozoic Ice Age (LPIA). Reconstructed using *PaleoWeb* software at 1:100000000 scale (The Rothwell Group LP, 2016).

During the Late Paleozoic, the North American continent was situated in tropical latitudes and was covered by a shallow sea. The North America Midcontinent Sea extended across humid and dry tropical zones (0-20°N) throughout the Pennsylvanian and sea-level was greatly affected by the intermittent waxing and waning of glacial sheets. Tectonic activity drove the northward shift of the Gondwana plate into the arid sub-tropical zone throughout the Late Pennsylvanian and Early Permian (Tabor & Poulsen, 2007; Joachimski & Lambert, 2015). This tectonic activity would have been a principal factor in the long-term trend from wetland to dry floral assemblages in the terrestrial record of this region (Tabor & Poulsen, 2007; Dimichele et al., 2009). Another important geologic phenomenon was the presence of multiple locations of mountain building (orogeny) along the margins of the Gondwanan sub-continent during the Late Paleozoic. Notably, the primordial Rocky Mountain uplift began in the Late Mississippian, peaked in the Middle Pennsylvanian, and reached its fullest extent in the Early Permian. This orogeny greatly isolated the Midcontinent Seaway from the Panthalassic Ocean and allowed limited exchange between these water bodies (Wells et al., 2007; Joachimski & Lambert, 2015).

Glacial cycling in the Midcontinent region has received much study (e.g., Isbell, 2003; Algeo & Heckel, 2008; Heckel, 2008). Modern synthesis of the glacial history of western Gondwana indicates that the Morrowan to Early Desmoinesian represented a localized glacial period, the Late Desmoinesian to Early Virgilian represented a widespread interglacial period with minor glaciation, and the Late Virgilian to Early Wolfcampian represented the apex of widespread glaciation during the Late Paleozoic Ice Age (Montanez & Poulsen, 2013). The rock record of the Midcontinent region of North America is characterized by numerous sedimentary successions known as cyclothems that represent repeated changes in sea-level throughout Pennsylvanian strata. Heckel (2008) indicated that each cyclothem can be divided into four distinct parts based on rock composition: transgressive deposits (during periods of glacial melting as sea-levels rose); high-stand deposits (during interglacial periods at maximum sea-level); forced-regressive (during glacial build-up as sea-levels fell); and low-stand (during maximum ice volume and minimum sea-level). Each correlates with the repeated waxing and waning of the Gondwanan ice sheet (Algeo & Heckel, 2008; Heckel, 2008). Although various stages within the time interval studied can be generally characterized as glacial or interglacial on a global scale, it is important to note that there may be varying degrees of localized glaciation in the Midcontinent throughout the LPIA. Modeling predicts that sea-level oscillations in the Late Pennsylvanian were between 50 - 100 meters depending upon the number and volume of melting ice sheets, and that water temperatures are estimated to have been between 4 - 7°C cooler during glacial maxima than inter-glacial periods (Heckel, 1986; Isbell, 2003; Montanez, 2007; Tabor, 2007; Heckel, 2008; Cecil et al., 2014). The sea-level and temperature changes would have had an important influence on species distribution and geographic range size and there is evidence for a global shift in marine invertebrate ranges and species diversity from high latitude habitats to low latitude habitats with the onset of the LPIA (Waterhouse & Shi, 2010).

Stable isotope studies have been used to understand chemical trends through the Late Paleozoic and the extent to which global carbon cycling played a role in glaciation. Mii et al. (1999) identified strong coupling between δC^{13} and δO^{18} signatures in the Paleozoic brachiopods of North America as evidence for the feedback of carbon storage on global temperature trends. Elevated δC^{13} values are indicative of high rates of carbon storage and subsequent decrease in global CO_2 concentrations while elevated δO^{18} concentrations are indicative of cooling temperature influenced by the amount of evaporation experienced by the sample (Dawson et al., 2002). Montanez et al. (2007) and Grossman et al. (2008) utilized fossilized δC^{13} rise documented in brachiopods from the Carboniferous of the Midcontinent and Russia, and from soil-formed calcite and fossilized plant matter from the Late Paleozoic of southern Gondwana, respectively, to infer atmospheric concentrations of CO_2 and surface temperature. Their findings support the notion that there were three major glaciations during the LPIA and that changes in Paleozoic climate and glaciation cycles are coupled with CO_2 concentrations (Montanez, 2007).

Paleoecology of the North American Midcontinent Sea:

As mentioned previously, the Late Carboniferous-Late Permian was a time of global transition from an icehouse to greenhouse climate (Montanez & Poulsen, 2013). However, within the larger trend towards a greenhouse climate, there were varying degrees of glacial cycling around the globe. The cyclicity of the LPIA, based the depositional sedimentology of this period, oscillated on 1-4 million year spans for major glaciation cycles and within stages on ~100,000 and ~400,000 year cycles (Heckel, 1986; Isbell, 2003; Fielding, Frank, & Isbell, 2008; Cecil, DiMichele, & Elrick, 2014). Glacial periods are characterized as wet periods of low seasonality while interglacial periods are characterized as arid periods of high seasonality; there was an overarching trend towards a warm, arid climate in the Late Permian (Tabor & Poulsen, 2007; Montanez, 2007; Grossman et al., 2008; Montanez & Poulsen, 2013).

The Pennsylvanian Midcontinent Sea was warm, tropical and hosted a diverse fauna, including fish, bivalves, cnidarians, and cephalopods. Research indicates that the Pennsylvanian Midcontinent Sea was highly stratified, periodically anoxic, and subject to varying degrees of input from freshwater sources (Wells et al., 2007; Algeo & Heckel, 2008). The Midcontinent Sea reached its greatest extent during glacial high-stands through the Middle to Late Pennsylvanian (Algeo & Heckel, 2008) and stable isotope analysis of δO^{18} concentrations from conodonts suggests that the salinity of the Midcontinent Sea varied significantly throughout this period, correlating with freshwater input during glacial and inter-glacial phases (Joachimski & Lambert, 2015). Paleotemperatures in Gondwana are estimated to have been analogous to modern low latitude temperatures and rose 5-10°C throughout the Late Pennsylvanian and Permian (Tabor, 2007).

These environmental dynamics would have had considerable influence over the biogeographic distribution of marine species throughout the Midcontinent Sea. As mentioned before, a marked global shift was documented in marine invertebrate ranges and species diversity from high latitude to low latitude environments with the onset of the LPIA (Waterhouse & Shi, 2010). Marine biogeographic dynamics can be affected by the ease of dispersal across large areas (Carr et al., 2003). An important control over modern marine ecosystem dynamics and distribution is temperature because of its effect on both biotic and abiotic processes, including oceanic chemistry, stratification, nutrient availability, organismal metabolic rates, and timing of life history events (Powell, 2007; Hoegh-Guldberg & Bruno, 2010; Badyrka et al., 2013). Many marine organisms are dependent on temperature cues for reproduction and development and are thus highly sensitive to changes in temperature (Powell, 2007). In this way, changes in species distributions and geographic range size can give insight into ecological change and feedback into evolutionary dynamics through species sorting (Lieberman & Vrba, 1995; Jablonski, 2008).

Previous Work:

Geographic Range Size and its Association with Various Macroevolutionary Phenomena:

In this thesis, I investigate the turnover rates of nautiloids and ammonoids in the North American Midcontinent Sea and the extent to which geographic range size relates to turnover rates throughout the Pennsylvanian and Early Permian. Much work has focused on the relationship between geographic range size, evolutionary success, and climate change (Vrba, 1980; Eldredge, 1989; Lieberman, 2000, 2008). There are three biotic responses to changing climate: (1) ecologic persistence and/or evolutionary stasis; (2) shift of species' geographic ranges to regions with suitable environmental conditions; and (3) extinction (Vrba, 1980; Davis et al., 2005). The use of Geographic Information Systems (GIS) has greatly facilitated investigations into the response of communities to environmental change as it enables the construction of species ranges incorporating spatial, temporal, and environmental aspects (Stigall & Lieberman, 2006).

Theory suggests that population range size and stability influences the differential survival of species; larger geographic range size enhances the probability of survival compared to species with smaller geographic range size (Stanley, 1990). Stanley (1990; pg. 116) summarized this pattern; "*For species that are characterized by stable, relatively continuous geographical distributions, effective dispersal will retard rate of speciation by opposing the formation of isolates. (Rates of extinction will also be low because the total population will be large, widespread and stable.) On the other hand, for species characterized by patchy or unstable populations, effective dispersal will promote speciation by generating isolates. (Rates of extinction will also be high because of the instability.)*" While this may be an important general observation, it is important to note that this pattern is likely dependent on the life-history of an organisms and its' propensity to disperse. There are a few fossil-based studies that have investigated the interplay between geographic range size and turnover rates using GIS. Rode & Lieberman (2004) found that Devonian brachiopods and bivalve species had speciation rates that decreased as geographic range size increase. By contrast, Myers et al. (2013) found no relationship between geographic range size and turnover rate in invertebrates of the Cretaceous Interior Seaway. Dunhill & Willis (2015) found that geographic range size was typically correlated with extinction rate, though not during times of mass extinction. These finding are intriguing as they suggest that geographic range size may increase or decrease turnover rates depending on abiotic factors.

Numerous studies have explored the biogeography of paleo-communities through periods of climate change using GIS to inform the development of evolutionary theory (Rode & Lieberman, 2004; Rode & Lieberman, 2005; Rode & Lieberman, 2004; Myers et al., 2013; Dunhill & Willis, 2015) such that using this approach to investigate the sluggish macroevolutionary dynamics of the LPIA seems appropriate. Sepkoski (1998) formalized the notion that there was a marked decline in evolutionary rates of Carboniferous and Permian marine fauna. Two hypotheses have been proposed to explain the unusually low rates of turnover at this time: (1) environmental conditions created an ecosystem with low carrying capacity; or (2) environmental conditions reduced turnover probabilities (Stanley & Powell, 2003). Further, Stanley & Powell (2003) specified a number of species traits, including: a broad ecological niche and a sufficiently large stable population with high dispersal rates that would facilitate low turnover rates. Although the cause of the sluggish turnover rates throughout the LPIA is still under debate, there are several studies that have explored the speciation and extinction rates across a number of marine invertebrates. Low levels of taxonomic turnover in marine invertebrate fauna and ecologic persistence was documented in the Illinois basin during the onset of the LPIA despite repetitive high amplitude glacial cycling (Bonelli & Patzkowsky, 2011). Late Paleozoic brachiopod biogeographic data provides evidence that sluggish evolutionary rates and latitudinal distribution during the LPIA was effectively controlled by climate and, further, provides evidence for the pattern that genera with narrow distribution were restricted to low latitudes while genera with wider distributions were typically more widespread across latitudes (Powell, 2007). Cluster analysis of Pennsylvanian-Early Permian brachiopod communities of Bolivia corroborated these findings with a few caveats: there was an increase in abundance of warm-water North American taxa rather than replacement (i.e., extinction) of regional cold-water taxa, and there was higher overall diversity during glacial periods than in inter-glacial periods (Badyrka et al., 2013).

These results suggest that ecologic persistence and evolutionary stasis, rather than change, is a more realistic response of communities to climate change. The concept of paleontological stasis at the species level is not new. Eldredge and Gould (1972) and Gould and Eldredge (1977) first proposed ‘evolutionary stasis’ (see also: Eldredge et al., 2005) to account for the lack of evolutionary change in individual species lineages over the course of millions of years within the fossil record. Vrba’s (1985) ‘Turnover Pulse Hypothesis’ extended this concept from individual species to the level of entire biogeographic faunas. Later, Morris et al. (1995) expounded on the associated phenomenon of ‘coordinated stasis’ which essentially is the phenomena of ecologic and evolutionary stability over vast periods of time despite repeated events of minor to moderate environmental disturbance (Morris et al., 1995). The sluggish macroevolutionary dynamics of the North American Midcontinent despite repeated environmental disturbances may suggest that the Late Paleozoic represents a protracted period of coordinated stasis. Investigating speciation and extinction rates within the Pennsylvanian and Early Permian cephalopod community of the North American Midcontinent will help shed light on the patterns and processes involved.

Cephalopods of the North American Midcontinent Sea:

One of the most characteristic marine invertebrates of the Late Paleozoic North American Midcontinent Sea are the cephalopods. Modern cephalopods inhabit a wide array of ecologic niches and are organized into two groups; the Nautiloidea; and the Coleoidea (or Angusteradulata) which includes squids, octopi, and extinct ammonoids (Jacobs & Landman, 1993; Engeser, 1996; Kroger et al., 2011). Phylogenetic study has established that ammonoids are more closely related to coleoids based on key synapomorphies shared between these groups and not with Nautiloidea (Boardman, 1994; Engeser, 1996). Cephalopoda diverged from other mollusks during the early Cambrian and nautiloids diverged from coleoids in the Mid-Paleozoic (Kroger et al., 2011). Ammonoids were both diverse and numerous through the Paleozoic and Mesozoic until their extinction ~65.5 million years ago, (Kruta et al., 2011). There are only two extant genera of Nautiloidea: *Nautilus* and *Allonautilus*.

Much of what is known of fossil nautiloids and ammonoids has been inferred from observation of the modern forms, *Nautilus* and *Allonautilus*. Nautiloids and ammonoids are believed to have been similar in behaviors due to their common conch (shell) morphology although, in recent years, the validity of this claim has been disputed (see: Jacobs & Landman, 1993). Nautiloids and ammonoids are readily distinguished from each other by several features. The most apparent feature is shell morphology: ammonoids are generally characterized by bulky, complex conchs while nautiloids are characterized by streamlined, simple conchs. Further, ammonoids and nautiloids differ in suture morphologies. Sutures are growth lines visible on the conch surface. In ammonoids, suture lines are typically far more complex in patterning than in nautiloids. Ammonoids and nautiloids also differ in the position of the siphuncle (the opening through the internal shell that contains the propulsive organs). In ammonoids, the siphuncle is positioned marginally while in nautiloids the siphuncle is positioned centrally to sub-centrally.

It has traditionally been thought that nautiloids were more dynamic, efficient, quick swimmers than their ammonoid counterparts (Jacobs & Landman, 1993). Both groups utilized neutral buoyancy via the phragmocone (chambered section of the internal shell) for locomotion but the efficiency and velocity of locomotion was most likely determined by conch shape and the position of the hyponome (jet-propulsion funnel) (Jacobs & Landman, 1993). Ammonoid mobility has been directly correlated with the degree of shell-coiling and it has recently been established that ammonoids with more tightly coiled shells likely had comparable mobility to nautiloids (Klug & Korn, 2004). Both nautiloids and ammonoids are found in a variety of paleo-environments across a range of inferred paleo-depths, and this has been interpreted as evidence for their dynamic use of different habitats (Ritterbush et al., 2014). A number of key differences between nautiloids and ammonoids in morphologyand life history strategy are detailed in Table 1. Further discussion of ammonoid and nautiloid biology can be found in Chapter 2 and 3.

Character	**Ammonoids**	**Nautiloids**
Siphuncle (position, size)	Marginal, small	Central, large
Retractor Muscles (position, size)	Medial, small	Ventral, large
Septa	Folded	Straight
Eyes	Yes	Yes, Pinhole
Arms (number)	10+	90
Diet	Carnivorous	Carnivorous
Habitat	Shallow, Intermediate, Deep	Shallow, Intermediate, Deep
Lifestyle	Pelagic (Planktonic?)	Pelagic-Planktonic
Reproduction	Sexual	Sexual
Reproductive Mode	R-Selected	K-Selected
Embryo (size, number)	Small, many	Large, few

Table 1: A comparison of morphological features and life-history strategies in nautiloids and ammonoids. Character state information compiled from various sources. Please see; (Jacobs & Landman, 1993; Engeser, 1996; Ritterbush et al., 2014).

Ammonoid fossils have commonly been used as stratigraphic indicators within the geologic record because of their diversity, abundance, and high rates of turnover (or volatility *sensu* Lieberman & Melott, 2013). By contrast, nautiloids have been less frequently used for biostratigraphic purposes. Both groups have been well characterized from the Pennsylvanian and Permian systems of North America (Miller et al., 1933; Newell, 1936; Plummer & Scott, 1937; Miller & Youngquist, 1949) and are numerous and diverse within the collections of the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas (KUMIP) and other major natural history museums. For this reason, Pennsylvanian-Permian cephalopods provide an excellent group to study biogeographic and evolutionary patterns during the LPIA of the North American Midcontinent Sea.

Materials & Methods:

Geographic ranges were reconstructed for 27 genera of cephalopods from the LPIA North American Midcontinent Sea. For this project, I focused on the nautiloid and ammonoid species within the Pennsylvanian and Permian strata of the Midcontinent region that had a significant presence within museum collections to better understand the biogeographic responses of these taxa to climate fluctuations and glacial cycling throughout the LPIA. The data set used for this analysis included thirteen genera of nautiloids: *Brachycycloceras, Domatoceras, Ephippioceras, Euloxoceras, Hebetorthoceras, Knightoceras, Liroceras, Metacoceras, Millkoninckioceras, Mooreoceras, Orthoceras, Pseudorthoceras,* and *Solenochilius,* and fourteen genera of ammonoids: *Gonioloboceras, Gonioloboceratoides, Megapronorites, Mescalites, Properrinites, Phaneroceras, Properrinites, Pseudoparalegoceras, Schistoceras, Shumardites, Parashumardites, Pseudopronorites, Pronorites,* and *Vidrioceras*. These ultimately comprised 79 species. The genera used in this analysis were chosen based on their abundance within museum collections, the availability of and access to reference material to enable the validity of taxonomic identifications, and the fact that they are typically well preserved. Any specimens that lacked well resolved stratigraphic and geographic information or could not be identified to the species level were not used in this analysis. Specimens from the following institutions, the major repositories of the relevant material, were examined: the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas (KUMIP); the University of Iowa Paleontology Repository (UI); and the Yale University Peabody Museum of Natural History (YPM). Further, these institutions contained many of the type specimens of the species examined for this analysis. All specimens were personally examined and taxonomically-vetted, with species assignments and determinations made by the author.

Data Collection:

A temporal occurrence database was created for the 79 cephalopod species from the North American Midcontinent Sea used in this analyses. Data collection for biogeographic analysis of Pennsylvanian-Early Permian cephalopods was a multistep process involving determining the identity, temporal and geographic ranges of ammonites and nautiloids: I will detail these steps in the paragraphs below.

The first step of data collection was to identify ammonoid and nautiloid specimens to species. Accurate species-level determinations were necessary to ensure the accuracy of geographic ranges and to infer biogeographic patterns and macroevolutionary dynamics of cephalopods from the Pennsylvanian-Early Permian Midcontinent Sea. The most informative characters for species identification were: suture patterning and morphology; venter and umbilical shoulder morphology; the distance between sutures; cross section morphology; and siphuncle position. In most cases, these features could reliably and accurately determine the identification of specimens to species level. Further, I examined type materials from the KUMIP, UI, and the YPM. Over 1,100 specimens were identified to the species. In Chapters 2 and Chapter 3, I discuss the biology and taxonomy, respectively, of ammonoids and nautiloids. Please see these chapters for further information regarding informative characters, stratigraphic occurrence, and other pertinent specimen information.

The second step of data collection was to correlate stratigraphic information to the Pennsylvanian and early Permian temporal intervals. The time intervals used in this study included the following Pennsylvanian stages: the Virgilian, Missourian, Desmoinesian, Atokan, and Morrowan, and the Permian Wolfcampian Stage. Collection information regarding the stratigraphic range of specimens was correlated to temporal stages through review of stratigraphic literature. Resources used for this process included; the USGS National Geologic Map Database (U.S. Geological Survey, 2017) and the Kansas Geological Survey website (KGS Stratigraphic Nomenclature: Geology Resources , 2015). I would like to formally acknowledge Dr. Michelle Casey from Murray State University for her assistance with stratigraphic and temporal correlation (Zeller, 1968; Pope, 2012). The temporal values used for the boundaries of the stages derive from The *Geologic Time Scale* "Chapter 23 The Carboniferous Period" by Davydov et al., (2012). It is necessary to note that many strata can be correlated across the Midcontinent region although Texas localities were correlated with more difficulty due to the disparate nature of Texan stratigraphic nomenclature with the rest of the Midcontinent.

Geologic Period	**Geologic Stage**	**Upper Boundary (in Millions of Years)**
Mississippian	Chesterian	318
Pennsylvanian	Morrowan	312
	Atokan	310
	Desmoinesian	307
	Missourian	304
	Virgilian	299
Permian	Wolfcampian	285
	Leonardian	270

Table 2: Temporal boundaries used for calculations of Late Paleozoic cephalopod speciation and extinction rates (Davydov et al., 2012).

The final step of data collection was to ensure that all specimens were georeferenced to highly resolved coordinates with little uncertainty. I followed the *KUMIP Geo-Referencing Protocol 2011* to georeference all localities used in this research project. I georeferenced localities using the *GeoLocate* software developed by Tulane University (2015) and the *MaNIS Georeferencing Calculator* (Wieczorek, 2015) to obtain coordinates and uncertainty radii. All points were calculated in decimal degrees within the WGS84 model in the *GeoLocate* World topo layer to ensure consistency and accuracy in determinations. The largest uncertainty radius allowed for this study was at the county level, although most radii were below 10,000 meters (6-miles). Any specimens with questionable locality information were discarded for biogeographic analysis. After specimens were correlated to temporal bins and georeferenced, I was able to create Microsoft *Excel* files for each temporal stage to be imported into GIS for range reconstruction. After all necessary culling of specimens, I had over 950 specimens to use for range reconstruction and statistical comparison of geographic range through geologic time.

Range Reconstruction:

Geographic Information Systems (GIS) provide a valuable tool for biogeographic range reconstruction in both modern and paleo- ecological studies. *ArcGIS v. 10.3* software allows for both the mapping of fossil geographic ranges through the *PaleoWeb* extension (The Rothwell Group LP, 2016) and calculation of range area throughout temporal bins. In this way, it is possible to use GIS to understand biogeographic changes through geologic time and infer evolutionary dynamics. Methods for paleo-range reconstruction of Pennsylvanian-Early Permian cephalopods were taken from Rode & Lieberman (2004 & 2005), Stigall & Lieberman (2006), Myers & Lieberman (2011) and M. Casey (personal communication, 2016).

After specimen occurrence data were georeferenced and assigned to temporal bins, *Excel* CSV files were compiled for the occurrence points of all specimens within species. CSV files were imported into *ArcGIS* and layers were created using geographic coordinate system 'WGS 1984' and projected coordinate system 'WGS 1984 World Mercator' (see Figure 2). These layers were input into *PaleoWeb* to rotate coordinates into continental configuration and geographic position of the Midcontinent Region during the Pennsylvanian-Early Permian (see section "Geologic Setting of the LPIA in the Midcontinent Region of North America" for further information) and to minimize any error in species range reconstruction (Myers & Lieberman, 2011). Paleo-coordinates were generated for each specimen occurrence point in each species layer using *PaleoWeb* (see Figure 3). These paleo-coordinate layers were then re-projected into *ArcMap*.

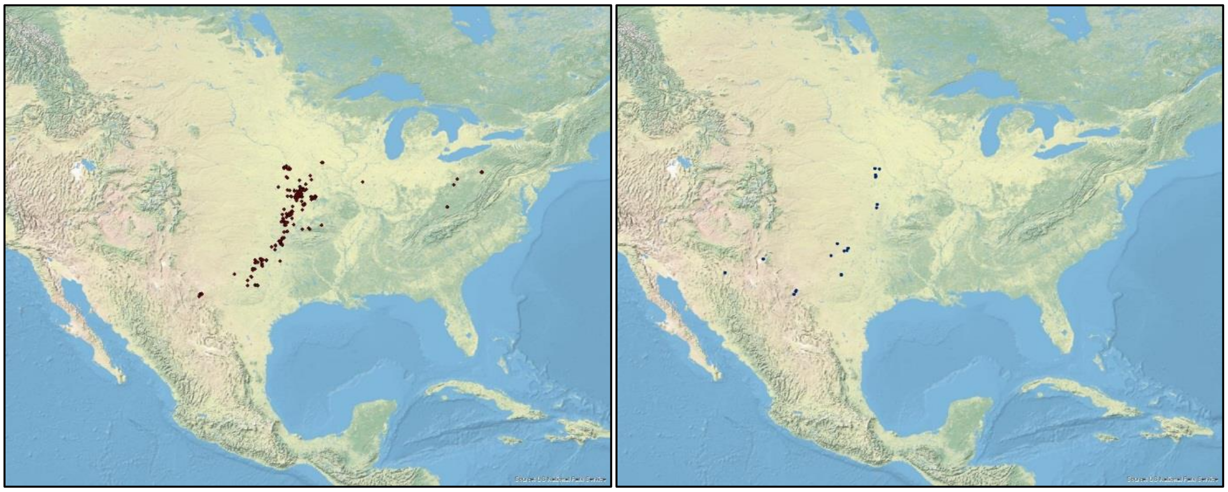


Figure 2: Distribution of Pennsylvanian nautiloid and ammonoid data points (red) and Permian nautiloid and ammonoid data points (blue) across the Midcontinent region of the United States. Plotted using *ArcGIS v. 10.3* software at 1: 20,000,000.

Ranges were reconstructed using minimum bounding geometry; convex hulls or buffers were given to every specimen occurrence point in each species and these shapefiles were re-projected in 'South America-Albers Equal Area Conic'. This model was used to accommodate the rotation of species occurrence coordinates into the southern hemisphere during the Late Paleozoic. Species with three or more occurrence points were given a convex hull that spanned the entire area between occurrences. In this way, multiple occurrence points were combined to recreate the geographic range of a single species. Species with only one occurrence point were given a $10km^2$ buffer, while species with two occurrence points were each given a $10km^2$ buffer and combined using map geometry. This 'buffering' method gives an area to species with only one or two occurrence points and allows for incorporation of these species into biogeographic

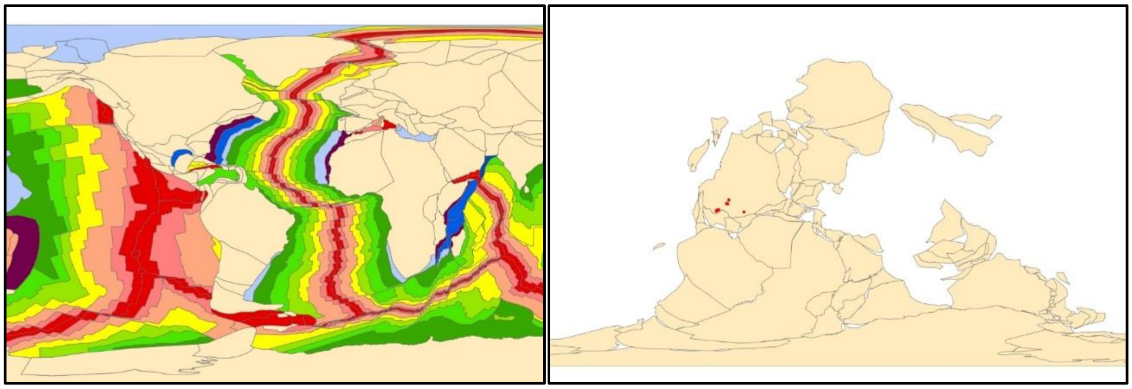


Figure 3: PaleoWeb reference map (left) and reconstructed map of *Metacoceras* sp. & *Mooreoceras* sp. occurrence points during the Virgilian (299) at 1:1,000,000,000 scale (The Rothwell Group LP, 2016).

analysis. After this step, it was possible to calculate range area for each species using map geometry. All species range values are recorded in Appendix 2: Reconstructed Range Values.

Analysis of fossil record bias:

A common concern when studying the fossil record is that there might be biases that can lead to inaccurate findings. This concern can be manifold, but the two most pertinent issues here involve incomplete sampling and/or issues of stratigraphic bias. While it is important to be cognizant of the fact that the fossil record is incomplete, it is worth recognizing that there is a large body of research that demonstrates many of the biogeographic patterns preserved in the fossil record, particularly in marine settings, represent real biological phenomena, rather than taphonomic artifacts (Heim & Peters, 2011; Myers & Lieberman, 2011; Rook et al., 2013). Further, it is also prudent to realize that sampling bias is a common issue even in studies of extant biodiversity and species distribution, and much work needs to be done in this area to alleviate the biases of the extant biota (Carrasco, 2013).

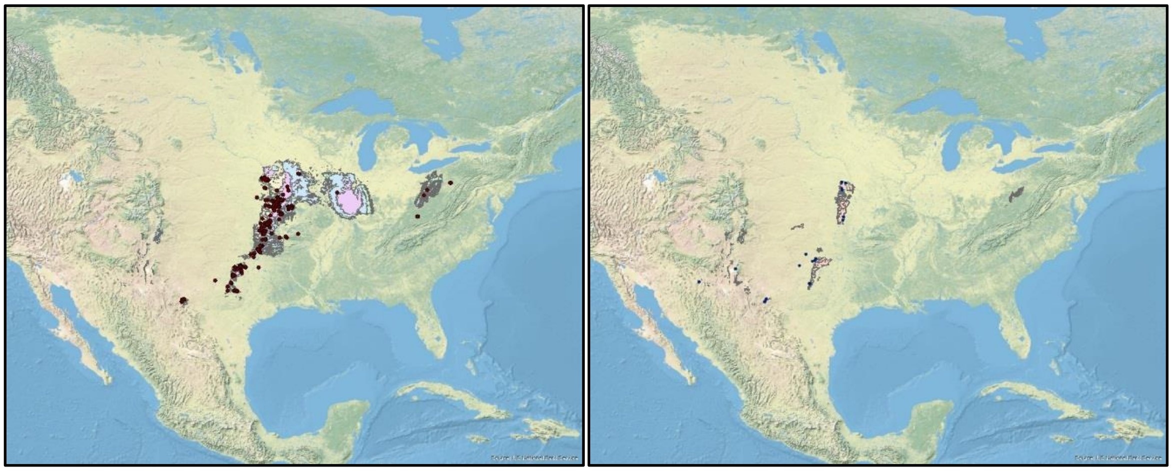


Figure 4: Distribution of Pennsylvanian nautiloid and ammonoid occurrence points with all Pennsylvanian geologic overlays (left) and distribution of Permian nautiloid and ammonoid occurrence points with Wolfcampian geologic overlay (right) using *ArcGIS v. 10.3* software at 1: 20,000,000.

I assessed whether the fossil record might be biasing my results in a few different ways. First, I considered the relationship between outcrop availability and the geographic range of Pennsylvanian and Permian cephalopods (see Figure 4). I created a percent coverage table of the range size of species overlaid against temporal outcrop availability using GIS mapping software. A low percentage of overlap between range size and outcrop area would suggest species distributions reflect 'real' biogeographic patterns while a high percentage of overlap would suggest the presence or absence of outcrop was significantly influencing our results (Myers & Lieberman, 2011). The low percentage of overlap between the cephalopod species geographic range and available outcrop suggest our results reflect 'real' biogeographic and that there is little bias within these analyses. The second test used to analyze to what extent the fossil record might be biasing results was an "n-1" jack-knifing analysis. This procedure sub-sampled species range size within each temporal bin to test the resilience of data to outliers. Mean range size estimations were generated for each temporal bin that were input into a one-way ANOVA to compare jackknife estimates and the 'real' geographic range size as an estimation of bias (Myers

& Lieberman, 2011; Myers et al., 2013). The results of the Jackknife bias estimator test and the secondary ANOVA indicate no bias within these analyses (see Statistical Appendix: Analysis of Bias section for complete printout).

Statistical Analyses:

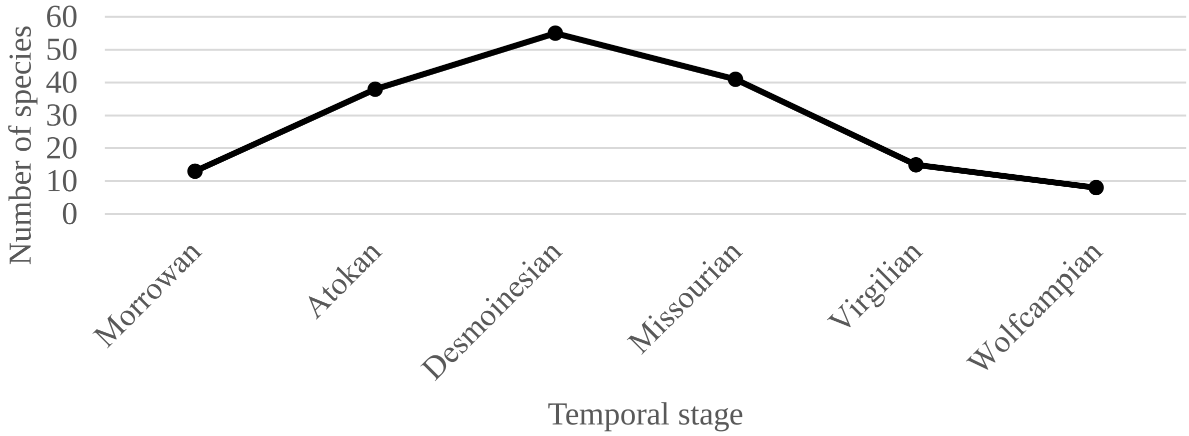
All statistical analyses were performed using Minitab® Statistical Software *Minitab* v. 17 and *R-Studio Version 3.4.0 (2017-04-21 "You Stupid Darkness").* Geographic range data were analyzed separately across all cephalopods, as well as individually for nautiloids and ammonoids. Species geographic range size data was tested for normality within each temporal stage through Anderson-Darling normality test and review of histograms of data distribution throughout temporal stages. The Anderson-Darling normality test revealed that the geographic range size data distribution within each temporal stage was not normally distributed ($p<0.005$). Further, review of histograms revealed that distributions were left skewed across all temporal stages within every data grouping. (For a complete output of histograms and Anderson-Darling normality test see Appendix 1: Statistical Analyses; Tests for Normality.) Data was transformed using the log-transformation to normalize data; further, non-parametric analyses were utilized on untransformed data to account for non-normality and to minimize assumptions. Descriptive statistics for non-transformed data and non-transformed data are contained in Appendix 1: Statistical Analyses; Descriptive Statistics Table 1.1, 1.2, and 1.3 and Table 2.1, 2.2, and 2.3, respectively.

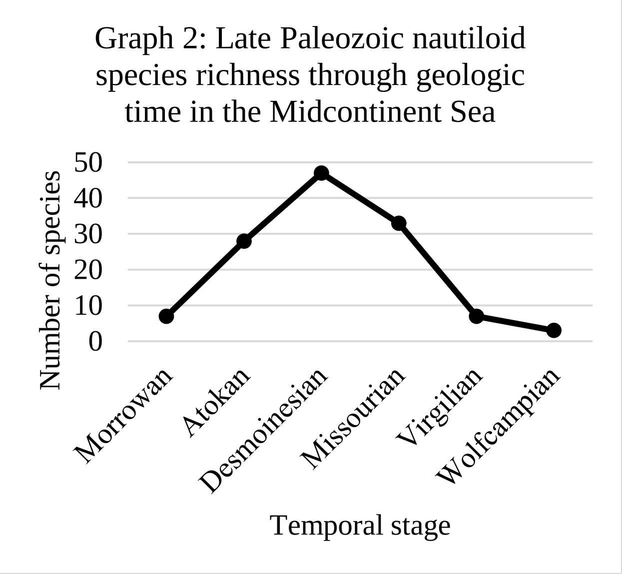
Statistical analyses were performed on both transformed and non-transformed data. Analyses performed on non-transformed data used the Mann-Whitney U test, and the Kolmogorov Smirnov test. By contrast, the two-sample t-test, ANOVA, and analyses considering the relationship between speciation and extinction rates and geographic range (mentioned below) were performed using the transformed data set. Speciation and extinction rates were calculated for nautiloids using the formula presented in Rode & Lieberman (2005); this was implemented using *Excel*. Correlations between geographic range size and speciation and extinction rates were assessed using the Pearson’s Rank Correlation Test.

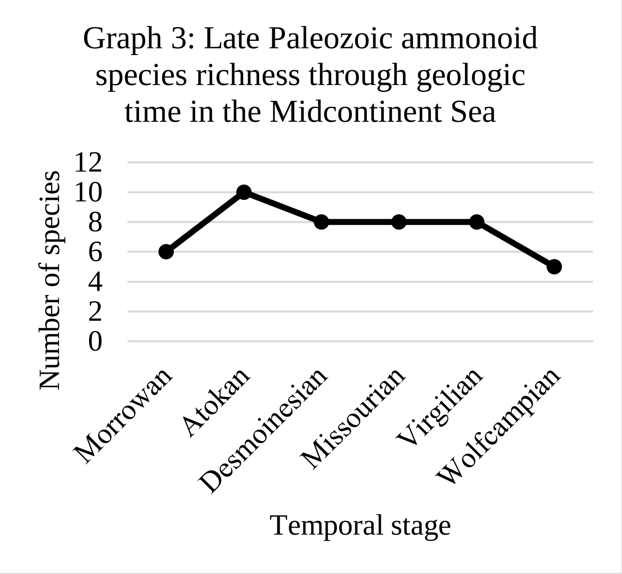
Results:

Paleoecologic Patterns in Late Paleozoic Cephalopods from the Midcontinent Sea:

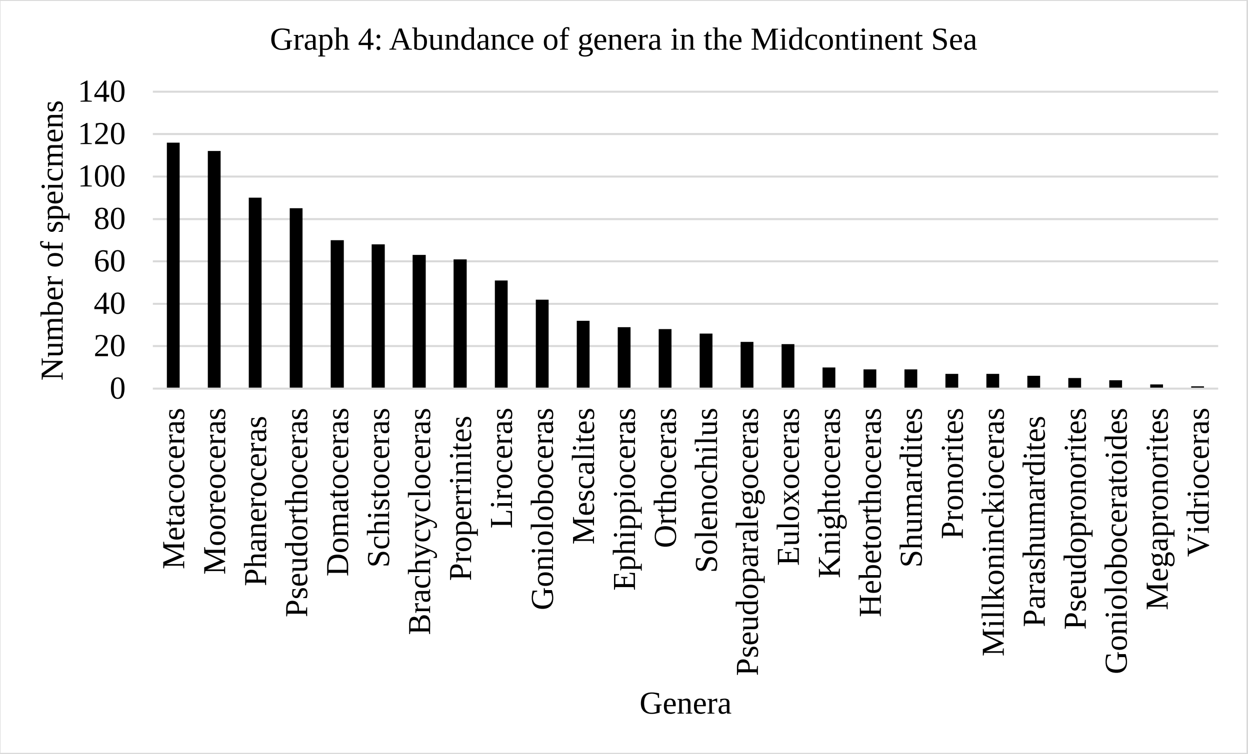
Simple occurrence metrics, such as species richness, are often used in modern ecologic studies as indicators of ecological health. Although their use in paleontological studies is more complicated due to the presumed problem of uneven sampling of the fossil record, such ‘biodiversity indices’ can reflect overall ecological trends through time, given adequate sampling. Further, various indices of biodiversity can be used to account for sampling bias. I will report the species richness as a function of temporal stage, and plot community rank abundance curves for the Midcontinent Sea to better understand the ecological deployment of Late Paleozoic cephalopods in the Midcontinent Sea.




Graph 2: Late Paleozoic nautiloid species richness through geologic time in the Midcontinent Sea


Graph 3: Late Paleozoic ammonoid species richness through geologic time in the Midcontinent Sea

Species richness is a simple measure of species diversity within a given community based solely upon sample size (Colwell, 2009). Across all cephalopods, species richness increased from the Morrowan to the Atokan, peaked in the Desmoinesian, and decreased through the Wolfcampian (see Graph 1). This trend reflects the pattern observed in the nautiloids (see Graph 2). However, the ammonoids (see Graph 3) demonstrate an earlier peak in the Atokan, followed by a Desmoinesian to Virgilian plateau, with a decrease in the Wolfcampian. Interestingly, there seems to be little association between species richness trends and glacial cycling in the Midcontinent Sea during time interval: localized glaciation is associated with an increase in species richness throughout the Morrowan to Early Desmoinesian, an interglacial period with minor glaciation is associated with a decrease in species richness throughout the Late Desmoinesian to Early Virgilian, and widespread glaciation is associated with a decrease in species richness throughout the Late Virgilian to Early Wolfcampian (Montanez & Poulsen, 2013). Of course, with these data by themselves, it is not possible to determine the causation behind this correlation. Notably, previous studies of Late Paleozoic brachiopod communities in Bolivia showed a consistent trend with glacial cycling: increased diversity during glacial periods and decreased diversity during inter-glacial periods (Badyrka et al., 2013).



A rank abundance plot was generated to better understand species occurrence throughout the Late Paleozoic (see Graph 4). While this rank abundance plot is not stage specific, it does elucidate the overall trends in species occurrence and distribution throughout the interval under analyses. Particularly, it elucidates which species were most common and which species were most rare in the Late Paleozoic- Early Permian fossil record. The most common species were *Metacoceras* while the least common were *Vidrioceras*. Note that these curves are markedly uneven compared to evenness of post- Paleozoic marine ecosystems (Clapham et al., 2006) (Wagner et al., 2006).

Group	**Genus**	**Rank**	**Individuals**	**Mean Range Size (km^2)**
Nautiloid	*Metacoceras*	1	116	4740.45
Nautiloid	*Mooreoceras*	2	112	2236.75
Ammonoid	*Phaneroceras*	3	90	8334.30
Nautiloid	*Pseudorthoceras*	4	85	34962.71
Nautiloid	*Domatoceras*	5	70	8795.53
Ammonoid	*Schistoceras*	6	68	32561.03
Nautiloid	*Brachycycloceras*	7	63	750.45
Ammonoid	*Properrinites*	8	61	78.54
Nautiloid	*Liroceras*	9	51	18776.41
Ammonoid	*Gonioloboceras*	10	42	16382.15
Ammonoid	*Mescalites*	11	32	78.54
Nautiloid	*Ephippioceras*	12	29	44590.33
Nautiloid	*Orthoceras*	13	28	1563248190
Nautiloid	*Solenochilus*	14	26	3896.72
Ammonoid	*Pseudoparalegoceras*	15	22	0.25
Nautiloid	*Euloxoceras*	16	21	3833.18
Nautiloid	*Knightoceras*	17	10	39.34
Nautiloid	*Hebetorthoceras*	18	9	0.31
Ammonoid	*Shumardites*	19	9	0.07
Ammonoid	*Pronorites*	20	7	78.54
Nautiloid	*Millkoninckioceras*	21	7	393.30
Ammonoid	*Parashumardites*	22	6	78.54
Ammonoid	*Pseudopronorites*	23	5	4497.30
Ammonoid	*Gonioloboceratoides*	24	4	0.47
Ammonoid	*Megapronorites*	25	2	78.54
Ammonoid	*Vidrioceras*	26	1	78.54

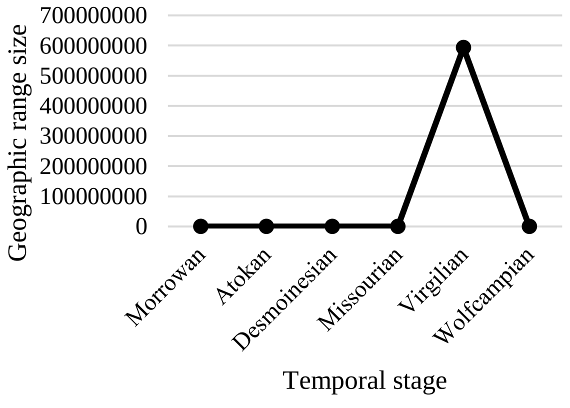
Table 3: This table depicts the rank, occurrence, and mean geographic range size for Late Paleozoic cephalopod genera in the Midcontinent Sea. This table is useful as supplementary information to the rank abundance plot depicted in Graph 4.

A Pearson correlation test was performed to test the association of occurrence points and geographic range size to assess the overall quality of the fossil record and whether the biogeographic signature recovered from the taxa studied were an artifact of the fossil record or a ‘real’ biogeographic pattern (see Appendix 1: Statistical Analyses; Correlation Analyses). Theses analyses showed no correlation between the number of occurrence points and geographic range size and provides further evidence that the biogeographic signatures of the Late Paleozoic cephalopods are ‘real’ and not an artifact of the fossil record. In the future, additional ecological analyses could be conducted on the cephalopod species from this period. For instance, ecological niche modeling would be worthwhile. Further, in conjunction with information that could be derived from phylogenetic analyses, it might be possible to look at the relationships between inferred generalist and specialist species, and see how these differ in their patterns of taxonomic turnover.

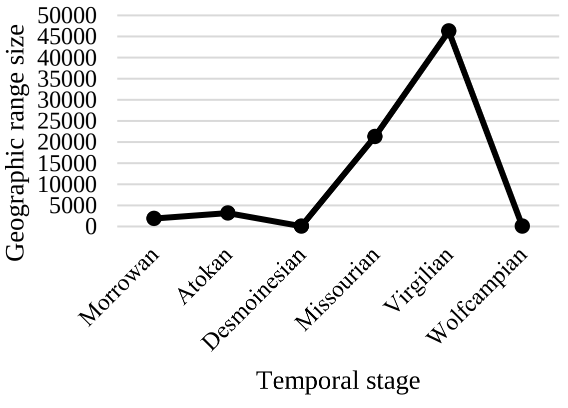
Paleobiogeographic Patterns in Late Paleozoic Cephalopods from the Midcontinent Sea:

Several tests were used to address the degree to which geographic range size changed through geologic time. First, plots of the mean geographic range size for each temporal bin (see Graph 5 & 6) shows a marked increase in mean ammonoid and nautiloid range size during the Missourian and Virgilian stages. This range expansion loosely correlates with a time of sea-level rise and warming during the inter-glacial period between Late Desmoinesian to Early Virgilian (Isbell, 2003; Montanez & Poulsen, 2013).

Graph 5: Nautiloid species mean geographic size through geologic time (km^2)



Graph 6: Ammonoid species mean geographic size through geologic time (km^2)



Mann-Whitney U Tests were used to compare the medians of geographic range data between temporal stages separately across all cephalopods, as well as individually for nautiloids and ammonoids (see Appendix 1: Statistical Analyses; Mann-Whitney U Tests). None of these tests found statically significant changes (at $P \leq 0.05$) in median geographic range size through time. A two-sample t-test was also performed to detect statistically significant differences in the mean geographic range size values between temporal stages, using log-transformed data (see Appendix 1: Statistical Analyses; Two-Sample T-tests). Again, none of these tests founds statistically significant changes (at $P \leq 0.05$) in mean geographic range size though time. Furthermore, a One-Way ANOVA (without the assumption of equal variance) was used to test the effect of temporal stage on log-transformed mean geographic range size across all cephalopods, as well as individually for nautiloids and ammonoids (see Appendix 1: Statistical Analyses; ANOVA). Again, no statistically significant effect (at $P \leq 0.05$) was found. Finally, a Kolmogorov-Smirnov test was used to compare the distribution of data points within each grouping (see Appendix 1: Statistical Analyses; Kolmogorov Smirnov) (Minitab Inc., 2016), but no statistically significant difference in distribution (at $P \leq 0.05$) was found.

Analysis of Macroevolutionary Rates in Late Paleozoic Cephalopods from the Midcontinent Sea:

Speciation and extinction rates were also calculated (see Table 4) to better understand macroevolutionary dynamics in cephalopods from the Late Paleozoic Midcontinent Sea. The specific aim was to uncover any association between changing climate and evolution. Macroevolutionary rates were calculated using the following equation, presented in Foote (2000) and Rode and Lieberman (2005):

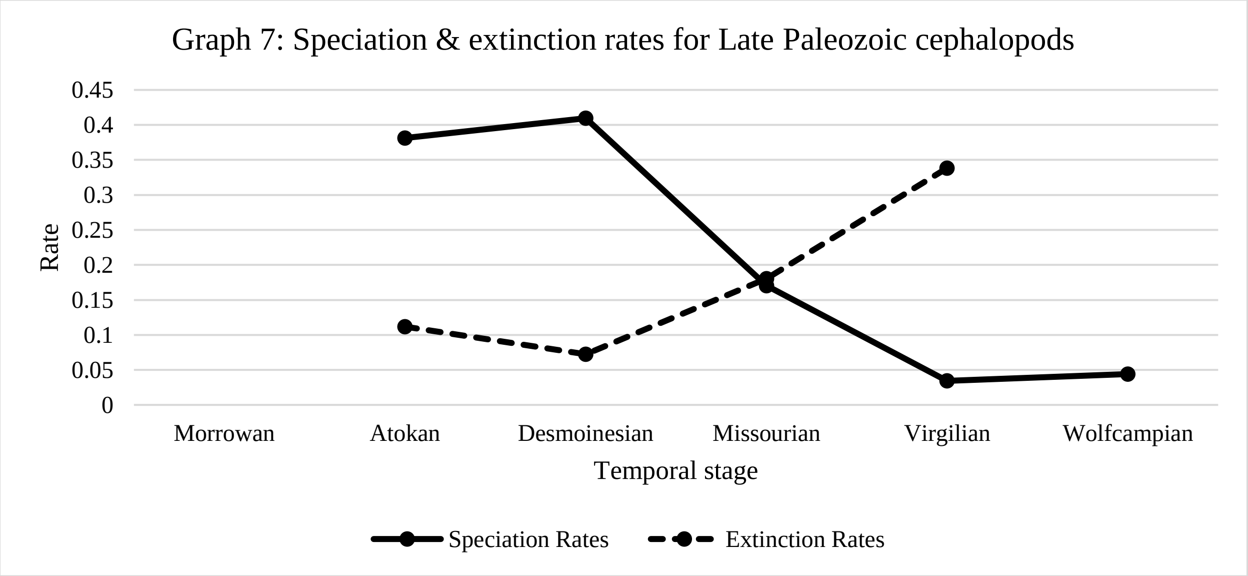
$$N_f=N_0e^{rt}$$

In this equation, N_0 is the species richness at the beginning of a temporal bin, N_f is the species richness at the end of a temporal bin, t is the duration of a temporal bin, and r is the total rate of diversity change. Species richness values (N_f) were determined for each temporal bin and were parsed into ‘carry-over’ (N_0) and ‘new’ species richness values to ensure the accuracy of speciation and extinction rate calculation. In this way, it was possible to calculate the rate of diversity change between bins; $r_{Atokan} = (\ln N_{0\text{-}Desmoinesian} - \ln N_{0\text{-}Atokan}) / t_{Atokan}$. Speciation rate within each temporal bin was calculated using the equation; $S_{Atokan} = (\ln N_{f\text{-}Atokan} - \ln N_{0\text{-}Atokan}) / t_{Atokan}$, and extinction rate within each temporal bin was calculated using the equation; $E_{Atokan} = S_{Atokan} - r_{Atokan}$ for each temporal stage (Foote, 2000; Rode & Lieberman, 2005).

An important caveat to the calculation of speciation rates is that many of the species used in these analyses belong to genera that were widely distributed beyond the Midcontinent during the Late Paleozoic. None of the species considered in these analyses seem to have a range extending beyond the region considered but their close relatives do. It is conceivable that although speciation events and rates are treated as occurring *in situ*, this might not always be the case. Instead, some speciation events could be occurring outside of the Midcontinent with subsequent invasion events into that region. These invasions would appear as *in situ* speciation events, although these events were not. In the absence of phylogenetic hypotheses for the many genera considered (which would require revisionary systematic work), it is not possible to currently consider this phenomenon. Further, a related phenomenon could affect the calculation of extinction rates; at times, extinction events in the Midcontinent Sea might be local extinctions or emigration to other regions. As mentioned previously, it does not appear that any of the species considered occur outside of the Midcontinent Sea but the taxonomic literature and quality of photographs make precise taxonomic determinations challenging. One final caveat worth noting: Due to the dependence of calculations on diversity metrics from both adjacent stages, it was not possible to accurately calculate the rate of biodiversity change, extinction, or speciation rate, for the first stage considered, the Morrowan, nor the rate of biodiversity change or extinction rate for the last stage considered, the Wolfcampian. (These values are shown as "0" in Table 4.) While it might have been possible to infer the speciation and extinction rates using other methods, to do so would exaggerate the significance of 'edge effects' (Foote, 2000).

Stage	**Species Richness**	**No**	**Nf**	**Duration**	**R**	**S**	**E**
Wolfcampian	13	7	13	14	0	0.044217086	0
Virgilian	38	32	38	5	-0.303965151	0.034370051	0.338335202
Missourian	55	33	55	3	-0.01025722	0.170275208	0.180532427
Desmoinesian	41	12	41	3	0.337200304	0.409555139	0.072354835
Atokan	15	7	15	2	0.26949825	0.381070026	0.111571776
Morrowan	8	0	8	6	0	0	0

Table 4: This table reflects the speciation and extinction rates calculated across all cephalopods. The equations used come from Foote (2000) and Rode & Lieberman (2005).



Speciation and extinction rate were calculated for the Atokan, Desmoinesian, Missourian, and the Virgilian periods across all cephalopods (see Figure 11) and within ammonoid and nautiloid groups. Across all cephalopods, speciation rates were high in the Atokan and Desmoinesian and fell through the Virgilian while extinction rates were low in the Atokan and Desmoinesian and rose through the Virgilian stage. This trend in speciation and extinction rates is also seen in isolation within both the ammonoid and nautiloid groups (see Appendix 1: Statistical Analyses; Speciation & Extinction Rate Calculations). Essentially, when speciation rate is high, extinction rate is low, and when speciation rate is low, extinction rate is high: Precisely the opposite of the pattern you would expect from an ecological opportunity model of speciation (Simões et al., 2016).

The Relationship between Biogeography and Macroevolutionary Rates of Late Paleozoic Cephalopods:

The extent to which geographic range size was correlated with speciation and extinction rates of cephalopods within the Late Paleozoic Midcontinent Sea was examined using the Pearson correlation test in *Minitab 17*. Recall that plotting of the mean geographic range size for each temporal bin showed a marked increase in mean cephalopod range size during the Missourian and Virgilian stages; geographic range expanded after the Desmoinesian and shrank after the Virgilian (see Figures 6 & 7). Moreover, across all cephalopods, speciation rates were high in the Atokan and Desmoinesian and fell through the Virgilian while extinction rates were low in the Atokan and Desmoinesian and rose through the Virgilian stage. Thus, there is seemingly no direct association between geographic range and speciation rate or geographic range and extinction rate and statistical analyses showed no significant (at $P \leq 0.05$) correlation between evolutionary rates and range size across temporal stages either across all cephalopods or within nautiloids and ammonoids (see Appendix 1: Statistical Analyses; Correlation Analyses).

Discussion:

A premise regarding the relationship between biogeography and macroevolution is that geographic range often plays a key role in determining species survival. Indeed, many paleontological studies have identified a positive relationship between geographic range size and species survivorship, i.e., that species with larger geographic ranges tend to outlive species with more narrow geographic range sizes through evolutionary time (Stanley, 1990; Rode & Lieberman, 2004; Stigall & Lieberman, 2006; Payne & Finnegan, 2007; Stigall, 2010; Harnik, 2011; Hopkins, 2011) For the remainder of this section, I will, again, summarize the results of statistical tests and discuss their implications for our understanding of the biotic response of cephalopods from the North American Midcontinent Sea to the changing climate regime of the LPIA.

Together, the results of the Mann Whitney U Test, Two-Sample T-Test, and the ANOVA imply no change in mean geographic range size though geologic time. Previous analyses have found that geographic range size is affected by fluctuations in climate regimes in both terrestrial and marine organisms through geologic time (Rode & Lieberman, 2004; Dimichele et al., 2009; Falcon-Lang & DiMichele, 2010). There are a few different modes of change in geographic range size that have been characterized into three categories: gradual range shifts, dispersal jumps, and range collapse (Brown et al., 1996). In terrestrial ecosystems of the Late Paleozoic, there is a recurrent pattern of geographic range shifting and collapse within vegetational regimes through glacial and interglacial periods during the Late Paleozoic (Dimichele et al., 2009; Falcon-Lang & DiMichele, 2010). While few studies on the biogeographic patterns of marine ecosystems of the Late Paleozoic focus specifically on range size, there is a marked geographic range shift in the latitudinal distribution of brachiopods (Powell, 2007) and range collapse (Leighton, 2005) that were directly correlated to regional climate change.

By contrast, the results from the analyses presented here suggest that mean (and median) cephalopod range size did not significantly fluctuate through time, despite significant changes in species richness throughout the Pennsylvanian and Early Permian, as well as repeated events of glacial cycling in the North American Midcontinent Sea. It is difficult to generalize the exact mode of change in geographic range size utilized in ammonoid and nautiloid species. It seems that pelagic organisms seem to be having a different type of response relative to the benthic (at least as adults) brachiopods. Thus, it seems that the increase in diversity within this ecosystem is not associated with a decrease in individual species geographic range (see Appendix 1: Statistical Analyses; Correlation Analyses). To examine the connection between species' niches and geographic range in the Midcontinent Sea, additional approaches would need to be applied, such as ecological niche modeling (e.g., Saupe et al. 2015).

The seeming 'flip-flop' of macroevolutionary rates observed herein for the cephalopods during the Pennsylvanian is intriguing considering the typical characterization of Pennsylvanian rates of evolution as 'sluggish' or 'stolid' (across all marine animals). Sepkoski (1998) formalized the notion that there was a marked decline in evolutionary rates of Carboniferous and Permian marine faunas. Stanley & Powell (2003) identified low mean macroevolutionary rates and a weak biotic rebound for marine invertebrate taxa of the LPIA. The results from the analyses presented may indicate that macroevolutionary rate, at least within Late Paleozoic cephalopods, were more dynamic than previously thought. This is perhaps not surprising given that cephalopods are likely to be fairly evolutionarily volatile (Lieberman & Melott, 2013) relative to many other marine invertebrate groups, and thus 'generally' have higher rates of speciation and extinction. Notably, species richness metrics for cephalopods do follow speciation and extinction rates throughout this period: richness increases as speciation rates are high and extinction rates are low throughout the Morrowan to Desmoinesian; richness decreases as extinction rates become high and speciation rates fall throughout the Missourian to Wolfcampian. It could ultimately be the case that speciation and extinction rates, as well as species richness, are tracking glacial cycles within the Midcontinent Sea. In particular, speciation rates were relatively higher and extinction rates were relatively lower during warm interglacial periods; whereas extinction rates were relatively higher and speciation rates were relatively lower during glacial periods, which matches aspects of the Turnover Pulse phenomenon identified by Vrba (1985). In the case of the cephalopods, it would be necessary to create a detailed stratigraphic-temporal map of *within* stage glacial cycles throughout the Late Paleozoic to precisely examine the interplay of glacial cycling with macroevolutionary rates and cephalopod diversity. The analyses conducted herein could only focus at the stage level, and unfortunately not within, given the constraints on species distribution, stratigraphic correlation, and chronostratigraphic resolution. However, perhaps at some point a more detailed level of resolution may be possible.

The results observed herein pertaining to the lack of association between geographic range size and macroevolutionary rates are worth considering in the context of previous studies. For instance, Rode & Lieberman (2004) found that Devonian brachiopods and bivalve species had speciation rates that decreased as geographic range size increase. By contrast, Myers et al. (2013) found no relationship between geographic range size and turnover rate in invertebrates of the Cretaceous Interior Seaway. Dunhill & Wills (2015) found that geographic range size was typically correlated with extinction rate, though not during times of mass extinction. The findings of the present study seem to most closely match those of Myers et al. (2013); that is, there was no statistically significant relationship between geographic range size and turnover rate in cephalopods from the Late Paleozoic Midcontinent Sea. There may be a few explanations for this finding. First, it may be that, ecologically, cephalopod species were not significantly affected by the glacial cycling within the Midcontinent Sea, nor were they significantly interacting ecologically with one another. Geographic range size (G-space) may be related to ecologic niche space (E-space) occupied (Brown et al., 1996; Peterson, 2011) though not always in a direct way, see discussion in Saupe et al. (2015) and Lieberman & Saupe (2016). To investigate this more fully, it would be useful to conduct ecological niche modeling analyses to better understand utilization of niche space within the ecosystem of the Midcontinent Sea.

A second possible explanation, perhaps coupled to the first, is that since cephalopods are highly mobile they can more easily occupy a greater portion of their potential range, relative to taxa that are benthic (at least as adults), such as brachiopods. Further, perhaps the available potential range of cephalopod species does not change much in glacial relative to interglacial regimes. It has been shown that marine biogeographic dynamics can be affected by the ease of dispersal across large areas (Carr et al., 2003; Hendricks et al., 2008). The nautiloids and ammonoids within the Midcontinent Sea may have had broad ecologic niches and thus been tolerant to the fluctuating climate regime of the LPIA. Moreover, the glacial cycling of the LPIA had a negligible effect on their geographic distribution through geologic time. This may seem unlikely given the vast fluctuations in sea level occurring at this time, but pelagic organisms may have more easily maintained consistently broad geographic range relative to benthic counterparts. As mentioned before, there is a marked global shift in marine invertebrate ranges from high latitude to low latitude environments with the onset of the LPIA (Waterhouse & Shi, 2010). The analyses presented herein did not explicitly investigate the location of geographic ranges although there does not appear to be change in a general sense across all cephalopods.

Still, a shift in the location of geographic range could still occur without a change in mean geographic range. To fully ascertain the role that pelagic lifestyle has on biogeographic patterns, it would be necessary to perform a pair-wise comparison with benthic organisms within the same geographic region and temporal stages.

A final set of explanations might be related to the issue of sampling. First, it was more difficult for the analyses presented herein to detect a relationship between geographic range size and macroevolutionary rate because speciation and extinction rates could only be calculated for four stages. This small sample size diminishes the statistical power of the analyses. Further, a common concern when studying the fossil record is that there might be biases that can lead to inaccurate findings. This concern can be manifold, but the two most pertinent issues here involve incomplete sampling and/or issues of stratigraphic bias. This secondary explanation is unlikely due to the results from the outcrop area vs. geographic range test and the jackknifing procedure. A further explanation may pertain to specimen collection methods. It may be that the way cephalopod specimens were collected or identified by paleontologists differs fundamentally from the way benthic taxa are collected and identified. Finally, the results of these analyses may be because species distribution are being examined at the scale of geological stages, the precise details of when and why species geographic ranges and turnover rates are being obscured.

Conclusion:

The Late Paleozoic Ice Age (LPIA) was the longest lived glacial period in the Phanerozoic and represents one of the only well documented transitions in Earth history from an icehouse to greenhouse climate (Montanez & Poulsen, 2013). The Pennsylvanian Midcontinent Sea was warm, tropical and hosted a diverse fauna, including fish, bivalves, brachiopods, cnidarians, and cephalopods that would have been subject to a variety of abiotic phenomena. For instance, the North American Midcontinent Sea was highly stratified, periodically anoxic, and subject to varying degrees of input from freshwater sources throughout the LPIA (Wells et al., 2007; Algeo & Heckel, 2008) and each of these would be expected to have had a significant influence over the biogeographic distribution of marine species (Stanley & Powell, 2003). The similarities between the LPIA and the Quaternary Ice Ages suggest that elucidating biogeographic patterns from Late Paleozoic taxa will be useful for enhancing our understanding of evolutionary rates and biogeographic responses during protracted intervals of glaciation, followed by icehouse-greenhouse climate transitions (Dietl & Flessa, 2011).

The analyses presented herein indicate that cephalopod species diversity did fluctuate throughout the Pennsylvanian and Early Permian and this follows the finding of other studies that examined the Late Paleozoic marine invertebrate fauna (Bonelli & Patzkowsky, 2011; Balseiro, 2016). However, contrary to studies that focused on benthic taxa, my analyses found that mean geographic range size of cephalopod species did not change through time, despite climate oscillations. Further, I found that geographic range size did not correlate with macroevolutionary rates. Finally, in the case of cephalopods, macroevolution was also less ‘sluggish’ and more ‘dynamic’ than previously characterized.

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Chapter 2: Systematic Paleontology of Ammonoidea

An important aspect of my Master’s thesis project was taxonomic inspection and analysis to determine species identifications of all specimens. These species determinations would be used as the data necessary to reconstruct species range area to infer the macroevolutionary patterns during the Pennsylvanian and Early Permian. This chapter focuses on the taxonomy of the species used in this project and includes a brief description of morphological characters used for species determinations. For this project, I focused on fossil cephalopod specimens that were both well-preserved and abundant within the museum collections at the University of Kansas to sample an array of diversity from the Midcontinent Sea. Prior to this study, the biogeographic patterns and turnover rates of the cephalopod clade within the Midcontinent region had not been examined in detail. Moreover, many of the taxa used in this study have not been the subject of taxonomic revision since before the 1950’s. Cephalopods were chosen as the focus of this analysis because they constitute an abundant and diverse pelagic organism of the Pennsylvanian and Permian ecosystems of the North American Midcontinent Sea that persisted throughout the Late Paleozoic Ice Age (LPIA) despite numerous climate oscillations (Körn et al., 2015). Further, ammonoids and nautiloids of the Pennsylvanian and Permian systems of the North America have been well described and specimens are abundant in many institutions around the United States due to their frequent use as biostratigraphic indicators in the fossil record.

Description of Ammonoidea:

Phylum: Mollusca Cuvier 1797

Class: Cephalopoda Leach 1817

Subclass: Ammonoidea Zittel 1884

Ammonoids are extinct members of the Class Cephalopoda. The wide diversity of ammonoids suggests that these organisms would have inhabited a variety of ecological niches within epi-continental seas as well as open ocean environments. Most of the ammonoids were believed to have been pelagic and can be classified as drifters, swimmers, and migrants within the water column. The remainder of organisms could be considered as demersal based on conch morphology (Westermann, 1996). Analysis of fossilized stomach contents indicates that ammonoids were carnivores feeding upon small invertebrates and other organisms within the water column (Kruta et al., 2011). The repeated occurrence of ammonoids in clusters may be indicative of spawning sites (Westermann, 1996) although it is difficult to ascertain whether the specimens used in this study are associated with these sites. Further information regarding ammonoid biology and behavior has been difficult due to the extinction of lineage and (Westermann, 1996).

Ammonoids arose in the Early Devonian and experienced numerous oscillations in diversity and abundance throughout the Carboniferous (Becker & Kullman, 1996). They have been characterized as a ‘highly volatile’ group by Lieberman & Melott (2013). The Late Paleozoic ammonoid fossil record is characterized by fluctuating diversity and abundance across the globe; an extinction event across the Mississippian-Pennsylvanian, the establishment of two highly diverse groups in Russia and the American-Midcontinent, and increase in diversity during the Early Permian, and an extinction event at the end-Permian (Körn et al., 2015). Ammonoids went extinct ~65.5 million years ago although the exact cause of this extinction is still debated (Kruta et al., 2011; Landman et al., 2015). Theories for this extinction include surface water acidification, a global collapse in oceanic primary productivity, or a predisposition to extinction because of the long-term volatility of the ammonoid group (Lieberman & Melott, 2013; Landman et al., 2015).

Comparison of Ammonoid & Nautiloid Morphology & Behaviors:

Ammonoidea and Nautiloidea have traditionally been treated as each other's closest relatives and much of their behavior and life-history has been deemed as similar for this reason. However, recent phylogenetic study has shown that Ammonoidea are more closely related to Coleoidea (Engeser, 1996). There are several plesiomorphic characters that are shared between extinct ammonoids and nautiloids. Both groups of organisms had an external shell and utilized neutral buoyancy for locomotion through internal propulsive organs. Both groups of organisms had a radula and beak, a crop, and several arms to facilitate feeding and digesting prey items (Engeser, 1996; Kruta et al., 2011). Finally, both groups utilized a direct mode of development without larval forms (Engeser, 1996). While these characters that are shared across all Cephalopoda, there are several morphological and inferred biological differences between fossil ammonoids and nautiloids that justify the separation of these groups into separate lineages. These differences include conch morphology, the morphology of propulsive organs, and the biostratigraphy of fossil remains.

Ammonoids are most readily distinguished from nautiloids by differences in conch morphology. Particularly, the aperture of the ammonoid conch is positioned above the phragmacone while nautiloid conchs are orientated in the reverse manner (Miller & Furnish, 1957). Ammonoids are characterized by a bulky conch morphology with elaborate suture patterns while nautiloids are characterized by a simple, stream-lined conch morphology with comparatively simple suture morphology. There is a marked trend towards suture folding and increasing complexity in suture patterning throughout ammonoid evolutionary history (Saunders et al., 1999). In addition to conch morphology, there are a number of differences in the morphology and position of propulsive organs. Perhaps most characteristic is the siphuncle position (the opening through the internal shell that contains propulsive organs) (Miller & Furnish, 1957). The position of the siphuncle in ammonoids is marginal while it is central (or sub-central) in nautiloids (Engeser, 1996). The hyponome (funnel for locomotion) was present in Ammonoidea however the degree of maneuverability of this funnel was most likely reduced in ammonoids compared to Nautiloidea (Engeser, 1996). Further, the number of retractor muscles, which were used to force water through the hyponome, is reduced in ammonoids and positioned on the dorso-lateral walls of the body chamber (Jacobs & Landman, 1993; Engeser, 1996). It is for these reasons, it has traditionally been thought that nautiloids were more dynamic, efficient, quick swimmers than their ammonoid counterparts (Jacobs & Landman, 1993). However, it has been established that Ammonoid mobility was directly correlated to the degree of shell-coiling and that ammonoids with a coiled shell morphology would have had comparable mobility to nautiloids (Klug & Körn, 2004).

Both nautiloid and ammonoid genera are found in a variety of paleo-environments across a variety of depths which has been interpreted as evidence for their dynamics use of warm and cold water habitats (Ritterbush et al., 2014). However, the fossil record has revealed some key differences in ammonoid and nautiloid life history strategies, particularly, in regard to developmental strategies. All Cephalopoda are interpreted to have separate sexes that reproduced sexually in ‘spawning’ events (Engeser, 1996). However, the fossil record has implied that there was a difference in reproductive strategies between groups. Particularly, numerous small ammonoid eggs have been found in clusters throughout the fossil record which strongly implies an R-Selected reproductive mode while nautiloids are known to engage in a K-selected reproductive mode (Jacobs & Landman, 1993; Engeser, 1996; Ritterbush et al., 2014). It follows that ammonoids would probably have engaged in a ‘live-fast, die young’ lifestyle as do modern organism with R-selected reproductive modes. Please reference Table 1 of Chapter 1 for a comparison of ammonoid and nautiloid characters.

Important sources regarding the terminology of ammonoid morphology includes; the Treatise on Invertebrate Paleontology Part L: Mollusca Cephalopoda Ammonoidea (Arkell et al., 1957), “A key for the description of Palaeozoic ammonoids” (Körn , 2010), and The Position of the Ammonoidea within the Cephalopoda (Engeser, 1996).

Notes on Species Determinations:

Ammonoid genera included in this study were: *Gonioloboceras, Gonioloboceratoides,* *Megapronorites, Mescalites, Properrinites, Phaneroceras, Properrinites, Pseudoparalegoceras, Schistoceras, Shumardites, Parashumardites, Pseudopronorites, Pronorites,* and *Vidrioceras*. Genera are organized first by order, (Goniatitida and Prolecanitida) then by family (Vidrioceratidae, Gonioloboceratidae, Pseudoparalegoceratidae, Schistoceratidae, Perrinitidae, Parashumarditidae, Shumarditidae, and Pronoritidae) and finally by species in alphabetical order. For each genus, the occurrence information, diagnostic characters, and taxonomic issues pertaining to the entire group will be discussed. Further, for each species, the resources used for species identifications and the specimen numbers of the research materials are included.

Resources employed for species identifications include examination of relevant publications and study of type specimens. Type specimen numbers are included if these were personally examined or were readily available through literature review. In some cases, type material has been lost and only photographs remain. All specimens utilized in this project come from the continental United States.

Repositories:

Collections from the following institutions were visited to inspect the type materials and obtain specimens for my biogeographic analyses: The Yale University Peabody Museum of Natural History (YPM), the University of Iowa Paleontological Repository (UI), and University of Kansas Museum of Invertebrate Paleontology (KUMIP). Special thanks to YPM Senior Collection Manager; Susan Butts, UI Special Collections Manager; Tiffany Adrian, and KU Collections Manager; Julien Kimmig, for their assistance in planning of respective research trips and access to type materials and additional specimens for use in my research project.

Order: Goniatitida Hyatt 1884

Family: Gonioloboceratidae Spath 1934

Genera: *Gonioloboceras* (Hyatt 1900), *Mescalites* Furnish & Glenister 1971, & *Gonioloboceratoides* Nassichuk 1975

Occurrence Information: Specimens of *Gonioloboceras* are from the Desmoinesian, Missourian, Virgilian, and Wolfcampian strata of Missouri, Oklahoma, and Texas. Specimens of *Gonioloboceratoides* are from the Desmoinesian strata of Missouri. Specimens of *Mescalites* are from the Wolfcampian strata of New Mexico. These genera are known throughout the Pennsylvanian and Permian strata of the United States, Canada, Russia, and China (Furnish et al., 2009).

Diagnostic features: *Gonioloboceras, Gonioloboceratoides,* and *Mescalites* are characterized by a discoidal, involute conch and are most easily distinguished through comparison of shell ornamentation and suture shape. The diagnostic features used to distinguish species are the morphology of the ventral lobe, particularly the degree of lobe constriction and angularity, and the spacing between lateral lobes and saddles on the umbilical shoulders as well as the lateral side of the conch.

Figure 5: KUMIP-65780 & 65781 *Gonioloboceras goniolobum*.

Genus: *Gonioloboceras* (Hyatt 1900)

Type Species: *Goniatites goniolobus* Meek 1877

Gonioloboceras bridgeportense Plummer & Scott 1937

- *Gonioloboceras bridgeportense* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516. (p. 33 fgs. 1-4)

Species Determination: The species description and holotype photos in Plummer & Scott (1937) (p. 33 fgs. 1-4) proved useful for species determinations. The holotype is reportedly maintained at the Bureau of Economic Geology at the University of Texas (University of Texas P-7604). The diagnostic features of *G. bridgeportense* are the compressed whorl, wide ventral lobes, and wide venter in comparison with other species.

Material Examined: YPM IP-015930

Gonioloboceras goniolobum (Meek 1877)

SYN *Goniatites goniolobus* Meek 1877

- *Goniatites goniolobus* Meek, F. B. (1877). Part I. Paleontology. *Report of the Geological*

Exploration of the Fortieth Parallel 4, (1877),1-197.

- *Gonioloboceras goniolobum* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52,1-211.
- *Gonioloboceras goniolobum* Elias, M. K. (1938). Revision of Gonioloboceras from Late Paleozoic Rocks of the Midcontinent Region. *Journal of Paleontology,* 12(1), 91-100.

Species Determination: The original holotype specimen was reported lost by Maxim K. Elias. Elias (1938) include a photograph of a specimen that he treated as *G. goniolobum*. These photographs were used as the primary material for species determinations (see Elias, 1938, p. 33 fgs. 1-4). The diagnostic features of *G. goniolobum* are the compressed whorl, angularity of the ventral lobe, and angularity of the relatively short ventral saddles in comparison to other species.

Material Examined: KUM IP- 50268, 50494, 50495, 50496, 50587, 50589, 65780, 65781, 150984, 151231, 151232, 151234, 151236, 151237, 151238, 151239, 151240; UI- 001054, 1069, 8884B, 008884C, 010443, 10735, 13813, 51484; YPM IP-147525, 376326, 376327

***Gonioloboceras gracellenae* Miller & Cline 1934**

- *Gonioloboceras gracellenae* Miller, A. K. & Cline, L. M. (1934). The Cephalopod Fauna of the Pennsylvanian Nellie Bly Formation of Oklahoma. *Journal of Paleontology*, 8, 171-185 (p. 28 fgs. 14-18)
- *Gonioloboceras gracellenae* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III,* 3701, 1-516.

Species Determination: The species descriptions in Miller & Cline (1934) and Plummer & Scott (1937) (p. 28, fgs. 14-18) as well as review of the type material maintained at the UI proved useful for species determinations. This species closely resembles *G. welleri*. It differs from *G. welleri*, however, in having a more rounded ventral lobe. The diagnostic features of *G.*

gracellenae are the wide rounded ventral lobe, very short first saddle, and a narrower umbilicus (Plummer & Scott, 1937).

Holotype Material: UI-000631

Paratype Materials: UI-000632 & 000632A

Material Examined: YPM IP-015302

Gonioloboceras welleri Smith 1903

- *Gonioloboceras welleri* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211.
- *Gonioloboceras welleri* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516. (p. 33 fgs. 10 & 11 and p. 34 fgs. 1-5)
- *Gonioloboceras welleri* Elias, M. K. (1938). Revision of Gonioloboceras from Late Paleozoic Rocks of the Midcontinent Region. *Journal of Paleontology*, 12(1), 91-100. (p. 19 fgs. 1-8 and p. 20 f. 6a & 6b)

Species Determination: The species descriptions and photographs in Plummer & Scott (1937) (p. 33 fgs. 10 & 11 and p. 34 fgs. 1-5) as well as photographs of the holotype and paratype specimens in Elias (1938) (p. 19 fgs. 1-8 and p. 20 f. 6a & 6b) proved useful for species determinations. The diagnostic features of *G. welleri* are the wide rounded ventral lobe, very short first saddle, and narrow umbilicus.

Material Examined: KUMIP- 290330, 50586, 50588; UI-13808; YPM IP- 015062, 015060, 015305, 114193, 229940

Genus: *Gonioloboceratoides* Nassichuk 1975

Type Species: *Gonioloboceratoides curvatus* Nassichuk 1975

***Gonioloboceratoides eliasi* (Miller & Owen 1939)**

SYN *Gonioloboceras eliasi* Miller & Owen 1939)

- *Gonioloboceras* eliasi Miller, A. K. & Owen, J. B. (1939). An ammonoid fauna from the lower Pennsylvanian Cherokee Formation of Missouri. *Journal of Paleontology*, 13(2), 141-162. (p. 17 fgs. 6-13)
- *Gonioloboceratoides eliasi* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic Archipelago. *Geological Survey of Canada Bulletin*, 237, 1-240.

Species Determination: The species descriptions and photographs in Miller &Owen (1939) (p. 17 fgs. 6-13) as well as review of the type material maintained at the UI proved useful for species determinations. This species is most easily distinguished from other species by being an intermediate in size, shape, and width of the ventral lobe relative to *G. goniolobum* and *G. welleri*. The key characters of *G. eliasi* are the narrow umbilicus, a flat ventral portion of the conch, and the broader, more rounded appearance of suture lobe pattern.

Material Examined: UI- 013525, 013526, 013527, 013528, 013529, 013530

Genus: *Mescalites* Furnish and Glenister 1971

Type Species: *Gonioloboceras discoidale* Böse 1920

***Mescalites discoidalis* (Böse 1920)**

SYN *Gonioloboceras* discoidale Böse 1920

- *Gonioloboceras discoidale* Böse, E. (1920). On ammonoids from the Abo Sandstone of

New Mexico and the age of the beds which contain them. *American Journal of Science*, 49(289), 51-60.

- *Gonioloboceras discoidale* Elias, M. K. (1938). Revision of Gonioloboceras from Late Paleozoic Rocks of the Midcontinent Region. *Journal of Paleontology*, 12(1), 91-100.
- *Mescalites discoidalis* Furnish, W. M. & Glenister, B. F. (1971). Permian Goniolobоceratidae (Ammonoidea). *Smithsonian Contributions to Paleobiology*, 3, 301-312.

Species Determination: Review of the type material maintained at the YPM proved essential for species determinations. *Mescalites* features are more similar to *Gonioloboceras* than to *Gonioloboceratoides*. The key characters of *M. discoidalis* are cross section shape, the presence of an additional ventral element on the ventral lobe of the suture pattern, and the presence of a furrow on the lateral sides of the conch.

Paralectotype Material: YPM IP-013081-013083, 014022-014058

Material Examined: YPM IP-013081, 013083, 014022-014058

Notes on the taxonomy of *Gonioloboceras*, *Gonioloboceratoides,* and *Mescalites*: Elias (1938) argued that there were only two species within *Gonioloboceras*. He treated *G. gracellenae* and *G. discoidale* as immature forms of *G. welleri* or *G. goniolobum*. He made no mention of *G. bridgeportense*. Despite this claim, both *G. gracellenae* and *G. discoidale* have been used since 1938 and there are differences in morphological characters that justify the continued use of *G. gracellenae* and *G. discoidale. Gonioloboceras eliasi* (Miller & Owen 1939) was transferred to *Gonioloboceratoides eliasi* by Nassichuk (1975) thus creating *Gonioloboceratoides*. According to Furnish & Glenister (1971), *Gonioloboceras discoidale* (Böse 1920) is recognized as *Mescalites discoidalis* by Furnish & Glenister (1971).

Family: Pseudoparalegoceratidae Librovich 1957

Genera: *Pseudoparalegoceras* Miller 1934 & *Phaneroceras* Plummer & Scott 1937

Occurrence Information: Specimens of *Pseudoparalegoceras* come from Desmoinesian, Atokan, and Morrowan strata of Oklahoma, Arkansas, and Texas. Specimens of *Phaneroceras* come exclusively from the Atokan strata of Oklahoma. No specimens with usable data were obtained from younger strata. These genera are widely distributed throughout Pennsylvanian strata in the United States, Russia, southern Europe, and Africa (Miller & Furnish, 1940; Furnish et al., 2009).

Diagnostic features: *Pseudoparalegoceras* and *Phaneroceras* are characterized by a smooth coiled conch with a wide umbilicus and a simple suture line without accessory elements. Species of *Pseudoparalegoceras* and *Phaneroceras* were most easily distinguished using comparisons of the umbilicus width, suture patterning, second lobe height and width, and shell ornamentation. Of particular use was the key to North American species of *Pseudoparalegoceras* created by Mackenzie Gordon (1964). His publication gave highly detailed criteria for assigning specimens to species, including: Dimensions of umbilicus width to conch diameter; shell morphologies; and detailed sketches of shell patterning. Ultimately, despite his questionable assignment of *P. williamsi* and *P. compressum* to *Phaneroceras,* his key was one of the most useful resources for determining species identification in both genera.

Figure 6: KUMIP-51102 *Phaneroceras kesslerense*.

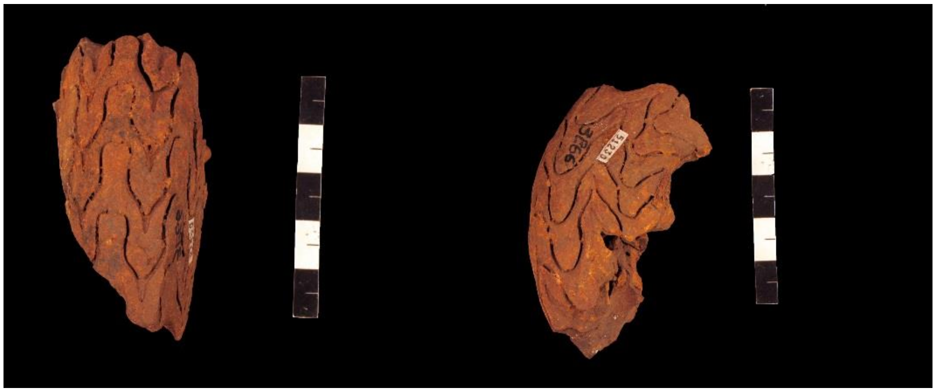

Figure 7: KUMIP-51230 *Pseudoparalegoceras brazoense*.

Genus: *Phaneroceras* Plummer & Scott 1937

Type Species: *Gastrioceras compressum* Hyatt 1891

Phaneroceras compressum (Hyatt 1891)

SYN *Gastrioceras compressum* Hyatt 1891; *Pseudoparalegoceras compressum* Miller & Furnish 1940

- *Gastrioceras compressum* Hyatt, A. (1891). Carboniferous cephalopods. *Texas Geological Survey Second Annual Report*, 1890, 327– 356. (pg. 355 fgs. 57-59)
- *Gastrioceras compressum* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211 (p. 9 fgs. 1-3)

- *Phaneroceras compressum* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Pseudoparalegoceras compressum* Miller, A. K. & Furnish, W. M. (1940). Studies of Carboniferous Ammonoids: Parts 5-7. *Journal of Paleontology*, 14, 521-543.
- *Pseudoparalegoceras compressum* McCaleb, J. A. (1963). The Goniatite Fauna from the Pennsylvanian Winslow formation of northwest Arkansas. *Journal of Paleontology,* 37(4), 110-115.
- *Phaneroceras compressum* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic Archipelago. *Geological Survey of Canada Bulletin*, 237, 1-240.

Species Determination: The species key in Gordon (1964, p. 29 fgs. 1-4) and the suture pattern drawings in Miller & Furnish (1940) proved useful for species determinations. Further, review of the type material maintained at the UI also proved useful for species determinations. The diagnostic features of *P. compressum* are the presence of the umbilical lobe centered on the umbilical wall and the width of the umbilicus as half the diameter of the conch.

Material Examined: UI-009775,013991,17062, 61769, 61770; KUM IP- 51101, 51116, 51126, 51127, 51133, 51147, 51168, 51169, 51197, 51211, 51217, 51234, 51244, 50375, 50365, 50368, 50420, 50431, 50438, 50457, 50367

Phaneroceras kesslerense **(Mather 1915)**

SYN *Gastrioceras kesslerense* Mather 1915; *Phaneroceras kesslerense* Miller & Moore 1938; *Pseudoparalegoceras williamsi* Miller & Downs 1948; *Pseudoparalegoceras (Phaneroceras) kesslerense* Gordon 1964

- *Gastrioceras kesslerense* Mather, K. F. (1915). The fauna of the Morrow group of

Arkansas and Oklahoma. *Bulletin of Science Laboratories of Denison University*, 18, 59–284.

- *Phaneroceras kesslerense* Miller, A. K. & Moore, A. (1938). Cephalopods from the Carboniferous Morrow group of northern Arkansas and Oklahoma. *Journal of Paleontology*, 22(4), 341-354. (p. 44 fgs. 1 & 2)
- *Pseudoparalegoceras williamsi* Miller, A. K. & Downs, R. (1948). A Cephalopod Fauna from the Type Section of the Pennsylvanian "Winslow Formation" of Arkansas. *Journal of Paleontology*, 22(6), 672-680. (p. 101 f. 5, p. 102 fgs. 1-5, p. 103, fgs. 6-9)
- *Pseudoparalegoceras (Phaneroceras) kesslerense* Gordon, M. (1964). Carboniferous Cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322. (p. 29 fgs. 5-17)
- *Phaneroceras kesslerense* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic Archipelago. *Geological Survey of Canada Bulletin*, 237, 1-240.

Species Determination: The species key in (1964) (p. 29 fgs. 5-17 & 84) proved useful for species determinations. The diagnostic features of *P. kesslerense* are the presence of the umbilical lobe centered on the umbilical wall and the width of the umbilicus as one-eighth the diameter of the conch.

Material Examined: KUMIP- 50354, 50361, 50362, 50366, 50370, 50391, 50399, 50413, 50415, 50416, 50434, 50437, 50447, 50448, 50449, 50450, 50451, 50455, 50459, 50460, 51102, 51106, 51115, 51117, 51119, 51121, 51125, 51128, 51136, 51138, 51239, 51150, 51156, 51157, 51158, 51161, 51165, 51170, 51175, 51176, 51180, 51182, 51185, 51186, 51187, 51189, 51207, 51221, 51224, 51246, 51247, 51249, 65631, 65632, 65633, 65634; UI-9741, 9743, 9744, 9745, 9747-

9749; YPM IP-010160

Genus: *Pseudoparalegoceras* Miller 1934

Type Species: *Gastrioceras russiense* Tsvetaeva 1888

Pseudoparalegoceras brazoense Plummer & Scott 1937

- *Pseudoparalegoceras brazoense* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516. (p. 10 fgs. 10-14)

Species Determination: The species descriptions and figures in Plummer & Scott (1937) (p. 10, fgs. 10-14) and the suture pattern drawings in Miller & Furnish (1940) proved useful for species determinations. Further, I used the undefined figured specimens from the UI for comparison with other specimens. The diagnostic features of *P. brazoense* are the presence of the umbilical lobe centered outside of the umbilical wall and the presence of a number of fine growth lines on the conch surface.

Material Examined: KUM IP-50374, 50376, 50377, 50378, 50394, 50412, 50421, 51103, 51104, 51113, 51135, 51164, 51179, 51188, 51208, 51210, 51213, 51230, 51252; UI-1432, 9814, 013992

Notes on the taxonomy of *Pseudoparalegoceras* & *Phaneroceras*: There is a dispute regarding the placement of specimens into *Pseudoparalegoceras* or *Phaneroceras*. This debate seems to have arisen after *Phaneroceras* was erected as a sub-genus of *Pseudoparalegoceras* by Plummer and Scott (1937). The creation of *Phaneroceras* as a sub-genus of *Pseudoparalegoceras* is based on both the position of the umbilical lobe and the chronostratigraphic position of the genera. *Phaneroceras* is defined as having the umbilical lobe centering on the umbilical shoulder and is reportedly found only in Early and Middle Pennsylvanian strata while *Pseudoparalegoceras* is defined as having an umbilical lobe centering on the outside of the umbilical shoulder and is reportedly found only in Middle Pennsylvanian strata (Gordon, 1964). *Phaneroceras* was established as a distinct genus by Nassichuk (1975). Nassichuk (1975) transferred *Pseudoparalegoceras compressum* and *Pseudoparalegoceras williamsi* to *Phaneroceras*.

Family: Schistoceratidae Schmidt 1929

Genus: *Schistoceras* Hyatt 1884

Occurrence Information: Specimens of *Schistoceras* are from the Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian strata distributed widely throughout the Midwest. This genus is widely distributed throughout the Pennsylvanian and Permian strata of the United States, China, and Russia (Furnish et al., 2009).

Diagnostic features: *Schistoceras* is characterized by a smooth, discoidal conch with a narrow umbilicus and a complex suture formula. The diagnostic features used to distinguish species are cross section shape, suture patterning, presence/absence of nodes, and the shape of the umbilicus.

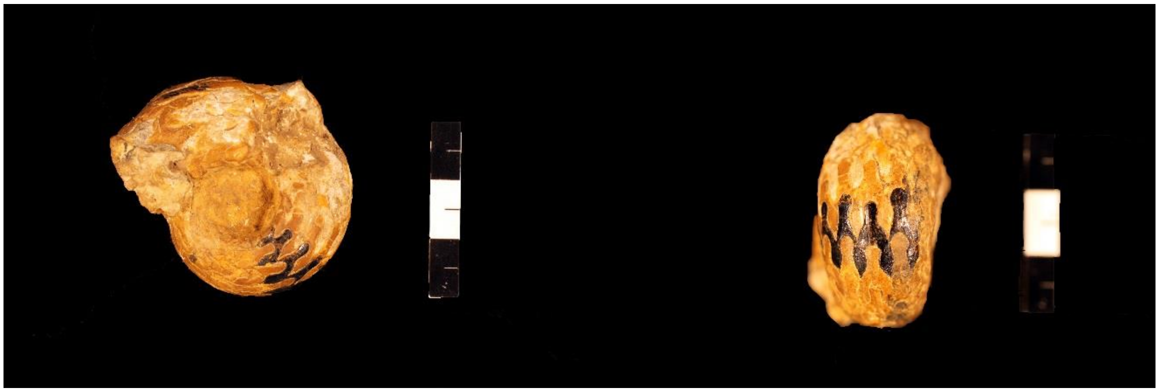

Figure 8: KUMIP-50272 *Schistoceras hildrethi*.

Genus: *Schistoceras* Hyatt 1884

Type Species: *Schistoceras hyatti* Smith 1903

Schistoceras hildrethi (Morton 1836)

SYN *Ammonites hildrethi* Morton 1836; *Paraschistoceras hildrethi* (Morton 1836)

- *Ammonites hildrethi* Morton, S. G. (1836). Being a notice and description of the organic remains embraced in the preceding paper [Hildreth, S. P., Observations on the Bituminous coal deposits of the Valley of the Ohio]. *American Journal of Science*, 29, 149–154.
- *Shistoceras hildrethi* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211.
- *Paraschistoceras hildrethi* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Schistoceras hidrethi* Miller, A. K. & Furnish, W. M. (1940). Studies of Carboniferous Ammonoids: Parts 5-7. *Journal of Paleontology*, 14, 521-543. (p. 65 fgs. 10 & 11)

Species Determination: The species descriptions and figures in Miller & Furnish (1940) (p. 65 fgs. 10 & 11) as well as review of type material maintained at the UI proved useful for species determinations. The key characters of *S. hildrethi* are the presence of nodes and a large umbilicus when compared to other species within this genus.

Material Examined: KUM IP-50272, 50493, 50653, 50954, 51194, 150988, 262460, 262461, 262484; UI- 001060, 001897, 003114, 003115, 10442, 12543, 13984, 17028, 17029, 48921, 61837, 61838; YPM IP-114226, 147469, 376325

***Schistoceras missouriense* (Miller & Faber 1892)**

SYN *Goniatites missouriensis* Miller & Faber 1892; *Schistoceras hyatti* Smith 1903; *Schistoceras smithi* Böse 1919

- *Goniatites missouriensis* Miller, S. A. & Faber, C. L. (1892). Description of some Subcarboniferous and Carboniferous Cephalopoda. *Journal of the Cincinnati Society of Natural History*, 14, 164–168.
- *Schistoceras hyatti* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211.
  (p. XX fgs. 1-8, p. XXI fgs. 10-13)
- *Schistoceras missouriense* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211. (p. VIII f. 1)
- *Schistoceras smithi* Böse, E. (1919). The Permo-Carboniferous ammonoids of the Glass Mountains, west Texas, and their stratigraphic significance. *Texas Bureau of Economic Geology Bulletin*, 1762, 1-241
- *Schistoceras missouriense* Miller, A. K. & Furnish, W. M. (1940). Studies of Carboniferous Ammonoids: Parts 5-7. *Journal of Paleontology*, 14, 521-543.
  (p. 65 fgs. 5-9)

Species Determination: The species descriptions and photographs in Miller & Furnish (1940) (p. 65 fgs. 5-9) and review of the type material of *Schistoceras missouriense* and *Schistoceras hyatti* at the University of Kansas, and paratype material of *Schistoceras missouriense* and *Schistoceras smithi* maintained at Yale Univeristy proved useful for species determinations. The key characters of *S. missouriense* are the absence of nodes, angular umbilical shoulders, and a small umbilicus.

Holotype Material: *Schistoceras missouriense* KUM IP-32273

Holotype Material: *Schistoceras hyatti* KUM IP-58844

Material Examined: KUM IP- 32273, 51337, 58844, 65775, 151244-151249, 151871; UI-001059, 1434, 1434, 005967A, 13983, 014000, 17030, 34793, 61818 61820, 61830; YPM IP-012936, 012936.A, 012936.B, 012940, 075586, 007979, 114228, 114229, 229227, 229252

Schistoceras unicum **Miller & Owen 1937**

- *Schistoceras unicum* Miller, A. K. & Owen, J. B. (1937). A new Pennsylvanian cephalopod fauna from Oklahoma. *Journal of Paleontology*, 11, 403-422.
  (p. 52, fgs. 16 & 17)

Species Determination: The species descriptions and photographs in Miller & Owen (1937) (p. 52 fgs. 16 & 17) proved useful for species determinations. The key characters of *S. unicum* are the presence of a single transverse rib running along the long axis of the conch and the rounded umbilical shoulder

Material Examined: KUM IP- 50192, 51268, 51269, 151339-151341, 151872; UI- 1433, 51480, 61827

Notes on the taxonomy of *Schistoceras*: *Schistoceras hyatti* Smith 1903 was transferred to *Schistoceras missouriense* (Miller & Faber 1892) by Miller & Furnish (1940). *Schistoceras smithi* Böse 1919 was transferred to *Schistoceras missouriense* by Miller & Furnish (1940).

Family: Perrinitidae Miller & Furnish 1940

Genus: *Properrinites* Elias 1938

Occurrence Information: Specimens of *Properrinites* are from the Wolfcampian strata of Texas and Kansas. This genus is found through the Permian strata of North America, China, and Indonesia (Furnish et al., 2009).

Diagnostic features: *Properrinites* is characterized by globular conch with depressed whorls, a depressed umbilicus, and a complex sutural formula; $(V_1V_1)L_2L_1(L_{2.1}L_{2.2})U_2U_1{:}U_2(I_{2.2}I_{2.1})I_1I_2D$. All specimens of the genus examined were type materials from the University of Kansas, the University of Iowa, and the YPM. The diagnostic features used to distinguish species was the width between the lateral lobes and saddles, the shape and size of the incisions on the lateral lobes and saddles, and the constriction of the mid-part of the ventral lobe.

Genus: *Properrinites* Elias 1938

Type Species: *Properrinites boesei* Plummer & Scott 1937

***Properrinites boesei* (Plummer & Scott 1937)**

SYN *Perrinites boesei* Plummer & Scott 1937

- *Perrinites boesei* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Properrinites boesei* Elias, M. K. (1938). *Properrinites plummeri* Elias, n. gen and sp., from Late Paleozoic Rocks of Kansas. *Journal of Paleontology*, 12, 101-105.
- *Properrinites boesei* Kues, B. S. (1995). Marine fauna of the Early Permian (Wolfcampian) Robledo Mountains Member, Hueco Formation, southern Robledo Mountains, New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 6, 63-90.

Species Determination: Review of the type material at the UI proved useful for species determinations. The diagnostic features of *P. boesei* are the spacing and relative constriction of the lateral lobes and shorter ventral lobe.

Syntype Material: UI-010616, 010618, 010620, 010621, 013607A, 013607B, 037418, 37419, 037420

Material Examined: UI-010616, 010618, 010620, 010621, 013607A, 013607B, 037418, 37419, 037420; YPM IP- 015964

***Properrinites cumminsi* (White 1889)**

SYN *Metaperrinites cumminsi* White 1889; *Waagenoceras cumminsi* (White 1889); *Perrinites cumminsi* (White 1889)

- *Metaperrinites cumminsi* White, C. A. (1889). On the Permian formation of Texas. *The American Naturalist*, 23(266), 109-128.
- *Waagenoceras cumminsi* Smith, J. P. (1903). The Carboniferous ammonoids of America. *Monographs of the United States Geological Survey*, 52, 1-211.
- *Perrinites cumminsi* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Perrinites cumminsi* Elias, M. K. (1938). Properrinites plummeri Elias, n. gen and sp., from Late Paleozoic Rocks of Kansas. *Journal of Paleontology*, 12, 101-105.
- *Properrinites cumminsi vicinus* Miller, A. K. & Furnish, W. M. (1940). Permian ammonoids of the Guadalupe Mountain region and adjacent areas. *Special Papers-Geological Society of America*, 26, 1-242.

Species Determination: Review of *Properrinites cumminsi* hypotypes at the YPM and the un-defined type materials at the UI proved useful for species determinations. The diagnostic features of *P. cumminsi* are the spacing and relative constriction of the lateral lobes and short ventral lobe.

Syntype Specimens: YPM IP- 025710, 025711, 031228, 031229, 031229, 031230, 031231, 031232, 031233, 031234, 031235, 031236, 031237, 031238, 031239, 031240, 031241

Type Material: UI-005983 & 052582

Material Examined: YPM IP-015967, 025710, 025711, 025712, 025713, 031227, 031228, 031229, 031230, 031231, 031232, 031233, 031234, 031235, 031236, 031237, 031238, 031239, 031240, 031241

***Properrinites plummeri* Elias 1938**

- *Properrinites plummeri* Elias, M. K. (1938). Properrinites plummeri Elias, n. gen and sp., from Late Paleozoic Rocks of Kansas. *Journal of Paleontology*, 12, 101-105.

Species Determination: Review of the holotype specimen at the University of Kansas proved useful for the species determinations. The diagnostic features of *P. plummeri* are the spacing and relative constriction of the lateral lobes and short ventral lobe.

Holotype Material: KUMIP-59718

Material Examined: KUMIP-59718

Notes on the taxonomy of *Properrinites*: There are no important notes on the taxonomy for the genus *Properrinites.* This genus was established by Elias (1938) to serve as an evolutionary intermediate between *Shumardites* and *Perrinites*.

Family: Parashumarditidae Boardman, Work, & Mapes 1994

Genus: *Parashumardites* Ruzhentsev 1939

Occurrence Information: Specimens of *Parashumardites* are from the Virgilian strata of Texas. This genus is known from the Pennsylvanian strata of United States, Canada, and Russia

(Furnish et al., 2009).

Diagnostic features: *Parashumardites* are characterized by an evolute, narrow coiled conch with undivided prongs in the ventral lobe of the suture. The diagnostic features used to distinguish species are the compression of the lateral lobes of the conch, the stepped appearance of the umbilicus, and cross-sectional shape (Miller & Cline, 1934).

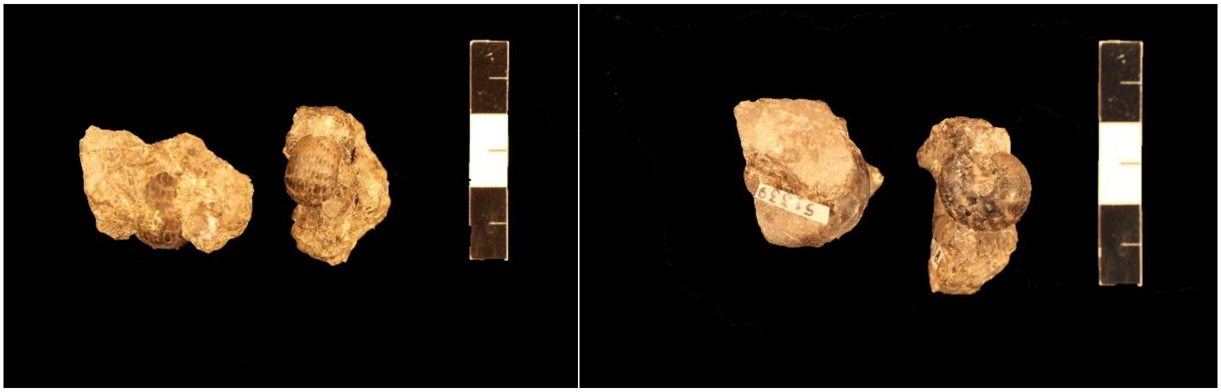

Figure 9: KUMIP-51338-51339 *Parashumardites senex.*

Genus: *Parashumardites* Ruzhencev 1939

Type Species: *Shumardites senex* Miller & Cline 1934

***Parashumardites senex* (Miller & Cline 1934)**

SYN *Shumardites senex* Miller & Cline 1934

- *Shumardites senex* Miller, A. K. & Cline, L. M. (1934). The Cephalopod Fauna of the Pennsylvanian Nellie Bly Formation of Oklahoma. *Journal of Paleontology*, 8(2), 171-185. (p. 28 fgs. 31-36)
- *Parashumardites senex* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic archipelago. *Geological Survey of Canada Bulletin*,

237, 1-240.

Species Determination: The photographs and species description in Miller & Cline (1934, p. 28 fgs. 31-36) were useful for species determinations. The diagnostic features of *P. senex* were the relative compression of the secondary lobes on the primary lateral lobes of the conch, the stepped appearance of the umbilicus, and cross-sectional shape (Miller & Cline, 1934).

Material Examined: KUMIP-51338, 51339

Notes on the taxonomy of *Parashumardites*: *Shumardites senex* was transferred to *Parashumardites* by Nassichuk (1975).

Family: Shumarditidae Plummer and Scott 1937

Genus: *Shumardites* Smith 1903

Occurrence Information: Specimens of *Shumardites* are from the Virgilian strata of Texas. This genus is known the Pennsylvanian strata of the United States and Russia (Furnish et al., 2009).

Diagnostic features: *Shumardites* is characterized by an evolute, narrow coiled conch with a marked bipartition of prongs in the ventral lobe of the suture. The diagnostic features used to distinguish species are comparison of the width and height of the lateral lobes and the presence/absence of lirae on the lateral side of the conch. Of particular use was the suture pattern figures in Miller and Downs (1950).

Figure 10: KUMIP-65823 *Shumardites cuyleri.*

Genus: *Shumardites* Smith 1903

Type Species: *Shumardites simondsi* Smith 1903

***Shumarites cuyleri* Plummer & Scott 1937**

- *Shumardites cuyleri* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Shumardites cuyleri* Miller, A. K. & Downs, R. H. (1950). Ammonoids of the Pennsylvanian Finis Shale of Texas. *Journal of Paleontology*, 24, 185-218.
  (p. 35 fgs. 7-10)

Species Determination: The species descriptions and figures in Miller & Downs (1950) (p. 35 fgs. 7-10 & in-text f. 9) as well as review of material at the UI proved useful for species determinations. The diagnostic features of *S. cuyleri* are the presence of fine lirae along the longitudinal axis of the conch and the rounded nature of the fourth lateral lobe.

Material Examined: KUMIP-65823; UI-001071, 001901, 001902, 51140; YPM IP-15301

***Shumardites simondsi* Smith 1903**

- *Shumardites simondsi* Smith, J. P. (1903). The Carboniferous ammonoids of America.

Monographs of the United States Geological Survey, 52, 1-211 (p. III fgs. 3-13)

- *Shumardites simondsi* Miller, A. K. & Downs, R. H. (1950). Ammonoids of the Pennsylvanian Finis Shale of Texas. *Journal of Paleontology*, 24, 185-218. (in-text f. 9)

Species Determination: The suture drawings in Miller & Downs (1950) and the conch drawings in Smith (1903) proved useful for species determinations. The diagnostic features of *S. simondsi* are the absence of fine lirae along the longitudinal axis of the conch and the more pronounced angularity and greater width of the first and fourth lateral lobe when compared to other species.

Material Examined: UI-38740, 38742, 53109

Notes on the taxonomy of *Shumardites*: There are no important notes regarding the taxonomy of this genus.

Family: Vidrioceratidae Plummer and Scott 1937

Genus: *Vidrioceras* Böse 1919

Occurrence Information: Specimens of *Vidrioceras* are from the Wolfcampian strata of Texas. This genus is known throughout the Pennsylvanian and Permian strata of North America, Russia, and Indonesia (Furnish et al., 2009).

Diagnostic features: *Vidrioceras* is characterized by a smooth, sub-discoidal to globular conch with a small closed umbilicus and a complex suture formula: $(V_1V_1)L_2L_1L_2(U_2U_1U_2){:}I_2I_1I_2D$ (Furnish et al., 2009). Particular attention was paid to the constriction of the lobes on the lateral sides of the conch to distinguish *Vidrioceras* from closely related *Shumardites*. The diagnostic features used to distinguish species are suture patterning, the presence and morphology of constrictions in lateral lobes, and umbilicus width and form.

Genus: *Vidrioceras* Böse 1919

Type Species: *Vidrioceras uddeni* Böse 1919

***Vidrioceras uddeni* (Böse 1919)**

SYN *Shumardites uddeni* (Böse 1919)

- *Vidrioceras uddeni* Böse, E. (1919). The Permo-Carboniferous ammonoids of the Glass Mountains, West Texas, and their stratigraphical significance. *Texas University Bulletin*, 1762.
- *Shumardites uddeni* Miller, A. K. & Furnish, W. M. (1940). Permian ammonoids of the Guadalupe Mountain Region and adjacent areas. *Special Papers-Geological Society of America*, 26, 1-238.
- *Vidrioceras uddeni* Miller, A. K. & Downs, R. H. (1950). Ammonoids of the Pennsylvanian Finis Shale of Texas. *Journal of Paleontology*, 24, 185-218.

Species Determination: The species description from Miller and Downs (1950) and review of type material maintained at the YPM proved very useful for species determinations. Extra care was utilized to ensure that specimens belonged to this genus and not to the closely related *Shumardites*. The diagnostic features of *V. uddeni* are the cross-section shape, relative size and length of lateral lobes, and the presence of transverse markings along the internal mold of the conch.

Holotype Material: YPM IP-016812

Material Examined: YPM IP-016812

Notes on the taxonomy of *Vidrioceras*: *Vidrioceras uddeni* is the original and current name for species previously considered *Shumardites uddeni* as designated by Miller & Downs (1950).

Order: Prolecanitida Miller & Furnish 1954

Family: Pronoritidae Frech 1901

Genera: *Megapronorites* Ruzhentsev 1949, *Pronorites* Mojsisovics 1882, & *Pseudopronorites* Nassichuk 1975

Occurrence Information: Specimens of *Megapronorites* are from the Atokan and Morrowan strata of Oklahoma. Specimens of *Pronorites* are from the Missourian and Morrowan strata of Oklahoma and Kansas. Specimens of *Pseudopronorites* are from the Atokan, Morrowan, Desmoinesian, Missourian, and Virgilian strata of Texas and Arkansas. These genera are widespread throughout the Carboniferous strata of Europe, Russia, Northern Africa, and the United States (Gordon, 1964; Furnish et al., 2009).

Diagnostic features: Species of *Megapronorites* are characterized by a large conch with a flat venter and a suture pattern with eighteen lobes (Furnish et al., 2009). Species of P*ronorites* are characterized as small, evolute conch with a flat venter and a suture pattern with fourteen lobes (Furnish et al., 2009). Species of *Pseudopronorites* are characterized by a large conch with transverse ribs along the venter and a stuture pattern with between twenty-two and twenty-four lobes (Furnish et al., 2009). The diagnostic features used to distinguish species are cross-section and suture morphology, and conch size.

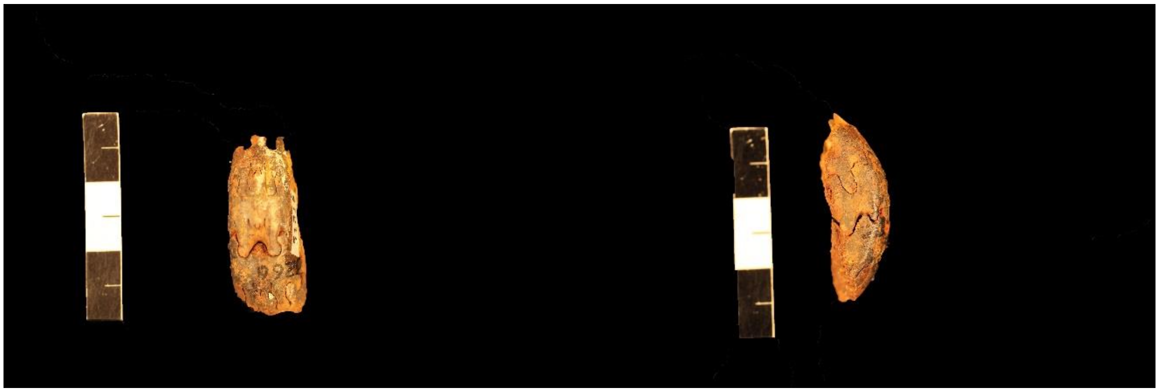

Figure 11: KUMIP-51218 *Megapronorites baconi*.

Genus: *Megapronorites* Ruzhencev 1949

Type Species: *Megapronorites sakmarensis* Ruzhencev 1949

***Megapronorites baconi* (Miller, Youngquist, & Nielsen 1952)**

SYN *Epicanites baconi* Miller, Youngquist, & Nielsen 1952; *Pronorites baconi* (Miller, Youngquist, & Nielsen 1952), *Megapronorites baconi* Ruzhentsev & Bogoslovskaya 1971

- *Epicanites baconi* Miller, A. K., Youngquist, W., & Nielsen, M. L. (1952). Mississippian cephalopods from western Utah. *Journal of Paleontology*, 26(2), 148-161.
- *Pronorites baconi* Gordon, M. (1964). Carboniferous Cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.
- *Megapronorites baconi* Ruzhentsev, V. E. & Bogoslovskaya, M. F. (1971). Namurskiy etap v evolyutsii ammonoidey. Rannenamyurskie ammonoidei. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta*, 133, 1-382.

Species Determination: The suture drawings in Gordon (1964) proved useful for species determinations. The diagnostic features of *P. baconi* are a small conch size, narrow shape, wide umbilicus, and suture pattern.

Material Examined: KUM IP-51218; UI-013945

Genus: *Pronorites* Mojsisovics 1882

Type Species: *Goniatites cyclolobus* Phillips 1836

Pronorites pseudotimorensis Miller 1930

- *Pronorites pseudotimorensis* Miller, A. K. (1930). A new ammonoid fauna of Late Paleozoic age from western Texas. *Journal of Paleontology*, (4), 383-412.

Species Determination: The suture drawings in Miller (1930) and review of the type materials at the YPM proved useful for species determinations. The diagnostic features of *P. pseudotimorensis* are a suture pattern with the first lateral saddle longer than the second saddle and the first lateral lobe longer than the second lateral lobe.

Syntype Materials: YPM IP-012931, 012931.B, 012931.C

Material Examined: YPM IP-012931, 012931.B, 012931.C, 147380; UI-011641

Genus: *Pseudopronorites* Nassichuk 1975

Type Species: *Pronorites cyclolobus* var. *arkansiensis* Smith 1896

Pseudopronorites kansasensis (Newell 1936)

SYN *Pronorites kansasensis* Newell 1936

- *Pronorites kansasensis* Newell, N. D. (1936). Some Mid-Pennsylvanian Invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology*, 10(6), 481-489. (p. 70 fgs. 3a & 3b)
- *Pseudopronorites kansasensis* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic archipelago. *Geological Survey of Canada Bulletin,*

237, 1-240.

Species Determination: The photographs and species description in Newell (1936, p. 70 fgs. 3a & 3b) proved useful for species determinations. The diagnostic features of *P. kansasensis* are a large conch, transverse ribs along the venter of the conch, and an angular suture pattern with elongate elements within the median lobe.

Material Examined: KUM IP-58810

***Pseudopronorites arkansiensis* (Smith 1896**)

SYN *Pronorites cyclolobus* var. *arkansiensis* Smith 1903; *Pronorites arkansiensis* (Smith 1903); *Stenopronorites arkansasensis* (Smith 1903)

- *Pronorites cyclolobus* var. *arkansiensis* Smith, J. P. (1896). Marine Fossils from the Coal Measures of Arkansas. *Proceedings of the American Philosophical Society*, 35(152), 213-285.
- *Pronorites arkansiensis* Plummer, F. B. & Scott, G. (1937). The Geology of Texas: Upper Paleozoic Ammonites of Texas. *University of Texas Bulletin III*, 3701, 1-516.
- *Stenopronorites arkansasensis* Gordon Jr., M (1964). Carboniferous Cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.
- *Pseudopronorites arkansiensis* Nassichuk, W. W. (1975). Carboniferous ammonoids and stratigraphy in the Canadian Arctic archipelago. *Geological Survey of Canada Bulletin*, 237, 1-240. (p. 3 f. 3 & in-text f. 17 & 18)

Species Determination: The species descriptions, photographs and text figures in Nassichuk (1975; p. 3 f. 3 & in-text f. 17 & 18) proved useful for species determinations. The diagnostic features of *P. arkansiensis*is are a small, narrow conch with transverse lateral ribs on the venter of the conch.

Material Examined: UI-011701, 013942, 013943, 013944

Notes on the taxonomy of *Megapronorites*, *Pronorites*, & *Pseudopronorites*: Miller, Youngquist, & Nielsen (1952) transferred *Pronorites baconi* to the genus *Megapronorites.* *Pronorites arkansiensis* Plummer & Scott 1937 and *Stenopronorites arkansasensis* Gordon 1964 were transferred to the genus *Pseudopronorites* by Nassichuk (1975).

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Chapter 3: Systematic Paleontology of Nautiloidea

An important aspect of my Master's thesis project was the careful taxonomic analysis and inspection of specimens to determine species identifications or verify preexisting species determinations. These species determinations would be used to reconstruct species range area and to infer the macroevolutionary patterns of the Pennsylvanian-Early Permian. This chapter focuses on the taxonomy of the nautiloid species considered in the project and includes a brief description of morphological characters used for species determinations. For this project, I focused on fossil cephalopod specimens that were both well-preserved and abundant within the museum collections at the University of Kansas to sample a broad array of diversity from the Midcontinent Sea. Prior to this study, the biogeographic patterns and turnover rates of the cephalopod clade within the Midcontinent region had not been examined in detail. Cephalopods were chosen as the focus of this analysis because they constitute an abundant and diverse organism of the Pennsylvanian and Permian ecosystems of the North American Midcontinent Sea that persisted throughout the Late Paleozoic Ice Age (LPIA) despite numerous climate oscillations (Korn et al., 2015). Further, ammonoids and nautiloids of the Pennsylvanian and Permian systems of the North America have been well described and specimens are abundant in many institutions around the United States due to their frequent use as biostratigraphic indicators in the fossil record.

Description of Nautiloidea:

Phylum: Mollusca Cuvier 1797

Class: Cephalopoda Leach 1817

Subclass: Nautiloidea Agassiz 1847

Nautiloids are members of the Class Cephalopoda that are represented in the form of two living genera; *Nautilus* Linnaeus 1758 and *Allonautilus* Ward & Saunders 1997. Due to the morphological resemblance of extant *Nautilus* to fossilized nautiloids the behaviors of extant nautiloids are considered to be analogous to those of extinct nautiloids. Modern nautiloids are pelagic and inhabit the reef-slope habitats of the southwestern Pacific Ocean (Furnish & Glenister, 1964; Saunders & Ward, 1987). Temperature is known to have an important control over biogeographic distribution of *Nautilus*. Nautiloid species have not been documented in water temperatures exceeding 28°C and primarily reside in water temperatures between 10-25°C (Saunders & Ward, 1987). *Nautilus* are known to migrate between the oceanic depths (~300 meters) during the day and the shallow tropical reef environments at night (Saunders & Ward, 1987). Observational studies and analysis of crop contents have shown that *Nautilus* are opportunistic scavengers that feed upon small crustaceans and vertebrates within the water column (Stenzel, 1964; Saunders & Ward, 1987). Although once thought of as nocturnal, *Nautilus* has been shown to opportunistically scavenge in both nocturnal and diurnal settings (Saunders & Ward, 1987). Further information regarding the reproduction and biology of Nautilus can be found in the proceeding sections.

Modern cephalopods are organized into two groups: Nautiloidea and Coleoidea (Engeser, 1996; Kröger et al., 2011). The coleoids are characterized by possessing an internal shell (which at times can be completely lost) and include squids, cuttlefish, and octopods (Kröger et al., 2011). The Nautiloidea lineage is believed to have diverged from one of three possible groups: the Orthocerida, the Oncocerida, or the Barrandeocerida, in the Late Silurian to Early Devonian (Sweet et al., 1964; Kröger et al., 2011). Although much debate exists around the timing of divergence, the coleoids are believed to have diverged from the Bactritida during the Early Carboniferous, and diversified during the Permian (Kröger et al., 2011).

The pattern of nautiloid evolutionary rates and abundance is complicated, and shows wide oscillations through time. The nautiloids formed an extremely diverse and common group from the Silurian to the Late Paleozoic after which evolutionary rates slowed for this group (Teichert & Matsumoto, 1987). Nautiloids survived the Late Triassic mass extinction event (Sweet et al., 1964) and underwent an evolutionary radiation across the K-T boundary after the extinction of the ammonoids (Teichert & Matsumoto, 1987). The group experienced a decline in diversity and abundance throughout the Cenozoic, and there is an apparent gap in nautiloid evolution in the Late Cenozoic, especially in the Pliocene and Pleistocene (Sweet et al., 1964; Teichert & Matsumoto, 1987). Although the precise phylogenetic relationships of *Nautilus* and *Allonautilus* are debated, the first appearance of this lineage is treated as the Eocene-Early Oligocene; within genus episodes of speciation are inferred to have occurred, at most, a few million years ago (Teichert & Matsumoto, 1987; Engeser, 1996; Bonacum et al., 2011).

Comparison of Ammonoid & Nautiloid Morphology & Behaviors:

Nautiloidea and Ammonoidea were traditionally treated as each other's closest relatives, and much of their behavior and life-histories had been deemed as similar for this reason. However, recent phylogenetic study has shown that Ammonoidea is more closely related to Coleoidea (Engeser, 1996; Klug et al., 2015) and Nautiloidea diverged from the coleoid lineage sometime around the Silurian-Devonian boundary (Kröger et al., 2011). There are several plesiomorphic characters that are shared between ammonoids and nautiloids. For instance, both organisms had an external shell and utilized neutral buoyancy for locomotion through internal propulsive organs. Both organisms also had a radula and beak, a crop, and several arms to facilitate feeding and digesting prey items (Engeser, 1996; Kruta et al., 2011). Finally, both groups had a direct mode of development without larval forms (Engeser, 1996). While these characters are shared across all Cephalopoda, there are several morphological and inferred biological differences between fossil ammonoids and nautiloids that justify the separation of these groups into distinct lineages. These differences include conch morphology and the morphology of propulsive organs.

Nautiloids are most readily distinguished from ammonoids by differences in conch morphology. Particularly, the aperture of the conch of the nautiloid is orientated below the phragmocone while the ammonoid conch is oriented in the reverse manner (Miller & Furnish, 1957). Nautiloids are characterized by a simple, stream-lined conch morphology with simple suture morphology (in comparison with ammonoids). Further, conch size is an important indicator of gender and populations of *Nautilus* are known to be sexually dimorphic. In particular, males are larger in size and have broader conch apertures than females. Further, there is an uneven sex ratio: 75% male dominated populations have been documented in various regions throughout the species distribution area (Stenzel, 1964; Saunders & Ward, 1987).

In addition to conch morphology, there are a number of differences in the morphology and position of propulsive organs. Perhaps most characteristic is the siphuncle position (the opening through the internal shell that contains propulsive organs (Miller & Furnish, 1957). The position of the siphuncle in is large and central (or sub-central) in nautiloids while it is small and marginal in ammonoids (Engeser, 1996). The hyponome (funnel for locomotion) of nautiloids is well developed an allows for a high degree of maneuverability in all directions compared to the likely limited maneuverability of this funnel in Ammonoidea (Engeser, 1996). Further, the retractor muscles, which were used to force water through the hyponome, are large and positioned on the ventral wall of the body chamber (Jacobs & Landman, 1993; Engeser, 1996). For these reasons, it has traditionally been thought that nautiloids were more dynamic, efficient, and quicker swimmers than their ammonoid counterparts (Jacobs & Landman, 1993).

Both nautiloid and ammonoid fossils are found in a variety of paleo-environments across a variety of depths. This has been interpreted as evidence for their dynamics use of warm and cold-water habitats (Ritterbush et al., 2014). However, the fossil record has revealed some key differences in ammonoid and nautiloid life history strategies, particularly, regarding developmental strategies. All Cephalopoda are interpreted to have had separate sexes that reproduced sexually in ‘spawning’ events (Engeser, 1996). However, investigation of the fossil record and modern observations of *Nautilus* implies that there was a difference in reproductive strategies between the groups. Reproduction in *Nautilus* is sexual and follows a K-selected mode (Jacobs & Landman, 1993; Engeser, 1996; Ritterbush et al., 2014). Unlike many other cephalopods, *Nautilus* has not been observed to engage in elaborate courtship rituals. Males will grasp the female and force the conch apertures together to initiate copulation (Arnold, 1987). The spermatophore is transferred to the female and the animals separate. The timing between copulation and egg deposition in unknown. Females will deposit between five and eight large eggs in small clusters on the marine substrate which will hatch to bear minute adults in approximately one year (Arnold, 1987; Lukeneder et al., 2010). Young take between five to six (and perhaps up to ten) years to reach sexual maturity based on long-term observations of

Nautilus macromphalus (Martin et al., 1978; Engeser, 1996). By contrast, ammonoids are believed to have had an R-Selected reproductive mode (Jacobs & Landman, 1993; Engeser, 1996; Ritterbush et al., 2014). A detailed comparison of ammonoid and nautiloid characters is given in Table 1 of Chapter 1.

Important sources regarding the morphological terminology for nautiloids includes <u>The Morphology of Hard Parts</u> (Tiechert, 1964) and the <u>Glossary of Morphological Terms used for Nautiloids</u> (Teichert, 1964) from the *Treatise on Invertebrate Paleontology*.

Notes on Species Determinations:

Nautiloid genera included in this study were: *Brachycycloceras, Domatoceras, Ephippioceras, Euloxoceras, Hebetorthoceras, Knightoceras, Liroceras, Metacoceras, Millkoninckioceras, Mooreoceras, Orthoceras, Pseudorthoceras,* and *Solenochilius*. Genera were organized first by order (Nautilida, Orthocerida, and Pseudorthocerida), then by family (Ephippoceratidae, Koninckioceratidae, Liroceratidae, Tainoceratidae, Solenochilidae, Brachycycloceratidae, Grypoceratidae, Spyroceratidae, Orthoceratidae, and Pseudorthoceratidae) and finally by species, in alphabetical order. For each genus, the occurrence information, diagnostic characters, and taxonomic issues pertaining to the group are discussed. Further, for each species, the materials used for species identifications and the specimen numbers of the research materials are included. Species identifications were made possible by examining of relevant publications and studying type specimens. Type specimen numbers are included if these were personally examined or were readily available through literature review. In some cases, the type material has been lost and only photographs remain. However, since the focus of this study was not on a taxonomic revision of the group, at this time I have not designated neotypes for these species. All specimens utilized in this project come from the continental United States.

Repositories:

Collections from the following institutions were visited to inspect the type materials and obtain specimens for my biogeographic analyses: The Yale University Peabody Museum of Natural History (YPM), the University of Iowa Paleontological Repository (UI), and University of Kansas, Biodiversity Institute, Division of Invertebrate Paleontology (KUMIP). Special thanks to YPM Senior Collection Manager: Susan Butts, UI Special Collections Manager: Tiffany Adrian, and KU Collections Manager: Julien Kimmig, for their assistance in planning research trips and providing access to type materials and additional specimens for use in my research project.

Order: Nautilida Agassiz 1847

Family: Ephippoceratidae Miller and Youngquist 1949

Genus: *Ephippioceras* Hyatt 1884

Occurrence Information: Specimens of *Ephippioceras* used in this study came from the Virgilian, Missourian, and Desmoinesian of Kansas, Missouri, Nebraska, Oklahoma, Kentucky, and Pennsylvania. This genus is widely distributed and known to occur throughout the Carboniferous of North America, Europe, and Russia (Teicheirt et al., 1964).

Diagnostic Features: Specimens of *Ephippioceras* are characterized by a large conch with a widely-rounded venter, a small umbilicus, a u-shaped cross section, a small and sub-centric siphuncle, and a large v-shaped suture pattern. The species of this genus are separated based on stratigraphic occurrence; all Pennsylvanian species are assigned to *E. ferratum* (Gordon, 1964).

Figure 12: KUMIP-38797 *Ephippioceras ferrartum.*

Genus: *Ephippioceras* Hyatt 1884

Type Species: *Nautilus ferratus* Cox 1857

***Ephippioceras ferrartum* (Cox 1857)**

SYN *Nautilus ferratus* Cox 1957; *Ephippioceras (Nautilus) ferratum* (Cox 1957); *Ephippioceras ferratum* (Cox 1957)

- *Nautilus ferratus* Cox, D. D. (1857). First report of a geological reconnoissance of the northern countries of Arkansas, made during the years 1857 and 1858. *Arkansas Geological Survey*, 1858.
- *Ephippioceras (Nautilus) ferratum* Hyatt, A. (1891). Carboniferous cephalopods. *Texas Geological Survey Annual Report*, 2, 329-356.
- *Ephippioceras ferratum* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240. (p. III fgs. 14-17)
- *Ephippioceras ferratum* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions,* 2, 1-11. (p.2 fgs. 7-10)
- *Ephippioceras ferratum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Ephippioceras ferratum* Gordon, M. Jr. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322. (p.16 fgs. 1-8)

Species Determination: The species descriptions in Miller, Dunbar, & Condra (1933) and Miller & Youngquist (1949), photographs in Gordon (1964) and review of the type material at the KUMIP proved useful for species determinations

Plesiotype Material: KUMIP-32028

Material Examined: KUMIP- 32021, 32028, 32035, 38640, 38670, 38730, 38751, 38752, 38797, 38800, 38810, 49937, 49938, 50052, 50082, 50930, 50963, 65641, 65642; UI-003128, 013390, 013391, 013392, 013388, 013389, 013437, 33091; YPM IP- 205173, 229145

Notes on the taxonomy of *Ephippioceras*: There are no important notes regarding the taxonomy of this genus.

Family: Koninckioceratidae Hyatt in Zittel 1900

Genus: *Knigthoceras* Miller & Owen 1934 & *Millkoninckioceras* Kummel 1963

Occurrence Information: Specimens of *Knightoceras* come from the Missourian and Desmoinesian of Kansas and Missouri. This genus is known from the Lower Carboniferous of North America and Europe (Teichert et al., 1964). Specimens of *Millkoninckioceras* are known from the Missourian of Kansa and Missouri. This genus is known from the Lower Carboniferous and Permian of North America and Europe (Teichert et al., 1964).

Diagnostic Features: Specimens of *Knightoceras* are characterized by having a nautiliconic conch (see Teichert C., Glossary of Morphological Terms Used for Nautiloids, 1964) that rapidly expands orad with rounded lateral walls, a deep, broad umbilicus, and a small siphuncle that is positioned sub-central towards the venter, a smooth conch, and simple, shallowly rounded sutures. Species of this genus are distinguished by the size of their conch, position of the siphuncle, and the morphology of the lateral zones of the conch. Specimens of *Millkoninckioceras* specimens are characterized by a nautiliconic conch with a deep, broad umbilicus, a small siphuncle that is positioned sub-central towards the venter, smooth conch, and straight sutures. Species of this genus are distinguished by examination of the sutures, the angularity of ventral and umbilical shoulders, and the nature of the dorsal depressed zone.

Figure 13: KUMIP-40877 *Knightoceras abundum.*

Genus: *Knigthoceras* Miller & Owen 1934

Type Species: *Knightoceras missouriense* Miller & Owen 1934

***Knightoceras abundum* Miller, Lane, & Unklesbay 1947**

- *Knightoceras abundum* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 3 fgs. 1-4)
- *Knightoceras abundum* Gordon, M., (1964): Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species description and figures contained in Miller, Lane, & Unklesbay (1947) (p. 3 fgs. 1-4) and species key in Gordon (1964) were useful for determinations. *Knightoceras abundum* is very similar in morphology to *K. missouriense* but is distinguished from the latter by having more rounded lateral zones on the phragmacone surface, the larger size of the conch, and the sub-central position of the siphuncle towards the venter of the conch.

Material Examined: KUMIP- 32080, 32081, 32082, 32083, 32084, 38684, 40871, 40877, 40928

***Knightoceras missouriense* Miller & Owen 1934**

- *Knightoceras missouriense* Miller, A. K. & Owen, J. B., (1934). Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History*, 16, 185–272. (p. XV fs. 6-8)
- *Knightoceras missouriense* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Knightoceras missouriense* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species descriptions contained in Miller & Youngquist (1949) and Gordon (1964), as well as the figure in Miller & Owen (1934) assisted in species determinations. Examination of the holotype specimen at the UI was also particularly useful for species determinations. *Knightoceras missouriense* is characterized by the small size of the conch, sub-central position of the siphuncle towards the venter, and highly arched character of the dorsal side of the conch.

Holotype Material: UI-13397

Material Examined: KUMIP-13397

Genus: *Millkoninckioceras* Kummel 1963

Type species: *Koninckioceras konincki* Miller & Kemp 1947

***Millkoninckioceras elaisi* (Newell, 1936)**

- *Koninckioceras elaisi* Newell, N. D. (1936). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology*, 10(6), 481-489. (p. 72 fgs. 2)

- *Koninckioceras elaisi* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.

Species Determination: The species description in Newell (1936) and review of the type material at the KUMIP was useful for species determinations. *Millkoninckioceras elaisi* is characterized by slightly flexed sutures, thickened connecting siphuncle rings between conch chambers, the position of the umbilical shoulder along the center of the lateral zone of the conch, and the broad, and the rounded nature of the margins of the dorsal depressed zone.

Holotype Material: KUMIP-32006

Material Examined: KUMIP- 32006, 40881

***Millkoninckioceras jewetti* (Newell, 1936)**

- *Koninckioceras jewetti* Newell, N. D. (1936). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology,* 10(6), 481-489. (p. 72 fgs. 1a &1b)
- *Koninckioceras jewetti* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.

Species Determination: The species description in Newell (1936) was useful for species determinations. *Millkoninckioceras jewetti* is characterized by strongly flexed sutures, thin connecting siphuncle rings between conch chambers, and the angular nature of the margins of the umbilical shoulder and dorsal depressed zone.

Material Examined: KUMIP- 38834

***Millkoninckioceras wyandottense* (Newell, 1936)**

- *Koninckioceras wyandottense* Newell, N. D. (1936). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology*, 10(6), 481-489. (p. 71 fgs. 1a-1c)

- *Koninckioceras wyandottense* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.

Species Determination: The species description and figures in Newell (1936) (p. 71 fgs. 1a-1c) as well as review of the type material at KUMIP was useful for species determinations. *Millkoninckioceras wyandottense* is characterized by moderately flexed sutures and the rounded nature of the lateral zones and the margins of the umbilical shoulder and dorsal depressed zone.

Holotype Material: KUMIP-32009

Material Examined: KUMIP-32009

Notes of taxonomy of *Knightoceras* & *Millkoninckioceras*: *Koninckioceras* was synonymized with *Millkoninckioceras* by Kummel (1963). Kummel (1963) established the later genus because he held that the original description was vague and the type specimen was indistinguishable. However, the only species Kummel (1963) recognized was *Millkoninckioceras konincki*. Miller & Youngquist (1949) suggested that *K. elaisi*, *K. jewetti,* and *K. wyandottense* were not valid species names of *Koninckioceras*. I diverge from this interpretation, as I noticed a difference in suture curvature and umbilical shoulder angularity and position between these three species. For this reason, I designate that these species should be added as valid species of *Millkoninckioceras.*

Family: Liroceratidae Miller and Youngquist 1949

Genus: *Liroceras* Teichert 1940

Occurrence Information: Specimens of *Liroceras* used in this study came from the Morrowan, Atokan, Desmoinesian, and Missourian strata of Oklahoma, Missouri, Kansas, and Pennsylvania.

This genus is known from the Lower Carboniferous and Permian of North America, Europe, Asia, and the East Indies (Teichert et al., 1964).

Diagnostic Features: *Liroceras* is characterized by a nautiliconic conch with a broad, rounded venter, rounded lateral zones, a small umbilicus, straight sutures, and a highly arched dorsal impressed zone. Species of this genus can be distinguished by the presence/absence of an umbilical plug, the presence/ absence of lirae along the longitudinal axis, and the shape of the sutures.

Figure 14: KUMIP-38564 *Liroceras* sp.

Genus: *Liroceras* Teichert 1940

Type species: *Liroceras liratum* (Girty 1912)

***Liroceras liratum* (Girty 1912)**

- *Coloceras liratum* Girty, G. H. (1912). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21(2), 119-156.
- *Coloceras liratum* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska*

Geological Survey Bulletin, 9, 1–240.

- *Liroceras liratum* Teichert C. (1940). Contributions to nautiloid nomenclature. *Journal of Paleontology*, 14(6), 590-597.
- *Liroceras liratum* Unklesbay, A. G. & Palmer, E. J. (1958). Cephalopods from the Burgner Formation in Missouri. *Journal of Paleontology,* 32(6), 1071-1076.
  (p. 138 fgs. 1-3)
- *Liroceras liratum* Hoare, R. D. (1961). Desmoinesian Brachiopoda and Mollusca from southwest Missouri. *Missouri University Studies*, 36, 1-262.
- *Liroceras liratum* Gordon, M., (1964): Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322.

Species Determination: The species descriptions and figures in Unklesbay & Palmer (1958) (p. 138 fgs. 1-3) and the species key in Gordon (1964) were useful for species determinations. *Liroceras liratum* is characterized by the absence of an umbilical plug and the presence of many longitudinal lirae along the umbilical shoulder of the conch.

Material Examined: KUMIP-38641, 38665, 38719, 38720, 288650, 288651, 288671, 288672, 288692, 289400, 289401, 289402, 289680; UI- 13939A, 13939B, 13940, 51461; YPM IP-229265

Liroceras milleri **Newell 1936**

- *Liroceras milleri* Newell, N. D. (1936). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology*, 10(6), 481-489.
- *Liroceras milleri* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 2 fgs. 1-6)

- *Liroceras milleri* Gordon, M., (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322.

Species Determination: The species description and figures contained in Miller, Lane & Unklesbay (1947) and species key in Gordon (1964) were useful for species determinations. *Liroceras milleri* is characterized by the presence of an umbilical plug.

Material Examined: KUMIP-32002, 32003, 32004, 32011, 32012, 32013, 32014, 32018, 32019, 32020, 32361, 32362, 32363, 32364, 32365, 32381, 32382, 38719, 38720, 38769, 51461, 61578, 65638, 65639, 151906, 151907, 282310, 288651, 288692, 288771, 289680; UI-051458, 051461

Notes on the taxonomy of *Liroceras*: *Coloceras* Hyatt 1893 is transferred to *Liroceras* by Teichert (1940).

Family: Tainoceratidae Hyatt 1883

Genus: *Metacoceras* Hyatt 1883

Occurrence Information: Specimens of *Metacoceras* used in this study came from the Desmoinesian, Missourian, Virgilian, and Wolfcampian of Oklahoma, Kansas, Missouri, Texas, Pennsylvania, Ohio, and Iowa. This genus has a global distribution and is known from the Pennsylvanian and Permian (Teichert et al., 1964).

Diagnostic Features: *Metacoceras* is characterized as having a coiled conch, shallow lobed sutures, and a small, sub-central siphuncle. Species are distinguished by comparison of the following features; cross-section shape, presence/ absence of nodes on the ventral and umbilical shoulders, angularity of conch margins, presence/ absence of lirae, and presence/absence of furrows on conch surface. It is important to note that an inordinate amount of species have been assigned to this genus so there is a need for further taxonomic work to ensure its validity.

Figure 15: KUMIP-38632 & 38633 *Metacoceras dubium*.

Genus: *Metacoceras* Hyatt 1883

Type Species: *Nautilus sangamonensis* Meek & Worthen

***Metacoceras angulatum* Sayre 1930**

SYN Metacoceras cavatiforme Miller 1892

- *Metacoceras cavatiforme* Miller, S. A. (1892). Palaeontology. *Geological Survey of Indiana Annual Report Advance Sheets*, 18, 1-79.
- *Metacoceras cavatiforme* var. *angulatum* Sayre, A. N. (1930). The fauna of the Drum Limestone of Kansas and western Missouri. *University of Kansas Science Bulletin*, 19(8), 1-203.
- *Metacoceras angulatum* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240. (p. XV fgs. 1-4)

Species Determination: The species description and figures contained in Miller, Dunbar, & Condra (1933) (p. XV fgs. 1-4) proved useful for species determinations. The key features of *M. angulatum* are the presence of nodes along every other suture line of the umbilical shoulder, angular umbilical shoulders, and a small umbilicus with steep sides.

Syntype Material: KUMIP-32017

Plesiotype Material: KUMIP-32039

Material Examined: KUMIP-32017, 32039, 38352, 38588, 38629, 38733, 38738, 38820, 40876, 40921, 40926, 50946, 282314, 282315, 282316, 282379, 288706, 288707, 288709; YPM IP-013992, 015056

***Metacoceras bituberculatum* Miller & Youngquist 1949**

- *Metacoceras bituberculatum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (p. 49 fgs. 3-4)

Species Determination: The species description and figures in Miller & Youngquist (1949) (p. 49 fgs. 3-4) proved useful for species determinations. The key features of *M. bituberculatum* are the presence of large nodes on the dorso-lateral shoulders, smaller nodes on the ventral-lateral shoulder, angular umbilical shoulders, and a small umbilicus.

Material Examined: UI- 13663

***Metacoceras bowmani* Miller & Breed 1964**

- *Metacoceras bowmani* Miller, H. W. & Breed, W. J. (1964). Metacoceras bowmani, a new species of nautiloid from the Toroweap Formation (Permian) of Arizona. *Journal of Paleontology*, 38(5), 877-880.

Species Determination: The species description in Miller & Breed (1964) proved useful for species determinations. The key features of *M. bowmani* are the presence of long dorso-lateral horns, a ventral furrow, lack of umbilical nodes, and a central siphuncle.

Material Examined: KUMIP-50924, 289659

Metacoceras cheneyi Miller & Youngquist 1947

- *Metacoceras cheneyi* Miller, A. K. & Youngquist, W. (1947). Lower Permian Cephalopods from the Texas Colorado River Valley. *The University of Kansas Paleontological Contributions*, 2, 1-15.
- *Metacoceras cheneyi* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
  (p. 45 fgs. 1-3 & p. 46 fgs. 6-8)

Species Determination: The species determinations and figures in Miller & Youngquist (1949) (p. 45 fgs. 1-3 & p. 46 fgs. 6-8) proved useful for species determinations. The key features of *M. cheneyi* are the presence of small protrusive nodes on the dorsolateral and ventrolateral shoulder along each suture line and the angularity of the umbilical shoulder.

Material Examined: KUMIP-38555, 50966, 151882, 151883, 282322; UI-13443; YPM IP-174015

Metacoceras cornutum Girty 1911

- *Metacoceras cornutum* Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21, 119-156.
- *Metacoceras cornutum* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353. (p. XXIX fgs. 4-5b)
- *Metacoceras cornutum* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240.
- *Metacoceras cornutum* Miller, A. K. & Youngquist, W. (1949). American Permian

nautiloids. *Geological Society of America Memoir*, 41, 1-218.

Species Determination: The species descriptions in Miller, Dunbar, & Condra (1933) and Miller & Youngquist (1949) as well as the figures in Girty (1915) (p. XXIX fgs. 4-5b) proved useful for species determinations. The key features of *M. cornutum* are angular lateral margins, the presence of nodes along the ventro-lateral shoulder on every other chamber, and broad, rounded sutures.

Material Examined UI-003118A, 003120, 003121, 003122, 003123, 013636, 013637, 008173; YPM IP-376050, 376071, 376072, 376150, 376051, 376052

***Metacoceras dubium* Hyatt 1891**

- *Metacoceras dubium* Hyatt, A. (1891). Carboniferous cephalopods. *Texas Geological Survey Annual Report*, 2, 329-356.
- *Metacoceras dubium* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353.
- *Metacoceras dubium* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240.
- *Metacoceras dubium* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.

Species Determination: The species description in Miller, Dunbar, & Condra (1933) and Miller & Youngquist (1949) proved useful for species determinations. The key features of *M. dubium* are the presence of subtle nodes along the dorsolateral shoulder at every other suture line, rounded lateral sides, the cross-section shape, and the rounded character of the umbilical shoulders.

Material Examined: KUMIP-38632, 38633, 38717, 50027, 151887, 151888, 151889, 151894, 289656; YPM IP-229106, 229114

Metacoceras inconspicuum **Hyatt 1891**

- *Metacoceras inconspicuum* Hyatt, A. (1891). Carboniferous cephalopods. *Texas Geological Survey Annual Report*, 2, 329-356.
- *Metacoceras inconspicuum* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353.
- *Metacoceras inconspicuum* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240. (in-text fgs. 29 & 30)
- *Metacoceras inconspicuum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (f.33)

Species Determination: The species descriptions and figures in Miller, Dunbar, & Condra (1933) (in-text fgs. 29 & 30) and Miller & Youngquist (1949) (f. 33) as well as review of the type material at YPM proved useful for species determinations. The key features of *M. inconspicuum* are the square appearance of the cross section, angularity of conch margins, and the convex nature of the lateral sides of the conch.

Hypotype Material: YPM IP-013993

Material Examined: YPM IP-013993

Metacoceras jacksonense **Miller, Lane, & Unklesbay 1947**

- *Metacoceras jacksonense* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson

Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 1 f. 9)

- *Metacoceras jacksonense* Unklesbay, A. G. (1954). Distribution of American Pennsylvanian cephalopods. *Journal of Paleontology*, 28(1), 84-95.

Species Determination: The species descriptions in Unklesbay (1954) and figures in Miller, Lane, & Unklesbay (1947) (p. 1 f. 9) proved useful for species determinations. The key features of *M. jacksonense* are the cross-section shape, the presence of distinct nodes on the ventro-lateral shoulders that increase in size through conch development, broad shallow ventral lobes, and the presence of a ridge of elongate nodes along the umbilical shoulder.

Material Examined: KUMIP-32092, 38631, 38637, 38657, 38658, 38687, 38793, 49565

Metacoceras knighti **Miller & Thomas 1936**

- *Metacoceras knighti* Miller, A. K. & Thomas, H. D. (1936). The Casper Formation (Pennsylvanian) of Wyoming and its cephalopod fauna. *Journal of Paleontology*, 10, 715-738.
- *Metacoceras knighti* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (p. 47 fgs. 2 & 3)

Species Determination: The species description in Miller & Thomas (1936) as well as the figures in Miller & Youngquist (1949) (p. 47 fgs. 2 & 3) proved useful for species determinations. The key features of *M. knighti* are the smooth, elongate nodes on the ventrolateral and umbilical shoulders, large conch, and large umbilicus.

Material Examined: KUMIP- 32092, 38631, 38637, 38657, 38658, 38687, 38793, 49565

Metacoceras mutabile Miller, Lane, & Unklesbay 1947

- *Metacoceras mutabile* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 1 fgs. 5-8)
- *Metacoceras mutabile* Unklesbay, A. G. (1954). Distribution of American Pennsylvanian cephalopods. *Journal of Paleontology*, 28(1), 84-95.

Species Determination: The species description and figures in Miller, Lane, & Unklesbay (1947) (p. 1 fgs. 5-8) and review of the type material maintained at KUMIP proved useful for species determinations. The key features of *M. mutabile* are shape of the cross section, angular umbilical shoulder, presence of nodes on ventrolateral and umbilical shoulders, and grooves running along the lateral sides.

Holotype Material: KUMIP-32040

Paratype Material: KUMIP-32032, 32036, 32070, 32071, 32072

Material Examined: KUMIP-32032, 32036, 32040, 32070, 32071, 32072, 38551, 38552, 38589, 38590, 38591,151881, 288784; UI-013399, 013402, 013403, 13443

Metacoceras nodosum Miller, Dunbar, & Condra 1933

- *Metacoceras nodosum* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240. (p. XV fgs. 5-7)

Species Determination: The species descriptions and figures in Miller, Dunbar, & Condra (1933) (p. XV fgs. 5-7) proved useful for species determinations. The key features of *M. nodosum* are the cross-section shape, rounded umbilical shoulders, and the presence of nodes below the umbilical shoulder at every suture line.

Material Examined: KUMIP-38553, 38661, 40885, 50945, 151884, 151885, 151886, 282384, 288831, 289439; YPM IP-205240

Metacoceras perelegans Girty 1915

- *Metacoceras perelegans* Girty, G. H. (1915): Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353. (p. XXX f. 5-6)
- *Metacoceras perelegans* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240.
- *Metacoceras perelegans* Sturgeon, M. T. et al. (1982). New and revised taxa of Pennsylvanian cephalopods in Ohio and West Virginia. *Journal of Paleontology*, 56(6), 1453-1479.

Species Determination: The species descriptions in Miller, Dunbar, & Condra (1933) as well as the figures in Girty (1915) (p. XXX f. 5-6) proved useful for species determinations. The key features of *M. perelegans* are the angular cross-section shape, the presence of large nodes on the ventro-lateral shoulder and smaller nodes on the umbilical shoulders, and nearly straight sutures.

Material Examined: UI-003124, 003125, 003126, 003127

Metacoceras sulciferum Miller & Thomas 1936

- *Metacoceras sulciferum* Miller, A. K. & Thomas, H. D. (1936). The Casper Formation (Pennsylvanian) of Wyoming and its cephalopod fauna. *Journal of Paleontology*, 10, 715-738.
- *Metacoceras sulciferum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (p. 47 fgs. 4-5)

Species Determination: The species descriptions and figures in Miller & Youngquist (1949) (p. 47 fgs. 4-5). The key feature of *M. sulciferum* are the cross-section shape and the presence of a longitudinal furrow that runs along the venter.

Material Examined: KUMIP-66751; YPM IP-205243

Metacoceras sublaeve Miller, Dunbar, & Condra 1933

- *Metacoceras sublaeve* Miller, A. K. et al. (1933): The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. VII fgs. 1-3)

Species Determination: The species description and figures in Miller, Dunbar, & Condra (1933) (p. VII fgs. 1-3) proved useful for species determinations. The key feature of *M. sublaeve* are the cross-section shape, the presence of rounded umbilical shoulders, and absence of nodes.

Material Examined: YPM IP-013995, 013996.A, 013996.B, 013996.C, 013996.D

Notes on the taxonomy of *Metacoceras*: An important note is the synonymy of *M. cavatiforme* Miller 1892 with *M. angulatum* by Sayre (1930).

Family: Solenochilidae Hyatt 1893

Genus: *Solenochilus* Meek & Worthen 1870

Occurrence Information: Specimens of *Solenochilus* came from the Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian strata of Kansas, Oklahoma, Missouri, Nebraska, Pennsylvania, Iowa, and Arkansas. This genus has a global distribution in Upper Carboniferous to Lower Permian strata (Teichert et al., 1964).

Diagnostic Features: *Solenochilus* is characterized by a smooth, nautilonic conch, angular umbilical shoulders with lateral spines at maturity, the presence of an isolated feature in the center of the suture on the venter, the siphuncle positioned sub-central toward the venter, and a deep umbilicus. Species can be distinguished by the direction of the isolated feature in the center of the suture, the morphology of the venter, the presence/absence of a keel along the umbilical shoulder, the presence/absence of flanks along the lateral sides of the conch, and the amount of depression of the umbilicus. Of particular use for species determinations was the species key created by Gordon (1964).

Figure 16: KUMIP-288741 *Solenochilus springeri*.

Genus: *Solenochilus* Meek & Worthen 1870

Type species: *Solenochilus springeri* (White & St. John 1867)

Solenochilius brammeri Miller, Dunbar, & Condra 1933

- *Solenochilius brammeri* Miller, A. K. et al. (1933): The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, *9,* 1-240. (p. XXII f. 6 & 7, p. XXIII f. 1, p. XXIV f. 1)
- *Solenochilius brammeri* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) and the species description and figures in Miller, Dunbar, & Condra (1933) proved useful for species determinations. Examination of the type material at YPM also proved useful for species determinations. The key features of *S. brammeri* are the presence of an isolated lobe in the center of the suture, rounded cross-section margins, a depressed venter, and the presence of a keel along the umbilical shoulder.

Holotype Material: YPM IP-14006

Paratype Material: YPM IP-14005

Material Examined: UI- 051366, 051367; YPM IP-14005, 14006

***Solenochilius kempae* Miller & Youngquist 1949**

- *Solenochilius kempae* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Solenochilius kempae* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322.

Species Determination: The species key in Gordon (1964) as well as the species description in Miller & Youngquist (1949) proved useful for species determinations. The key features of *S. kempae* are the presence of an isolated lobe in the center of the suture and more than ten camerae are contained within a space equal to the width of the whorl.

Material Examined: KUMIP-38755, 38756, 38757, 38794, 38806, 38819, 40886, 40888

***Solenochilus kerefordensis* Miller, Dunbar, & Condra 1933**

- *Solenochilus kerefordensis* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1–240. (p. XXII fgs. 1-3)

- *Solenochilus kerefordense* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322.

Species Determination: The species key in Gordon (1964) as well as the species description in Miller, Dunbar, & Condra (1933) proved useful for species determinations. The key features of *S. kerefordensis* are the presence of an isolated lobe in the center of the suture, rounded margins of the cross-section, the absence of flanks on the ventral side of the umbilical shoulder, four camerae equal to whorl width, and a moderately depressed whorl.

Holotype Material: YPM IP-14003

Material Examined: KUMIP-38824, 50077; YPM IP-014003

***Solenochilus missouriense* Miller, Lane, & Unklesbay 1947**

SYN *Solenochilus missouriensis* Miller, Lane, & Unklesbay 1947

- *Solenochilus missouriensis* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson County, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 4 fgs. 3 & 4)
- *Solenochilus missouriense* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species description and figures in Miller, Lane, & Unklesbay (1947) proved useful for species determinations. Review of the type material at the KUMIP also proved useful for species determinations. The key features of *S. missouriense* are the presence of an isolated lobe in the center of the suture, rounded margins of the cross-section, the presence of flanks on the ventral side of the umbilical shoulder, an umbilical shoulder without lateral projections, a depressed whorl with shallow concave zone on the dorsal side of the cross-section.

Holotype Material: KUMIP-110830

Material Examined: KUMIP-110830, 288587

***Solenochilus newloni* (Hyatt 1891)**

SYN *Asymptoceras newloni* Hyatt 1891

- *Asymptoceras newloni* Hyatt, A. (1891). Carboniferous cephalopods. *Texas Geological Survey Annual Report*, 2, 329-356. (fgs. 48 & 49)
- *Solenochilus newloni* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1–322.

Species Determination: The species key in Gordon (1964) as well as the species description and figures in Hyatt (1891) (fgs. 48 & 49) proved useful for species determinations. The key features of *S. newloni* are the presence of an isolated lobe in the center of the suture, rounded cross-section margins, a depressed venter, and the absence of a keel along the umbilical shoulder.

Material Examined: KUMIP- 38808

***Solenochilus peculiare* Miller & Owen 1934**

- *Solenochilus peculiare* Miller, A. K. & Owen, J. B. (1934). Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History*, 16, 185-272.
- *Solenochilus peculiare* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species description in Miller & Owen (1934) proved useful for species determinations. The key features of *S.*

peculiare are the presence of an isolated saddle in the center of the suture and the width of the whorl that is markedly greater than the height.

Material Examined: UI- 013435

***Solenochilus springeri* (White & St. John 1867)**

SYN *Nautilus (Cryptoceras) springeri* White & St. John 1867

- *Nautilus (Cryptoceras) springeri* White, C. A. & St. John, O. H. (1868). Descriptions of new Subcarboniferous and Coal Measure fossils collected upon the Geological Survey of Iowa; together with a notice of new generic characters observed in two species of brachiopods. *Transactions of the Chicago Academy of Sciences*, 1, 115-127.
- *Solenochilus springeri* Meek, F. B. & Worthen, A. H. (1870). Descriptions of new species and genera of fossils from the Palaeozoic rocks of the western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 22-56.
- *Solenochilus springeri* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) and the species description in Meek & Worthen (1870) proved useful for species determinations. The key features of *S. springeri* are the presence of an isolated lobe in the center of the suture, rounded cross-section margins, a depressed venter, the presence of a keel along the umbilical shoulder, the presence of flanks on the ventral side of the umbilical shoulder, and the presence of lateral projections along the umbilical shoulder.

Material Examined: KUMIP-50264, 288741; UI-012544, 011043

***Solenochilus syracusensis* Miller, Dunbar & Condra 1933**

- *Solenochilus syracusensis* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. XXII f. 4 & 5)
- *Solenochilus syracusense* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species description and figures in Miller, Dunbar, & Condra (1933) (p. XXII f. 4 & 5) proved useful for species determinations. Review of the type material at YPM also proved useful for species determinations. The key features of *S. syracusensis* are the presence of an isolated lobe in the center of the suture, rounded margins of the cross-section, the absence of flanks on the ventral side of the umbilical shoulder, six to seven camerae equal to whorl width, and a broadly depressed whorl.

Holotype Material: YPM IP-14004

Material Examined: YPM IP-14004

Notes on the taxonomy of *Solenochilus*: There are no important notes regarding the taxonomy of this genus.

Order: Orthocerida Kuhn, 1940

Family: Brachycycloceratidae Furnish, Glenister & Hansman, 1962

Genus: Brachycycloceras Miller, Dunbar & Condra 1933

Occurrence Information: Specimens of *Brachycycloceras* came from the Atokan, Desmoinesian, Missourian, and Virgilian of Texas, Kansas, Oklahoma, Missouri, and Kentucky. This species is known to occur throughout the Carboniferous of the United States, the United Kingdom, and Russia (Furnish et al., 1962; Niko & Mapes, 2009).

Diagnostic Features: *Brachyclcoceras* specimens are characterized by a short straight conch with repeated transverse lirae and/or annulations and a small, sub-centric siphuncle connected to an expanded 'deciduous' portion of the conch (Gordon, 1964). The key features used to distinguish species were the angularity of the conch, size of the conch, length, and presence/ absence of annulations (Gordon, 1964). The species key created by Gordon (1964) proved to be extremely useful for species determinations.

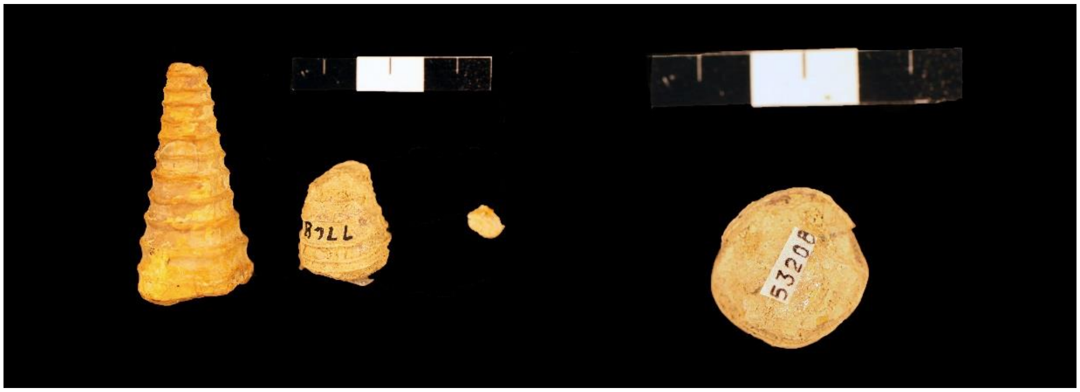

Figure 17: KUMIP-53207 & 53208 *Brachycycloceras crebricinctum.*

Genus: *Brachycycloceras* Miller, Dunbar & Condra 1933

Type Species: *Brachycycloceras normale* Miller, Dunbar, & Condra 1933

***Brachycycloceras bransoni* (Miller & Owen 1934)**

- *Poterioceras bransoni* Miller, A. K. & Owen, J. B. (1934). Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History*, 16, 185-272.
- *Brachycycloceras bransoni* Furnish, W. M. et al. (1962). Brachycycloceratidae, novum, deciduous Pennsylvanian nautiloids. *Journal of Paleontology*, 36(6), 1341-1356.
  (p. 180, f. 9 & In-text f. 3b)

Species Determination: The photographs and species description by Furnish, Glenister, & Hansman (1962; p. 180, f. 9 & In-text f. 3b) and review of the type materials at UI proved useful for species determinations. *Brachycycloceras bransoni* is characterized by a small conch with fine lirae, absence of annulations, and a disproportionately large deciduous portion with a high expansion rate.

Hypotype Material: UI-013347, 013348, 013349

Paratype Material: UI-013342, 013343, 013344, 013345, 013346

Material Examined: UI-004269, 013341, 013342, 013343, 013344, 013345, 013346, 013347, 013348, 013349

***Brachycycloceras crebricinctum* (Girty 1911)**

- *Protocycloceras rushense* var. *crebricinctum* Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21, 119-156. (pg. 144)

- *Protocycloceras rushense* var. *crebricinctum* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1-353.
- *Bracycycloceras crebricinctum* Gordon, M., (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key created by Gordon (1964) proved useful for species determinations. *Brachycycloceras crebricinctum* is characterized by a short conch, presence of annulations, and a widely flared conch and expanded deciduous portion.

Material Examined: KU-53207, 53208, 53209, 53210, 53211; UI- 000609, 004264A, 010790, 010795, 10796, 11041, 33052, 33087A; YPM IP- 010087, 015053

Brachycycloceras curtum **(Meek & Worthen 1860)**

SYN *Cyrtoceras curtum* Meek & Worthen 1860; *Poterioceras curtum (*Meek & Worthen 1860)

- *Cyrtoceras curtum* Meek, F. B. & Worthen, A. H., (1860). Descriptions of new Carboniferous fossils from Illinois and other western states. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 447-472.
- *Poterioceras curtum* Miller, A. K. & Unklesbay, A. G. (1942). Permian nautiloids from western United States. *Journal of Paleontology*, 16(6), 719-738.
- *Bracycycloceras curtum* Furnish, W. M. et al. (1962). Brachycycloceratidae, novum, deciduous Pennsylvanian nautiloids. *Journal of Paleontology*, 36, 1341-1356. (p. 179 f. 5-12 & p. 180 f. 1-6)

Species Determination: The photographs and species description from Furnish, Glenister, & Hansman (1962; p. 179 f. 5-12 & p. 180 f. 1-6) proved useful for species determinations. *Brachycycloceras curtum* is characterized by a small conch covered with fine lirae, the absence of annulations, and a widely flared, expanded deciduous portion of the conch.

Material Examined UI-003116, 003117, 4272, 35799; YPM IP- 015054

***Brachycycloceras longulum* Miller & Owen 1934**

- *Brachycycloceras longulum* Miller, A. K. & Owen, J. B. (1934). Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History*, 16, 185-272. (p. VII fgs. 1-4)
- *Brachycycloceras longulum* Sturgeon, M. T. (1946). Allegheny fossil invertebrates from eastern Ohio-Nautiloidea. *Journal of Paleontology*, 20, 8-37.
- *Brachycycloceras longulum?* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.
- *Brachycycloceras longulum* Niko, S. & Mapes, R. H. (2009). Redescription and New Information on the Carboniferous Cephalopod Brachycycloceras normale Miller, Dunbar and Condra, 1933. *Paleontological Research*, 13(4), 337-343.

Species Determination: The species key created by Gordon (1964), the photographs and species description from Miller & Owen (1934; p. VII fgs. 1-4), and review of the syntype material at UI proved useful for species determinations. *Brachycycloceras longulum* is characterized by a very long, slender conch, the absence of annulations, and a regularly expanding deciduous portion of the conch.

Syntype Material: UI-013378, 013379, 013380, 013381, 013382, 013384

Material Examined: UI-013378, 013379, 013380, 013381, 013382, 013384, 013385

***Brachycycloceras normale* (Miller, Dunbar & Condra 1933)**

SYN *Brachycycloceras kentuckiense* Miller, Dunbar, & Condra 1933

- *Brachycycloceras normale* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. III f. 3-5)

- *Brachycycloceras kentuckiense* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240.
- *Brachycycloceras normale* Furnish, W. M., Glenister, B. F., & Hansman, R. H. (1962). Brachycycloceratidae, novum, deciduous Pennsylvanian nautiloids. *Journal of Paleontology*, 36, 1341-1356. (p. 179 f. 2-4 & p. 180 f. 7-8 & 10-11)
- *Brachycycloceras normale* Niko, S. & Mapes, R. H. (2009). Redescription and New Information on the Carboniferous Cephalopod Brachycycloceras normale Miller, Dunbar and Condra, 1933. *Paleontological Research*, 13(4), 337-343.

Species Determination: The photographs and species descriptions in the publications from Miller, Dunbar, and Condra (1933; p. III f. 3-5) and Furnish, Glenister, and Hansman (1962; p. 179 f. 2-4 & p. 180 f. 7-8 & 10-11) as well as the species key created by Gordon (1964) proved useful for species determinations. Further, review of the type materials maintained at YPM was very useful for species determinations. *Brachycycloceras normale* is characterized by a short conch with fine lirae, the presence of annulations, and a regularly expanding deciduous portion of the conch.

Holotype Material: YPM IP- 013976

Hypotype Material: YPM IP-013977 & 046520

Material Examined: KUMIP- 38765, 38566, 212024; UI-004264, 10796A, 010801, 10802, 010853, 10854, 013383, 33087, 035784, 035796; YPM IP-013976, 013977, 015051, 015052, 046520, 584115

Notes on the taxonomy of *Brachycycloceras*: An important note is the transfer of *Poterioceras curtum (*Meek & Worthen 1860) to *B. curtum* by Furnish, Glenister, & Hansman, (1962) and the transfer of *B. kentuckiense* Miller, Dunbar, & Condra 1933 to *B. normale* by Furnish, Glenister, & Hansman (1962).

Family: Grypoceratidae Hyatt in Zittel 1900

Genus: *Domatoceras* Hyatt 1891

Occurrence Information: Specimens of *Domatoceras* came from the Wolfcampian, Virgilian, Missourian, and Desmoinesian of Nebraska, Missouri, Texas, Oklahoma, Kansas, and Pennsylvania. This genus is widespread throughout the Upper Carboniferous of North America, Europe, Africa, Asia, and Australia (Teichert et al., 1964).

Diagnostic Features: *Domatoceras* specimens are characterized by a large conch with flattened lateral sides, angular umbilical shoulders, a small sub-central siphuncle, and a smooth surface with wide rounded sutures. Key features used to differentiate the species of this genus are the cross-section shape, position of umbilical shoulder, angularity of lateral sides, and conch width and shape. Of particular use was the cross-section figures (shown below) contained in Kummel (1953).

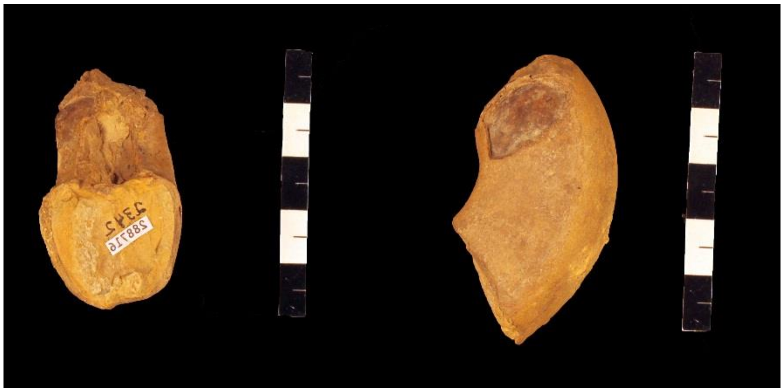

Figure 18: KUMIP-288716 *Domatoceras bradyi*.

Genus: *Domatoceras* Hyatt 1891

Type Species: *Domatoceras umbilicatum* Hyatt 1893

***Domatoceras bradyi* Miller & Unklesbay 1942**

- *Domatoceras bradyi* Miller, A. K. & Unklesbay A. G. (1942). Permian nautiloids from western United States. *Journal of Paleontology*, 16(6), 719-738.
  (p. 116 fgs. 5-6; p. 117 f. 2; text fgs, 1G & 1H)
- *Domatoceras bradyi* Miller, A. K. & Youngquist W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (p. 13 f. 2 & p. 14 fgs. 5-6)
- *Penascoceras bradyi* Ruzhentsev, V. E. & Shimanskiy, V. N. (1954). Nizhnepermskie svernutye i sognutye Nautiloidei yuzhnogo Urala. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta*, 50, 1-150.

Species Determination: The photographs and species descriptions from Miller & Unklesbay (1942; p. 116 fgs. 5-6; p. 117 f. 2; in-text fgs, 1G & 1H) and Miller & Youngquist (1949; p. 13 f. 2 & p. 14 fgs. 5-6) and cross section figures in Kummel (1953; in-text f. 23) were useful for species determinations. *Domatoceras bradyi* is characterized by a large, wide conch with a flat venter and rounded lateral sides (in-text f. 23; Kummel, 1953).

Material Examined: KUMIP-288716; YPM IP-228683

Domatoceras kleihegei Miller, Lane & Unklesbay 1947

- *Domatoceras kleihegei* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 5, fgs. 1-6)
- *Domatoceras kleihegei* Kummel, B. (1953). American Triassic Coiled Nautiloids. *Geological Survey Professional Paper*, 250, 1-149. (in text f. 23)

Species Determination: The photographs and species descriptions from Miller, Lane, & Unklesbay (1947; p. 5, fgs. 1-6), the cross-section figures in Kummel (1953; in-text f. 23), and examination of the type material maintained at KU were informative for species determinations. *Domatoceras kleihegei* is characterized by a conch with slightly rounded lateral sides and a flat venter, smooth rounded sutures, broad rounded nodes along the ventral shoulder of the conch.

Holotype Material: KUMIP-32342

Paratype Material: KUMIP-32091, 32343

Material Examined: KUMIP-32091, 32342, 32343, 38645, 50986, 282369

Domatoceras moorei Miller, Dunbar & Condra 1933

- *Domatoceras moorei* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. XXI fgs. 1-2)
- *Domatoceras moorei* Kummel, B. (1953). American Triassic Coiled Nautiloids. *Geological Survey Professional Paper*, 250, 1-149. (in text f. 23)

Species Determination: The photographs and species descriptions from Miller, Dunbar, and Condra (1933; p. XXI fgs. 1-2) and the cross-section figures in Kummel (1953; in-text f. 23) were useful for species determinations. *Domatoceras moorei* is characterized by a narrow, elongate conch with flat lateral sides and a slightly concave venter (in-text Figure 23; Kummel, 1953).

Material Examined: KUMIP-40872, 49570, 50952, 282318, 282319, 282320, 282321; UI-001408, 6997, 051365, 051473; YPM IP-517369

Domatoceras sculptile **(Girty 1911)**

SYN *Metacoceras sculptile* Girty 1911; *Metacoceras sculptile* (Girty 1911); *Pseudometacoceras sculptile* (Girty 1911)

- *Metacoceras sculptile* Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21, 119-156.
- *Metacoceras sculptile* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353.
- *Pseudometacoceras sculptile* Miller, A. K. et al. (1933): The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240.
- *Domatoceras sculptile* Kummel, B. (1953). American Triassic Coiled Nautiloids. *Geological Survey Professional Paper*, 250, 1-149. (in-text f. 23)

Species Determination: The cross-section figures in Kummel (1953; in-text f. 23) and review of the type material at UI was useful for species determinations. *Domatoceras sculptile* is characterized by a wide conch with flat lateral sides, an angular umbilical shoulder, and a convex venter (in-text f. 23; Kummel, 1953).

Syntype Material: UI-6186

Material Examined: UI-6186, 013431

Domatoceras umbilicatum **Hyatt 1893**

- *Domatoceras umbilicatum* Hyatt, A., (1893). Carboniferous cephalopods: Second paper. *Geological Survey of Texas Annual Report*, 4, 377-474.
- *Domatoceras umbilicatum* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240.
- *Domatoceras umbilicatum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218. (f. 5 & 6)
- *Domatoceras umbilicatum* Kummel, B. (1953). American Triassic Coiled Nautiloids. *Geological Survey Professional Paper* 250: 1-149. (in-text f. 23)

Species Determination: The species descriptions and figures in Miller & Youngquist (1949; f. 5 & 6) and cross-section figures in Kummel (1953; in-text f. 23) were useful for species determinations. *Domatoceras umbilicatum* is characterized by a moderate sized conch with rounded lateral sides, a flat venter, rounded umbilical shoulders, and u-shaped sutures (in-Text f. 23; Kummel 1953).

Material Examined: KUMIP-38619, 38621, 38624, 38653, 38654, 38674, 38675, 38677, 38678, 38681, 38685, 38686, 38689, 38690, 38692, 38832, 38833, 40882, 40883, 50944, 282307, 286896, 288739, 288786, 288896, 288897, 288898, 288899; YPM IP-205182

***Domatoceras williamsi* Miller & Owen 1934**

- *Domatoceras williamsi* Miller, A. K. & Owen, J. B., (1934). Cherokee nautiloids of the northern Mid-Continent region. *University of Iowa Studies in Natural History*, 16, 185-272. (p. XVI f. 4, p. XVII fgs. 1-4, & p. XVIII f. 1)
- *Domatoceras williamsi* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Domatoceras williamsi* Kummel, B. (1953). American Triassic Coiled Nautiloids. *Geological Survey Professional Paper*, 250, 1-149. (in-text f. 23)

Species Determination: The species descriptions and figures in Miller & Owen (1934; p. XVI f. 4, p. XVII fgs. 1-4, & p. XVIII f. 1) and cross section figures in Miller & Youngquist (1949) and Bernhard (1953, in-text f. 23) were useful for species determinations. *Domatoceras williamsi* is characterized by angular ventro-lateral and dorso-lateral shoulders, flat lateral sides, a circular siphuncle positioned off-center towards the venter, and shallow-rounded sutures.

Material Examined: KUMIP- 38618, 38676, 65643, 65644, 288740, 289320, 289429, 289430, 289431; UI- 013417, 013419, 013420, 013422, 013424, 013426, 013428, 013429, 013430, 013431, 013432, 013434; YPM IP-205196

Notes on the taxonomy of *Domatoceras*: An important note is the transfer of *Metacoceras sculptile* Girty 1915 to *Domatoceras sculptile* by Kummel (1953).

Family: Spyroceratidae Shimizu & Obata 1935

Genus: *Euloxoceras* Miller, Dunbar & Condra 1933

Occurrence Information: Specimens of *Euloxoceras* came from the Desmoinesian, Missourian, and Virgilian strata of Oklahoma, Kansas, and Texas. This genus is known from the Upper

Mississippian and Pennsylvanian of the United States (Teichert et al., 1964).

Diagnostic Features: *Euloxoceras* is characterized by a small, slender orthoconic conch, an ovular cross section shape, straight sutures, and the sub-central position of the siphuncle towards the dorsum. The species of this genus can be distinguished by comparison of cross section shape and conch expansion.

Figure 19: KUMIP-28885 *Euloxoceras greenei*.

Genus: *Euloxoceras* Miller, Dunbar, & Condra 1933

Type species: *Euloxoceras greenei* Miller, Dunbar, & Condra 1933

Euloxoceras greenei Miller, Dunbar & Condra 1933

- *Euloxoceras greenei* Miller, A. K. et al. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, *9*, 1-240. (p. 1 fgs. 12-15)
- *Euloxoceras greenei* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species descriptions and figures in Miller, Dunbar, & Condra (1933) (p. 1 fgs. 12-15) and the species key in Gordon (1964) were useful for species determinations.

Review of the type material maintained at YPM was particularly useful for species determinations. *Euloxoceras greenei* is characterized by having an ovular cross section shape and a conch that expands more moderately than other related species.

Holotype Material: YPM IP- 013964A

Paratype Materials: YPM IP- 013964, 013964B, 013965, 013965A, 013970, 013971, 013972, 013974

Material Examined: KUMIP- 38571, 38572, 38573, 38574, 38575, 38576, 38577, 38578, 38579, 38758, 288857, 288858; YPM IP- 013964, 013964A, 013964B, 013965, 013965A, 013970, 013971, 013972, 013974, 376171

Notes on the taxonomy of *Euloxoceras*: There are no important notes regarding the taxonomy of this genus.

Family: Orthoceratidae M'Coy 1844

Genus: *Orthoceras* Bruguiere 1789

Occurrence Information: Specimens of *Orthoceras* came from the Desmoinesian, Missourian, and Virgilian of Oklahoma, Texas, Kansas, and Missouri. This genus has a global distribution and is known from the Middle Ordovician to Permian (Teichert et al., 1964; Alroy, 2013).

Diagnostic Features: *Orthoceras* is characterized by a orthoconic conch, a small siphuncle positioned sub-central towards the venter, fine lirae across the conch surface, and longitudinal cross-section morphology. Species of this genus are distinguished by comparison of siphuncle position, cross-section shape, and the degree of conch tapering.

Genus: *Orthoceras* Bruguiere 1789

Type Species: *Orthoceras regularis* Schlotheim 1820

***Orthoceras longissimicameratum* Miller 1930**

- *Orthoceras longissimicameratum* Miller, A. K. (1930). A new ammonoid fauna of Late Paleozoic age from western Texas. *Journal of Paleontology*, 4(4), 383-412. (p. 38 fgs. 1 & 2)

Species Determination: The species description and figures in Miller (1930) (p. 38 fgs. 1 & 2) and review of the type material at YPM proved useful for species determinations. The key features of *O. longissimicameratum* are a circular cross-section, a small, central siphuncle, the surface of the phragmocone marked with several transverse ridges, straight sutures, and a characteristically long camerae.

Syntype Material: YPM IP-012928.A, 012928.B, 012928.C, 012928.D, 012928.E, 012928.F, 012928.G

Material Examined: YPM IP-009124, 012928.A, 012928.B, 012928.C, 012928.D, 012928.E, 012928.F, 012928.G, 416225

***Orthoceras dunbari* Foerste 1936**

- *Orthoceras dunbari* Foerste, A. F. (1936). Silurian cephalopods of the Port Daniel area on Gaspé Peninsula, in eastern Canada. *Bulletin of Denison University, Journal of the Scientific Laboratories*, 31, 21-92. (p. 17 fgs. 3a & 3b)
- *Orthoceras dunbari* White, R. D. & Skorina, L. K. (1999). A Type Catalog of Fossil Invertebrates (Mollusca: Actinoceratoiclea, Bactritoidea, Endoceratoidea, and Nautiloidea) in the Yale Peabody Museum. *Postilla*, 219.

Species Determination: Examination of the type material at YPM proved useful for species determinations. The key features of *O. dunbari* are an ovular cross section, a small siphuncle positioned towards the venter of the conch, and curved sutures.

Holotype Material: YPM IP-010549

Material Examined: YPM IP-010549, 228672

***Orthoceras kansasense* Sayre 1930**

- *Orthoceras kansasense* Sayre, A. N. (1930). The fauna of the Drum Limestone of Kansas and western Missouri. *University of Kansas Science Bulletin*, 19(8), 1-203.
  (p. XIX fgs. 9-12)

Species Determination: The species description and figures in Sayre (1930) (p. XIX fgs. 9-12) proved useful for species determinations. The key features of *O. kansasense* are the elliptical shape of the cross-section, lack of surface ornamentation, gradual tapering of the body chamber, and the sub-central position of the siphuncle towards the venter.

Material Examined: KUMIP-32016, 32271, 58200, 58201, 58202, 58203, 58204, 58798; YPM IP-015049, 015055, 228663, 228668, 228723, 228724, 376919, 376920

***Orthoceras occidentale* (Swallow 1858)**

SYN *Nautilus occidentalis* Swallow 1858

- *Nautilus occidentalis* Swallow, G. C. (1858). Rocks of Kansas with Descriptions of New Permian Fossils. *Transactions of the Academy of Sciences St. Louis*, 1(2), 1-27.
- *Nautilus occidentalis* Keyes, C. R. (1894). Paleontology of Missouri. *Missouri Geological Survey*, 4, 1-226.
- *Orthoceras occidentale* Sayre, A. N. (1930). The fauna of the Drum Limestone of Kansas

and western Missouri. *University of Kansas Science Bulletin*, 19(8),1-203.

(p. XIX fgs. 1-2a)

Species Determination: The species description and figures in Sayre (1930) (p. XIX fgs. 1-2a) proved useful for species determinations. The key features of *O. occidentale* are the tapering of the body chamber, the convex morphology of the sutures, and the sub-central position of the siphuncle towards the venter.

Material Examined: YPM IP- 015055, 228665; KUMIP-32026,32030

Notes on the taxonomy of *Orthoceras*: An important note is the synonymy of *Orthoceras unicamera* Smith 1938 with *Hebetorthoceras unicamera* by Kröger & Mapes (2005) and the transfer of *Nautilus occidentalis* Swallow 1858 to *O. occidentale* by Sayre (1930).

Order: Pseudorthocerida Barskov 1968

Family: Pseudorthoceratidae Flower & Caster 1935

Genus: *Hebetorthoceras* Kröger & Mapes 2005, *Mooreoceras* Miller, Dunbar, & Condra 1933, and *Pseudorthoceras* Girty 1911

Occurrence Information: Specimens of *Hebetorthoceras* came from the Desmoinesian of Arkansas, Oklahoma, and Texas. This genus is known from the Pennsylvanian of North America (Alroy, 2013). Specimens of *Mooreoceras* came from the Morrowan, Atokan, Desmoinesian, and Missourian strata of Missouri, Oklahoma, Kansas, Nebraska, and Kentucky. This genus is widely distributed through the Upper Devonian to Upper Permian strata of North America, Europe, Asia, and Australia (Teichert et al., 1964). Specimens of *Pseudorthoceras* came from the Atokan, Desmoinesian, Missourian, Virgilian, and Wolfcampian strata of Nebraska, Oklahoma, Kansas, Iowa, Texas, and Kentucky. This genus is known from the Upper Devonian to Lower Permian strata of North America, Europe, Asia, and Australia.

Diagnostic Features: *Hebetorthoceras* is characterized by an orthoconic conch, with little to no ornamentation along the conch surface, straight sutures, a circular cross-section, cylindrical connecting rings within the inner conch, a central siphuncle, and a very short first body chamber. Species are distinguished by comparison of degree of compression of the cross-section, the angularity of the conch, and shell ornamentation. *Mooreoceras* is characterized by a smooth surfaced, orthoconic conch, the shift of the siphuncle position from central to ventral in later conch development, the shift in suture morphology from straight to faintly arched in later conch development, and the lack of siphuncular deposits in conch cross-section. This genus has the reputation for being a ‘garbage can’ taxon as it had over 40 species when it was originally named

(Kröger & Mapes, 2005). Species can be distinguished by comparison of conch size, morphology of connecting rings in the inner conch, and cross-sectional morphology. Of particular use for species determinations was the species key created by Gordon (1964). *Pseudorthoceras* is very similar in form to *Mooreoceras* but can be distinguished through comparison of the following features: the presence of siphuncular deposits in conch cross-section; the shape of the cross-sections; siphuncle position; and conch shape. According to Miller & Youngquist (1949) there is only one valid species within this genus.

Figure 20: KUMIP-38584 *Mooreoceras* sp.

Genus: ***Hebetorthoceras*** Kröger and Mapes 2005

Genotype: Hebetorthoceras unicamera (Smith 1938)

Hebetorthoceras unicamera **(Smith 1938)**

SYN *Orthoceras unicamera* Smith 1938

- *Orthoceras unicamera* Smith, H. J. (1938). *The Cephalopod Fauna of the Buckhorn Asphalt*. University of Chicago Libraries: Chicago, 40.
- *Orthoceras unicamera* Gordon, M., (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

- *Michelinoceras unicamera* Hewitt, R. A. et al. (1989). Bathymetric limits of a Carboniferous orthoconic nautiloid deduced by finite element analysis. *Palaios*, 4, 157-167.
- *Hebetorthoceras unicamera* Kröger, B. & Mapes, R. H. (2005). Revision of some common Carboniferous genera of North American orthocerid nautiloids. *Journal of Paleontology*, *79*(5), 1002-1011.

Species Determination: The species description in Kröger & Mapes (2005) proved useful for species determinations. *Hebetorthoceras unicamera* is characterized by straight sutures, a circular cross-section, a central siphuncle, straight margins, and the presence of many transverse lirae along the conch surface.

Material Examined: KUMIP-500534, 500535, 500543, 500551, 500552, 500553; YPM IP-228656, 228657, 228658, 228662, 416223, 416224, 416226

Genus: *Mooreoceras* Miller, Dunbar, & Condra 1933

Type species: *Mooreoceras normale* Miller, Dunbar, & Condra 1933

***Mooreoceras bakeri* Miller, Dunbar, & Condra 1933**

- *Mooreoceras bakeri* Miller, A. K. et al. (1933): The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. II fgs. 11-13)
- *Mooreoceras bakeri* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species description and figures in Miller, Dunbar, & Condra (1933) (p. II fgs. 11-13) proved useful for species determinations. Review of the type material at YPM was also useful for species determinations. The key features of *M. bakeri* are the elliptical morphology of the cross-section and the pyriform morphology of the connecting rings within the interior conch.

Holotype Material: YPM IP-013959

Paratype Material: YPM IP-013961

Plesiotype Material: KUMIP- 32001

Material Examined: KUMIP- 32001, 32041; YPM IP-013959, 013961

Mooreocoeras condrai **Newell 1936**

- *Mooreoceras condrai* Newell, N. D. (1936). Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III. Cephalopoda. *Journal of Paleontology*, 10(6), 481-489. (p. 69 fgs. 3a-3e)
- *Mooreoceras condrai* Gordon, M. Jr. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species descriptions and figures in Newell (1936) (p. 69 fgs. 3a-3e) proved useful for species determinations. The key features of *M. condrai* are the circular morphology of the cross-section, the globular morphology of the connecting rings in the inner conch, and the ventral position of the siphuncle throughout conch development.

Material Examined: KUMIP-32007, 38342, 38343, 38664, 44102; UI-013635; YPM IP-205180, 228704

Mooreoceras conicum **Miller, Lane & Unklesbay 1947**

- *Mooreoceras conicum* Miller, A. K., Lane, J. H., & Unklesbay, A. G. (1947). A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions*, 2, 1-11. (p. 1 fgs. 2 & 3)

- *Mooreoceras conicum* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species descriptions and figures in Miller, Lane, & Unklesbay (1947) (p. 1 fgs. 2 & 3) proved useful for species determinations. The key features of *M. conicum* are the circular morphology of the cross-section, the globular morphology of the connecting rings in the inner conch, and the central position of the siphuncle throughout conch development.

Material Examined: KUMIP- 38601, 38604, 38609, 38696, 32074, 32075, 32076, 32077, 32078; UI-013367

***Mooreoceras giganteum* Clifton 1942**

- *Mooreoceras gigantea* Clifton, R. L. (1942). Invertebrate faunas from the Blaine and the Dog Creek formations of the Permian Leonard Series. *Journal of Paleontology*, 16, 685-699.
- *Mooreoceras giganteum* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
  (p. 3 f. 9, p. 4 fgs. 7-9, p. 5 f. 1)
- *Mooreoceras giganteum* Gordon, M. Jr. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species description and figures in Miller & Youngquist (1949) (p. 3 f. 9, p. 4 fgs. 7-9, p. 5 f. 1) proved useful for species determinations. The key features of *M. giganteum* are the circular morphology of the cross-section, the pyriform morphology of the connecting rings within the inner conch, and the enormous size of the conch.

Material Examined: KUMIP-38799

Mooreoceras normale Miller, Dunbar & Condra 1933

- *Mooreoceras normale* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. II fgs. 5-7)
- *Mooreoceras normale* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Mooreoceras normale* Gordon, M. Jr. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.
- *Mooreoceras normale* Kröger B. & Mapes R. H. (2005). Revision of some common Carboniferous genera of North American orthocerid nautiloids. *Journal of Paleontology*, 79(5), 1002-1011.

Species Determination: The species key in Gordon (1964) as well as the species description in Miller & Youngquist (1949) and figures in Miller, Dunbar, & Condra (1933) (p. II fgs. 5-7) proved useful for species determinations. Review of the type material at YPM also proved useful for species determinations. The key features of *M. normale* are the circular morphology of the cross-section, the pyriform morphology of the connecting rings within the inner conch, and the moderate size of the conch.

Holotype Material: YPM IP-013956

Material Examined: KUMIP-32096, 38339, 38340, 38341, 38502, 38503, 38504, 38505, 38506, 38507, 38508, 38509, 38510, 38511, 38523, 38524, 38526, 38528, 38529, 38531, 38532, 38534, 38539, 38594, 38595, 38598, 38599, 38600, 38603, 38605, 38608, 38613, 38646, 38749, 38750; UI-13351, 13352, 13353, 13354, 13356, 13357, 13358, 13359, 13360, 13361, 13362, 13363, 13364, 13365, 13366, 13368, 13369, 13370, 13371, 13372, 13373, 13375, 013376A, 013376B, 13684; YPM IP-013956, 013957, 228704, 229173

Mooreoceras ovale **Young 1942**

- *Mooreoceras ovale* Young, J. A. (1942). Pennsylvanian scaphopoda and cephalopoda from New Mexico. *Journal of Paleontology*, 16, 120-125. (p. 20 fgs. 10 & 14)
- *Mooreoceras ovale* Gordon, M. (1964): Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species descriptions and figures in Young (1942) (p. 20 fgs. 10 & 14) proved useful for species determinations. The key features of *M. ovale* are the elliptical morphology of the cross-section and the globular morphology of the connecting rings within the interior conch.

Material Examined: KUMIP- 38527, 38530, 38536, 38540, 38544, 38606, 38611, 38627, 38628, 38714, 38764; YPM IP- 228720

Mooreoceras tuba **(Girty 1911)**

SYN *Orthoceras tuba* Girty 1911

- *Orthoceras tuba* Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21, 119-156.
- *Orthoceras tuba* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1-353.

- *Mooreoceras tuba* Miller, A. K. et al. (1933): The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240. (p. II fgs. 2-4)
- *Mooreoceras tuba* Gordon, M. (1964): Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322.

Species Determination: The species key in Gordon (1964) as well as the species descriptions and figures in Miller, Dunbar, & Condra (1933) (p. II fgs. 2-4) proved useful for species determinations. Review of the type material at YPM also proved useful for species determinations. The key features of *M. tuba* are the circular morphology of the cross-section, the globular morphology of the connecting rings within the inner conch, and
the orad flaring of the body chamber.

Hypotype Material: YPM IP-013958

Material Examined: YPM IP-013958

***Mooreoceras wedingtonianum* Gordon 1964**

- *Mooreoceras wedingtonianum* Gordon, M. (1964). Carboniferous cephalopods of Arkansas. *United States Geological Survey Professional Paper*, 460, 1-322. (p. 8 fgs. 17 & 18)

Species Determination: The species key and figures in Gordon (1964) (p. 8 fgs. 17 & 18) proved useful for species determinations. The key features of *M. wedingtonianum* are the circular morphology of the cross-section, the globular morphology of the connecting rings within the inner conch, and the absence of flaring along the body chamber.

Material Examined: KUMIP- 38538, 38788

Notes on the taxonomy of *Hebetorthoceras* & *Mooreoceras*: An important note is the transfer of

Orthoceras unicamera Smith 1938 to *H. unicamera* by Kröger & Mapes (2005).

Genus: *Pseudorthoceras* Girty 1911

Type species: *Pseudorthoceras knoxense* (McChesney 1860)

Pseudorthoceras knoxense (McChesney 1860)

SYN *Orthoceras knoxense* McChesney 1860

- *Orthoceras knoxense* McChesney, A. M. (1860). Descriptions of new species of fossils from the Paleozoic rocks of the western states. *Transactions of the Chicago Academy of Sciences*, 1, 1-76.
- *Pseudorthoceras knoxense* Girty, G. H. (1911). On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, 21, 119-156.
- *Pseudorthoceras knoxense* Girty, G. H. (1915). Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1-353.
- *Pseudorthoceras knoxense* Miller, A. K., Dunbar, C. O., & Condra, G. E. (1933). The nautiloid cephalopods of the Pennsylvanian System in the Mid-Continent region. *Nebraska Geological Survey Bulletin*, 9, 1-240.
- *Pseudorthoceras knoxense* Miller, A. K. & Youngquist, W. (1949). American Permian nautiloids. *Geological Society of America Memoir*, 41, 1-218.
- *Pseudorthoceras knoxense* Kröger, B. & Mapes R. H. (2005). Revision of some common Carboniferous genera of North American orthocerid nautiloids. *Journal of Paleontology*, 79(5), 1002-1011.

Species Determination: The species descriptions in Miller, Dunbar, & Condra (1933), Miller &

Youngquist (1949), and Kröger & Mapes (2005) proved useful for species determinations. According to Miller & Youngquist (1949) there is only one valid species within the genus.

Material Examined: KUMIP- 288837, 288838, 288839, 288840, 288841, 32023, 32025, 32024, 38550, 38565, 38592, 38660, 38702, 500537, 500538, 500540, 52560, 65691, 65692, 65693, 65694, 65695, 65696, 65697; UI-013339, 012482, 012483, 012484, 012485, 012486; YPM IP - 228354, 228360, 228364, 228365, 228379, 228380, 228381, 228383, 228384, 228385, 228386, 228387, 228393, 228414, 228416, 228417, 228418, 228419, 228423, 228430, 228432, 229036, 229033, 229034, 229035, 229148, 229150, 229151, 229152, 229153, 229154, 229155, 229156, 229157, 229158, 229159, 229160

Notes on the taxonomy of *Pseudorthoceras*: An important note is the transfer of *Orthoceras knoxense* McChesney 1860 to *Pseudorthoceras knoxense* by Girty (1911).

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Appendix 1: Statistical Analyses

Statistical Analyses:

All statistical analyses were performed using Minitab® Statistical Software *Minitab* v. 17 and *R-Studio Version 3.4.0 (2017-04-21) "You Stupid Darkness"* with the *bootstrap* package. Geographic range data were analyzed separately across all cephalopods, as well as individually for nautiloids and ammonoids. Species geographic range size data was tested for normality within each temporal stage through Anderson-Darling normality test and review of histograms of data distribution throughout temporal stages. The Anderson-Darling normality test revealed that the geographic range size data distribution within each temporal stage was not normally distributed ($p<0.005$). Further, review of histograms revealed that distributions were left-skewed across all temporal stages within every data grouping. Data was transformed using the log-transformation to normalize data; further, non-parametric analyses were utilized on untransformed data to account for non-normality and to minimize assumptions. Descriptive statistics for non-transformed data are contained in Table 1.1, 1.2, and 1.3. Descriptive statistics for transformed data are contained in Table 2.1, 2.2, and 2.3.

Analyses performed on non-transformed data used the Mann-Whitney U test, and the Kolmogorov Smirnov test. By contrast, the two-sample t-test, ANOVA, and analyses considering the relationship between speciation and extinction rates and geographic range (mentioned below) were performed using the transformed data set. Speciation and extinction rates were calculated for nautiloids using the formula presented in Rode & Lieberman (2005); this was implemented using *Excel*. Correlations between geographic range size and speciation and extinction rates were assessed using the Kendall's Rank Correlation Test. Analysis of biases tests were performed in *Excel* and *R-Studio Version 3.4.0 (2017-04-21) –You Stupid Darkness*. In this appendix, please find copies of all outputs for statistical analyses performed in this study.

Descriptive Statistics:

Table 1.1

Descriptive Statistics: Wolfcampian, Virgilian, Missourian, Desmoinesian, Atokan, Morrowan (Non-Transformed Data) All Cephalopods

```
              Total
Variable      Count   N  N*       Mean    SE Mean       StDev     Variance  Median
Wolfcampian      79  13  66        508        436        1574      2476778      79
Virgilian        79  38  41  452535495  452518737  2789512842  7.78138E+18      79
Missourian       79  55  24      11670       4484       33258   1106072985      79
Desmoinesian     79  41  38       2800       1616       10348    107077601      79
Atokan           79  15  64       3759       2531        9804     96114562      79
Morrowan         79   8  71       2022       1288        3644     13277185      79
```

*All Cephalopod Data

Table 1.2

Descriptive Statistics: Wolfcampian_1, Virgilian_1, Missourian_1, Desmoinesian, Atokan_1, Morrowan_1 (Non-Transformed Data) Ammonoids

```
                Total
Variable        Count  N  N*   Mean  SE Mean  StDev    Variance  Median
Wolfcampian_1      22  6  16   65.5     13.0   31.8      1013.5    78.5
Virgilian_1        22  9  13  46264    22071  66214  4384298716      79
Missourian_1       22  8  14  21258    18017  50961  2596978574      79
Desmoinesian_1     22  8  14   59.0     12.8   36.1      1305.5    78.5
Atokan_1           22  8  14   3165     3109   8792    77302482      79
Morrowan_1         22  5  17   1846     1768   3952    15620364      79
```

*All Ammonoid Data

Table 1.3

Descriptive Statistics: Wolfcampian_2, Virgilian_2, Missourian_2, Desmoinesian_2, Atokan_2, Morrowan_2(Non-Transformed Data) Nautiloids

```
                Total
Variable        Count   N  N*       Mean    SE Mean       StDev     Variance  Median
Wolfcampian_2      57   7  50        888        810        2142      4588340      79
Virgilian_2        57  29  28  592963188  592955914  3193165320  1.01963E+19      79
Missourian_2       57  47  10      10038       4338       29741    884530277      79
Desmoinesian_2     57  33  24       3464       1996       11468    131513472      79
Atokan_2           57   7  50       4439       4360       11536    133071213      79
Morrowan_2         57   3  54       2316       2238        3876     15022137      79
```

*All Nautiloid Data

Table 2.1

Descriptive Statistics: Wolfcampian, Virgilian, Missourian, Desmoinesian, Atokan, Morrowan (Transformed)

```
              Total
Variable      Count   N  N*   Mean  SE Mean  StDev  Variance  Median
Wolfcampian      79  13  66  4.313    0.524  1.890     3.570   4.364
Virgilian        79  38  41  5.960    0.786  4.845    23.474   4.364
Missourian       79  55  24  5.646    0.488  3.618    13.092   4.364
Desmoinesian     79  41  38  4.362    0.489  3.134     9.823   4.364
Atokan           79  15  64   4.05     1.02   3.96     15.72    4.36
Morrowan         79   8  71  5.513    0.753  2.129     4.532   4.364
```

*All Cephalopods

Table 2.2

Descriptive Statistics: Wolfcampian_1, Virgilian_1, Missourian_1, Desmoinesian_1, Atokan_1, Morrowan_1 (Transformed Data)

```
                Total
Variable        Count  N  N*   Mean  SE Mean  StDev  Variance  Median
Wolfcampian_1      22  6  16  3.539    0.824  2.019     4.075   4.364
Virgilian_1        22  9  13   5.96     1.90   5.70     32.52    4.36
Missourian_1       22  8  14   6.02     1.10   3.10      9.63    4.36
Desmoinesian_1     22  8  14  3.092    0.832  2.355     5.544   4.364
Atokan_1           22  8  14   3.02     1.75   4.95     24.51    4.36
Morrowan_1         22  5  17  5.310    0.946  2.116     4.478   4.364
```

*All Ammonoids

Table 2.3

Descriptive Statistics: Wolfcampian_, Virgilian_2, Missourian_2, Desmoinesian, Atokan_2, Morrowan_2 (Transformed Data)

```
                Total
Variable        Count   N  N*   Mean  SE Mean  StDev  Variance  Median
Wolfcampian_2      48   7  41  4.977    0.613  1.622     2.632   4.364
Virgilian_2        57  29  28  5.962    0.866  4.661    21.729   4.364
Missourian_2       57  47  10  5.583    0.543  3.725    13.876   4.364
Desmoinesian_2     57  33  24  4.670    0.566  3.250    10.565   4.364
Atokan_2           57   7  50  5.216    0.852  2.255     5.083   4.364
Morrowan_2         57   3  54   5.85     1.49   2.57      6.63    4.36
```

*All Nautiloids

Tests for Normality:

Anderson-Darling normality test:

H_n: The data follows a normal distribution

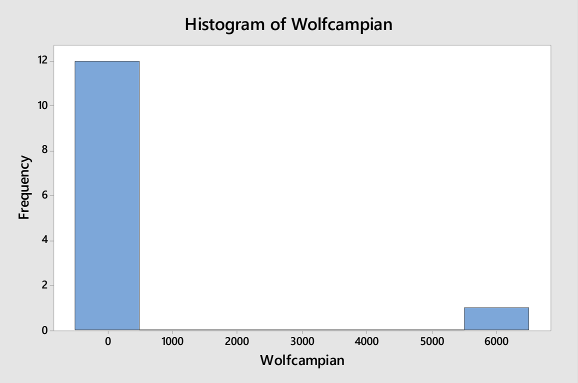
H_a: The data does not follow a specified distribution

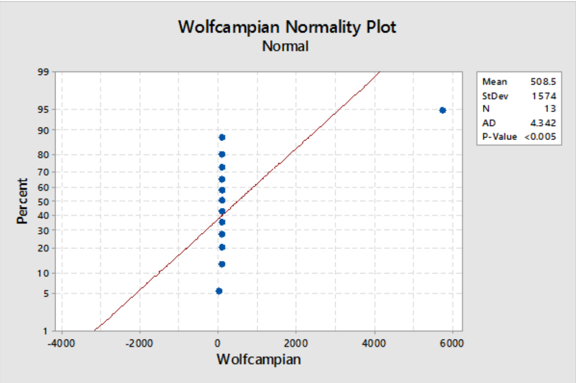
Probability plots were generated for distribution data in each temporal bin. Distribution data was significant ($p<0.005$) for Anderson-Darling normality test which indicates that the data is not normally distributed. See probability plots below.

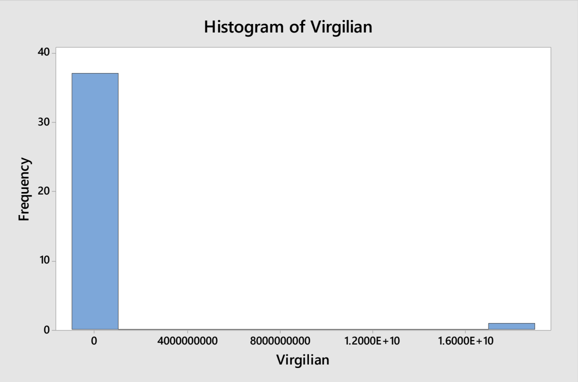
Histograms:

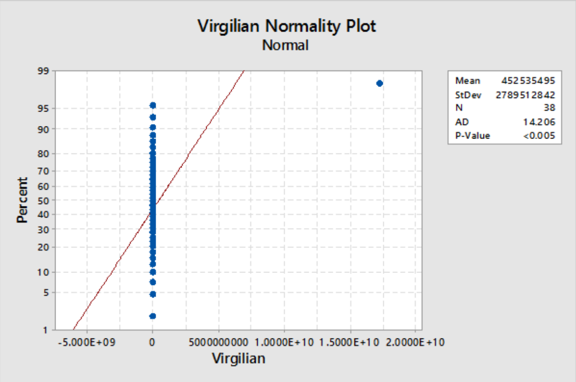
Review of histograms revealed that distribution was left-skewed in all data tiers. Data was transformed using the log-transformation to normalize data. Please see histograms for data distribution across all cephalopods below.

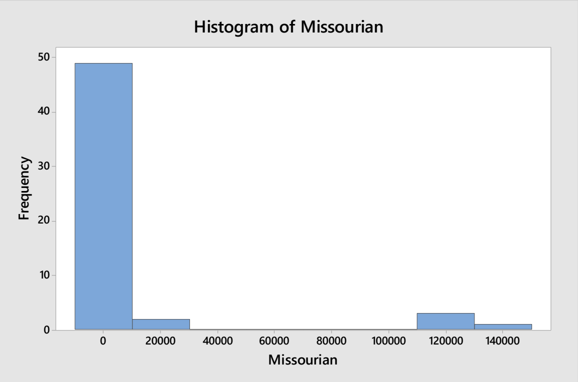
Normality Tests for Non-Transformed Data Set-All Cephalopods:

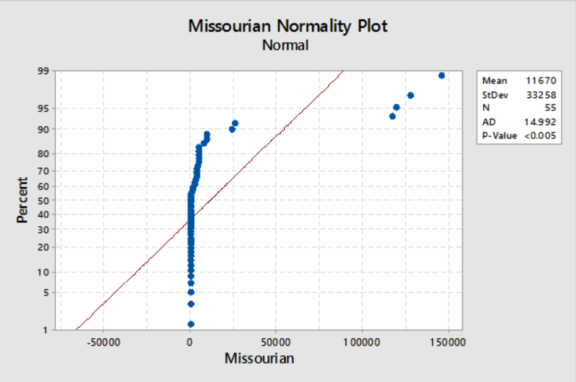


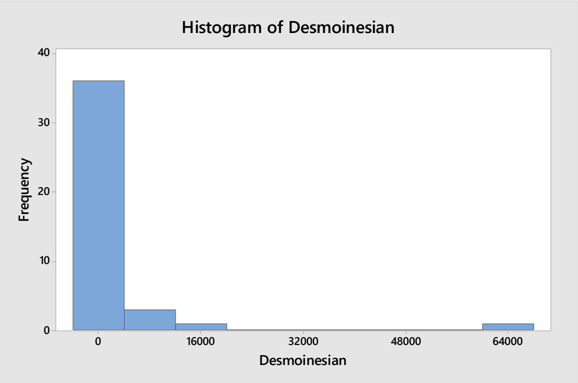


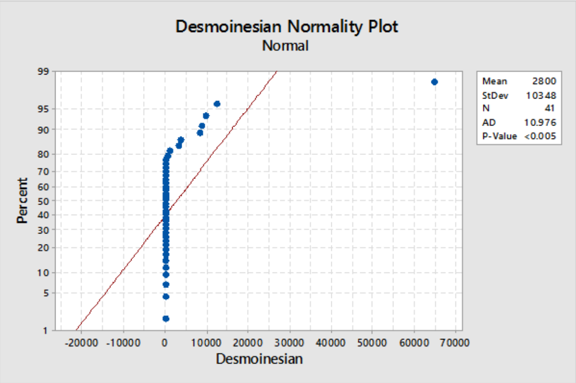


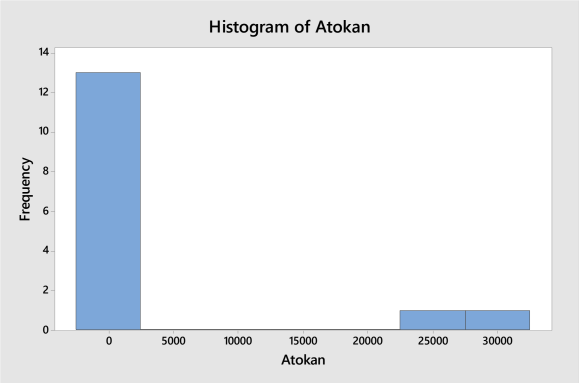


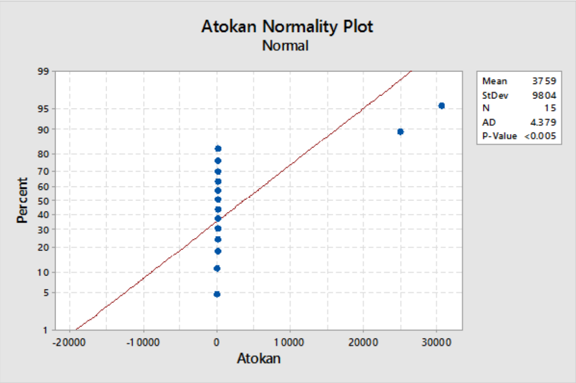


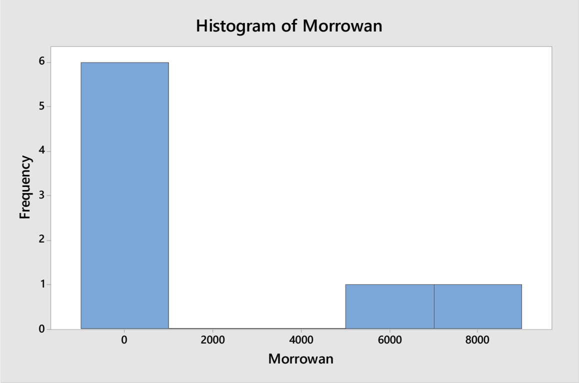


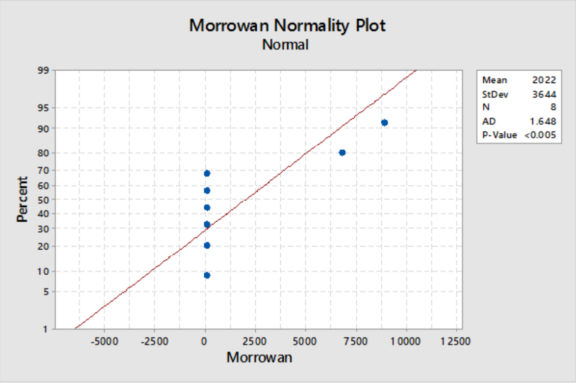




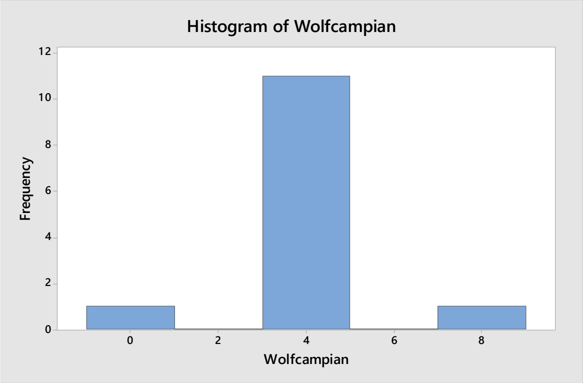


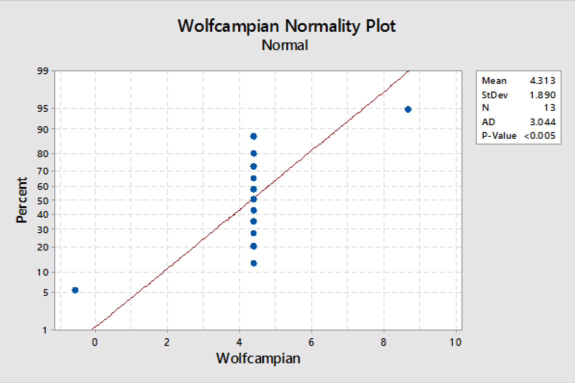


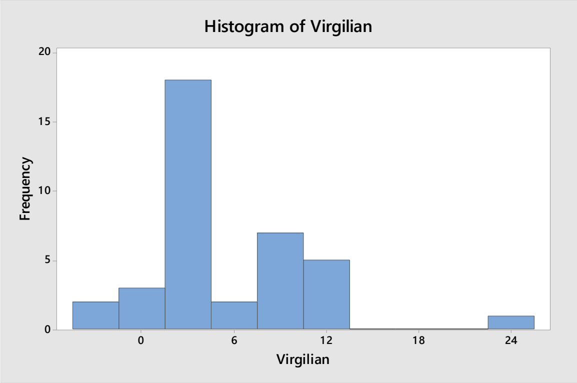


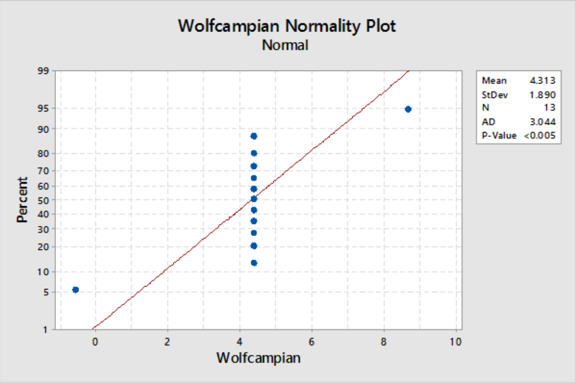


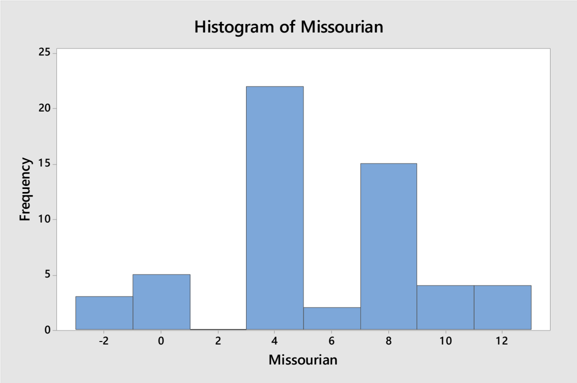
Normality Tests for Log-Transformed Data Set-All Cephalopods:

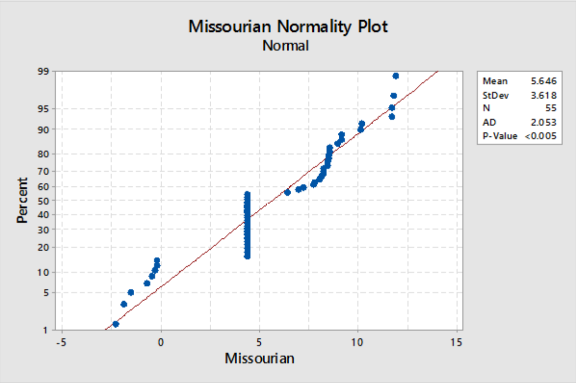


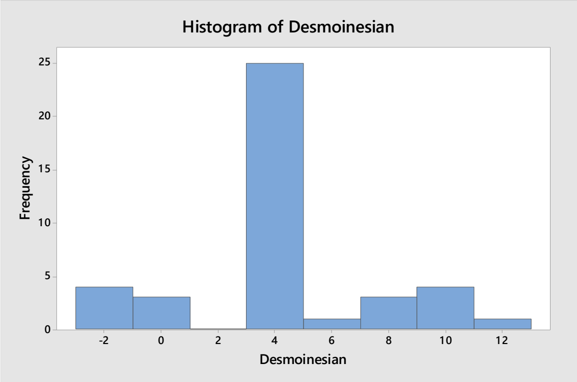


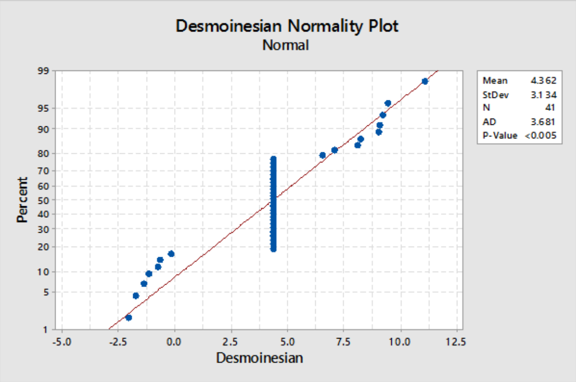


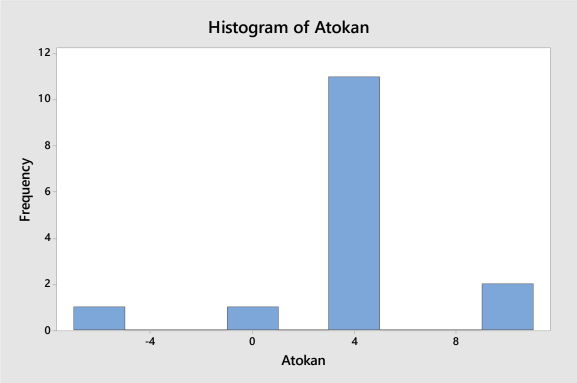


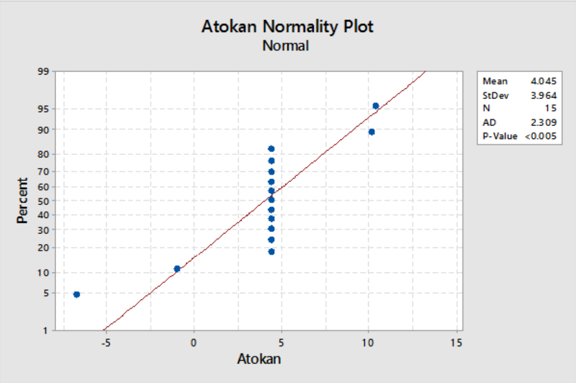

Histogram of Missourian

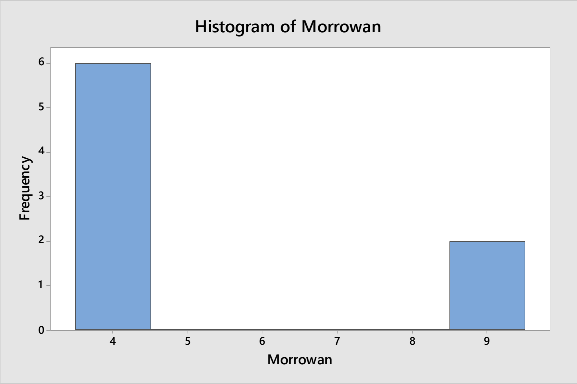

Missourian Normality Plot
Normal

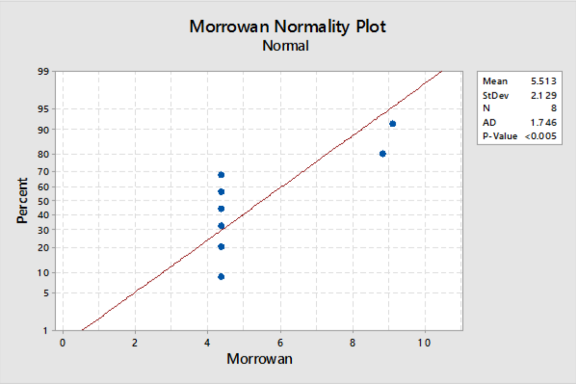

Histogram of Desmoinesian


Desmoinesian Normality Plot
Normal


Histogram of Atokan


Atokan Normality Plot
Normal


Histogram of Morrowan


Morrowan Normality Plot
Normal

Mann-Whitney U Test:

Hn: There is no difference in median between two groups

Ha: There is a statistically significant difference in medians between temporal bins

Mann-Whitney U Tests were non-parametric tests utilized to compare the non-transformed medians between temporal bins without the assumption of normality or equal variance. Data was significant if p≤0.05.

Mann Whitney U Test-Comparison across all cephalopods:

Mann-Whitney Test and CI: Wolfcampian, Virgilian

```
              N  Median
Wolfcampian  13      79
Virgilian    38      79
Point estimate for η1 - η2 is 43
95.2 Percent CI for η1 - η2 is (-2909,1352)
W = 257.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.0819
The test is significant at 0.0345 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian, Missourian

```
              N  Median
Wolfcampian  13    78.5
Missourian   55    78.5
Point estimate for η1 - η2 is 0.0
95.1 Percent CI for η1 - η2 is (-3361.6,-0.1)
W = 350.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.1264
The test is significant at 0.1044 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian, Desmoinesian

```
               N  Median
Wolfcampian   13    78.5
Desmoinesian  41    78.5
Point estimate for η1 - η2 is 0.0
95.0 Percent CI for η1 - η2 is (0.1,-0.0)
W = 347.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.8476
The test is significant at 0.8188 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian, Atokan

```
              N  Median
Wolfcampian  13    78.5
Atokan       15    78.5
Point estimate for η1 - η2 is -0.0
```

```
95.2 Percent CI for η1 - η2 is (-0.1,0.0)
W = 188.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian, Morrowan

```
              N  Median
Wolfcampian  13    78.5
Morrowan      8    78.5
Point estimate for η1 - η2 is -0.0
95.4 Percent CI for η1 - η2 is (-3170.2,-0.2)
W = 130.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.3653
The test is significant at 0.1867 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian, Missourian

```
             N  Median
Virgilian   38      79
Missourian  55      79
Point estimate for η1 - η2 is 95
95.1 Percent CI for η1 - η2 is (-2550,-588)
W = 1771.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.9098
The test is significant at 0.9001 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian, Desmoinesian

```
               N  Median
Virgilian     38      79
Desmoinesian  41      79
Point estimate for η1 - η2 is -37
95.1 Percent CI for η1 - η2 is (2111,-117)
W = 1679.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.1199
The test is significant at 0.0561 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian, Atokan

```
            N  Median
Virgilian  38      79
Atokan     15      79
Point estimate for η1 - η2 is -129
95.1 Percent CI for η1 - η2 is (-2568,-569)
W = 1097.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.1609
The test is significant at 0.0907 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian, Morrowan

```
            N  Median
Virgilian  38      79
Morrowan    8      79
Point estimate for η1 - η2 is -65
95.3 Percent CI for η1 - η2 is (1605,3033)
```

```
W = 919.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4599
The test is significant at 0.3934 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian, Desmoinesian

```
               N  Median
Missourian    55    78.5
Desmoinesian  41    78.5
Point estimate for η1 - η2 is -0.0
95.0 Percent CI for η1 - η2 is (-0.0,944.2)
W = 2915.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.0673
The test is significant at 0.0515 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian, Atokan

```
             N  Median
Missourian  55    78.5
Atokan      15    78.5
Point estimate for η1 - η2 is -0.0
95.0 Percent CI for η1 - η2 is (0.1,2260.6)
W = 2052.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.1565
The test is significant at 0.1342 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian, Morrowan

```
             N  Median
Missourian  55    78.5
Morrowan     8    78.5
Point estimate for η1 - η2 is -0.0
95.1 Percent CI for η1 - η2 is (-77.7,3361.3)
W = 1773.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.7964
The test is significant at 0.7870 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian, Atokan

```
               N  Median
Desmoinesian  41    78.5
Atokan        15    78.5
Point estimate for η1 - η2 is 0.0
95.0 Percent CI for η1 - η2 is (0.0,0.0)
W = 1177.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.8750
The test is significant at 0.8544 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian, Morrowan

```
               N  Median
Desmoinesian  41    78.5
Morrowan       8    78.5
Point estimate for η1 - η2 is -0.0
95.0 Percent CI for η1 - η2 is (-78.2,0.1)
W = 998.0
```

```
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4735
The test is significant at 0.4069 (adjusted for ties)
```

Mann-Whitney Test and CI: Atokan, Morrowan

```
           N  Median
Atokan    15    78.5
Morrowan   8    78.5
Point estimate for η1 - η2 is 0.0
95.1 Percent CI for η1 - η2 is (-78.6,0.0)
W = 169.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4979
The test is significant at 0.3803 (adjusted for ties)
```

Mann Whitney U Test-Comparison across all ammonoids:

Mann-Whitney Test and CI: Wolfcampian_1, Virgilian_1

```
               N  Median
Wolfcampian_1  6    78.5
Virgilian_1    9    78.5
Point estimate for η1 - η2 is -39.0
96.1 Percent CI for η1 - η2 is (-139797.5,78.3)
W = 40.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4094
The test is significant at 0.3709 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_1, Missourian_1

```
               N  Median
Wolfcampian_1  6    78.5
Missourian_1   8    78.5
Point estimate for η1 - η2 is 0.0
95.5 Percent CI for η1 - η2 is (-23836.4,0.0)
W = 36.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.2725
The test is significant at 0.1268 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_1, Desmoinesian_1

```
                N  Median
Wolfcampian_1   6   78.54
Desmoinesian_1  8   78.54
Point estimate for η1 - η2 is 0.00
95.5 Percent CI for η1 - η2 is (0.00,78.04)
W = 48.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.7469
The test is significant at 0.6534 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_1, Atokan_1

```
               N  Median
Wolfcampian_1  6    78.5
Atokan_1       8    78.5
Point estimate for η1 - η2 is -0.0
```

```
95.5 Percent CI for η1 - η2 is (-78.1,78.1)
W = 45.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_1, Morrowan_1

```
               N  Median
Wolfcampian_1  6    78.5
Morrowan_1     5    78.5
Point estimate for η1 - η2 is 0.0
96.4 Percent CI for η1 - η2 is (-8837.6,0.0)
W = 31.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4113
The test is significant at 0.2230 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_1, Missourian_1

```
              N  Median
Virgilian_1   9    78.5
Missourian_1  8    78.5
Point estimate for η1 - η2 is 0.0
95.1 Percent CI for η1 - η2 is (-78.5,115333.5)
W = 81.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_1, Desmoinesian_1

```
                N  Median
Virgilian_1     9    78.5
Desmoinesian_1  8    78.5
Point estimate for η1 - η2 is 78.0
95.1 Percent CI for η1 - η2 is (-0.2,139797.4)
W = 92.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.3123
The test is significant at 0.2740 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_1, Atokan_1

```
             N  Median
Virgilian_1  9    78.5
Atokan_1     8    78.5
Point estimate for η1 - η2 is 78.2
95.1 Percent CI for η1 - η2 is (-78.2,115411.9)
W = 91.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.3359
The test is significant at 0.3096 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_1, Morrowan_1

```
             N  Median
Virgilian_1  9    78.5
Morrowan_1   5    78.5
Point estimate for η1 - η2 is 0.0
95.4 Percent CI for η1 - η2 is (-78.6,139797.7)
```

```
W = 71.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.6892
The test is significant at 0.6693 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_1, Desmoinesian_1

```
                N  Median
Missourian_1    8    78.5
Desmoinesian_1  8    78.5
Point estimate for η1 - η2 is 0.0
95.9 Percent CI for η1 - η2 is (-0.2,23836.5)
W = 82.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.1563
The test is significant at 0.0625 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_1, Atokan_1

```
              N  Median
Missourian_1  8    78.5
Atokan_1      8    78.5
Point estimate for η1 - η2 is -0.0
95.9 Percent CI for η1 - η2 is (0.1,23836.3)
W = 78.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.3184
The test is significant at 0.2251 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_1, Morrowan_1

```
              N  Median
Missourian_1  8    78.5
Morrowan_1    5    78.5
Point estimate for η1 - η2 is 0.0
95.2 Percent CI for η1 - η2 is (-0.1,23836.4)
W = 58.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.8262
The test is significant at 0.7665 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian_1, Atokan_1

```
                N  Median
Desmoinesian_1  8    78.5
Atokan_1        8    78.5
Point estimate for η1 - η2 is -0.0
95.9 Percent CI for η1 - η2 is (-78.1,0.5)
W = 67.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.9581
The test is significant at 0.9491 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian_1, Morrowan_1

```
                N  Median
Desmoinesian_1  8    78.5
Morrowan_1      5    78.5
Point estimate for η1 - η2 is 0.0
95.2 Percent CI for η1 - η2 is (-8837.4,-0.1)
W = 48.0
```

```
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.2723
The test is significant at 0.1376 (adjusted for ties)
```

Mann-Whitney Test and CI: Atokan_1, Morrowan_1

```
            N  Median
Atokan_1    8    78.5
Morrowan_1  5    78.5
Point estimate for η1 - η2 is 0.0
95.2 Percent CI for η1 - η2 is (-8837.6,0.1)
W = 51.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.5101
The test is significant at 0.4211 (adjusted for ties)
```

Mann Whitney U Test-Comparison across all nautiloids:

Mann-Whitney Test and CI: Wolfcampian_2, Virgilian_2

```
                N  Median
Wolfcampian_2   7      79
Virgilian_2    29      79
Point estimate for η1 - η2 is -67
95.4 Percent CI for η1 - η2 is (-2652,-1619)
W = 105.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.3374
The test is significant at 0.2529 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_2, Missourian_2

```
                N  Median
Wolfcampian_2   7    78.5
Missourian_2   47    78.5
Point estimate for η1 - η2 is 0.0
95.3 Percent CI for η1 - η2 is (-3748.3,77.7)
W = 164.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4709
The test is significant at 0.4552 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_2, Desmoinesian_2

```
                 N  Median
Wolfcampian_2    7    78.5
Desmoinesian_2  33    78.5
Point estimate for η1 - η2 is 0.0
95.4 Percent CI for η1 - η2 is (-0.2,0.2)
W = 143.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_2, Atokan_2

```
               N  Median
Wolfcampian_2  7    78.5
Atokan_2       7    78.5
Point estimate for η1 - η2 is 0.0
```

```
95.9 Percent CI for η1 - η2 is (0.2,0.1)
W = 52.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

Mann-Whitney Test and CI: Wolfcampian_2, Morrowan_2

```
               N  Median
Wolfcampian_2  7    78.5
Morrowan_2     3    78.5
Point estimate for η1 - η2 is -0.0
96.0 Percent CI for η1 - η2 is (-6713.2,5667.4)
W = 36.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.6485
The test is significant at 0.5153 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_2, Missourian_2

```
               N  Median
Virgilian_2   29      79
Missourian_2  47      79
Point estimate for η1 - η2 is 54
95.1 Percent CI for η1 - η2 is (-2977,2036)
W = 1057.5
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.5316
The test is significant at 0.4926 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_2, Desmoinesian_2

```
                 N  Median
Virgilian_2     29      79
Desmoinesian_2  33      79
Point estimate for η1 - η2 is -176
95.0 Percent CI for η1 - η2 is (-2198,1292)
W = 970.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4295
The test is significant at 0.3413 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_2, Atokan_2

```
              N  Median
Virgilian_2  29      79
Atokan_2      7      79
Point estimate for η1 - η2 is -63
95.4 Percent CI for η1 - η2 is (-795,2925)
W = 558.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4013
The test is significant at 0.3171 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_2, Morrowan_2

```
              N  Median
Virgilian_2  29      79
Morrowan_2    3      79
Point estimate for η1 - η2 is 357
95.5 Percent CI for η1 - η2 is (-5378,12242)
```

```
W = 481.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.8971
The test is significant at 0.8818 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_2, Desmoinesian_2

```
                 N  Median
Missourian_2    47    78.5
Desmoinesian_2  33    78.5

Point estimate for η1 - η2 is 0.0
95.1 Percent CI for η1 - η2 is (0.0,1242.8)
W = 2032.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.2109
The test is significant at 0.1913 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_2, Atokan_2

```
               N  Median
Missourian_2  47    78.5
Atokan_2       7    78.5
Point estimate for η1 - η2 is 0.0
95.3 Percent CI for η1 - η2 is (-77.7,3679.5)
W = 1317.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.5365
The test is significant at 0.5221 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_2, Morrowan_2

```
               N  Median
Missourian_2  47    78.5
Morrowan_2     3    78.5
Point estimate for η1 - η2 is 0.0
95.0 Percent CI for η1 - η2 is (-6713.1,4836.4)
W = 1197.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.9674
The test is significant at 0.9666 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian_2, Atokan_2

```
                 N  Median
Desmoinesian_2  33    78.5
Atokan_2         7    78.5
Point estimate for η1 - η2 is -0.0
95.4 Percent CI for η1 - η2 is (-77.9,0.0)
W = 673.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.9150
The test is significant at 0.9023 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian_2, Morrowan_2

```
                 N  Median
Desmoinesian_2  33    78.5
Morrowan_2       3    78.5
Point estimate for η1 - η2 is -0.0
95.5 Percent CI for η1 - η2 is (-6713.1,3190.4)
```

```
W = 603.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.6887
The test is significant at 0.6546 (adjusted for ties)
```

Mann-Whitney Test and CI: Atokan_2, Morrowan_2

```
            N  Median
Atokan_2    7    78.5
Morrowan_2  3    78.5
Point estimate for η1 - η2 is 0.0
96.0 Percent CI for η1 - η2 is (-6713.0,30520.5)
W = 37.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.8197
The test is significant at 0.7450 (adjusted for ties)
```

Mann Whitney U Test-Comparison between ammonoids & nautiloids:

Mann-Whitney Test and CI: Wolfcampian_1, Wolfcampian_2

```
               N  Median
Wolfcampian_1  6    78.5
Wolfcampian_2  7    78.5
Point estimate for η1 - η2 is -0.0
96.2 Percent CI for η1 - η2 is (-77.9,0.0)
W = 36.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4320
The test is significant at 0.2116 (adjusted for ties)
```

Mann-Whitney Test and CI: Virgilian_1, Virgilian_2

```
              N  Median
Virgilian_1   9      79
Virgilian_2  29      79
Point estimate for η1 - η2 is -159
95.4 Percent CI for η1 - η2 is (-1793,113215)
W = 200.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4099
The test is significant at 0.3503 (adjusted for ties)
```

Mann-Whitney Test and CI: Missourian_1, Missourian_2

```
               N  Median
Missourian_1   8    78.5
Missourian_2  47    78.5
Point estimate for η1 - η2 is -0.0
95.1 Percent CI for η1 - η2 is (-2988.5,78.5)
W = 222.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.9714
The test is significant at 0.9705 (adjusted for ties)
```

Mann-Whitney Test and CI: Desmoinesian_1, Desmoinesian_2

```
                 N  Median
Desmoinesian_1   8    78.5
Desmoinesian_2  33    78.5
```

```
Point estimate for η1 - η2 is 0.0
95.3 Percent CI for η1 - η2 is (-592.0,-0.0)
W = 131.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.2298
The test is significant at 0.1722 (adjusted for ties)
```

Mann-Whitney Test and CI: Atokan_1, Atokan_2

```
          N  Median
Atokan_1  8    78.5
Atokan_2  7    78.5
Point estimate for η1 - η2 is 0.0
95.7 Percent CI for η1 - η2 is (-78.5,0.0)
W = 57.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 0.4519
The test is significant at 0.3343 (adjusted for ties)
```

Mann-Whitney Test and CI: Morrowan_1, Morrowan_2

```
            N  Median
Morrowan_1  5    78.5
Morrowan_2  3    78.5
Point estimate for η1 - η2 is -0.0
96.3 Percent CI for η1 - η2 is (-6713.2,8837.6)
W = 22.0
Test of η1 = η2 vs η1 ≠ η2 is significant at 1.0000
The test is significant at 1.0000 (adjusted for ties)
```

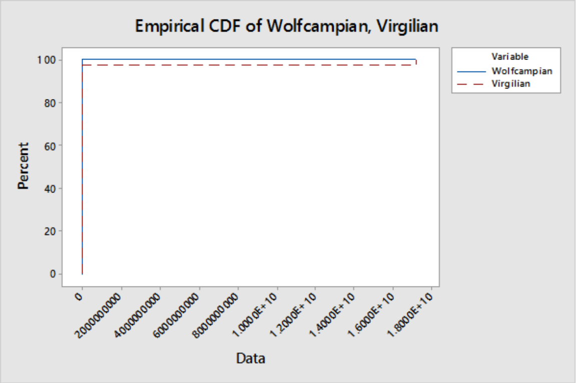
Kolmogorov Smirnoff:

H_n: The distributions of points between temporal bins is the same.

H_a: The distributions of points between temporal bins is different.

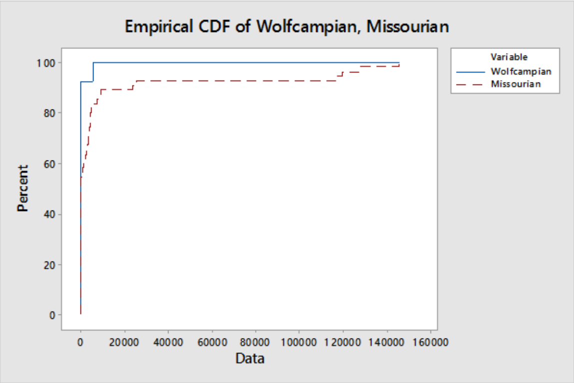
The Kolmogorov Smirnoff Test was a non-parametric test utilized to compare the distribution of non-transformed data points between temporal bins. The test is significant at $p \leq 0.05$

Kolmogorov Smirnoff-Comparison across all cephalopods:



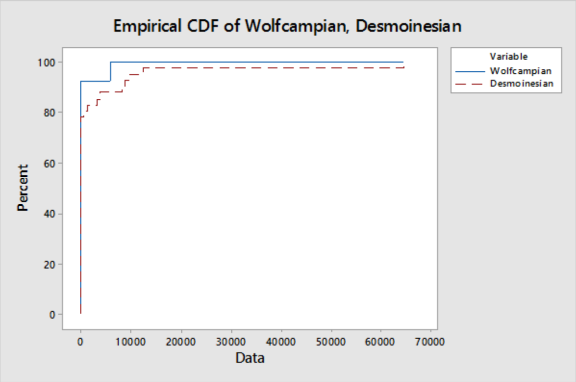
Kolmogorov-Smirnov 2-Sample Test: ALL WOLF VS ALL VIRG

```
K-S Test Statistic:             0.317
K-S Critical Value (Approx):    0.436
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



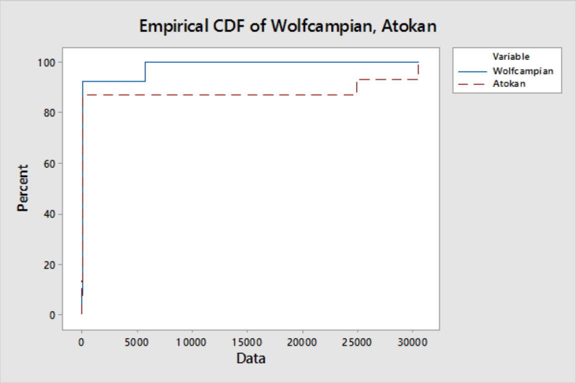
Kolmogorov-Smirnov 2-Sample Test ALL WOLF VS ALL MISS

```
K-S Test Statistic:              0.377
K-S Critical Value (Approx):     0.419
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



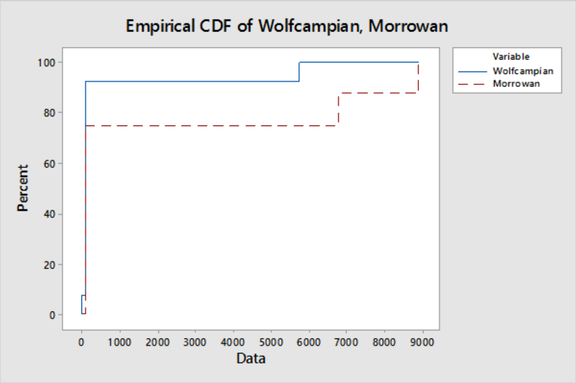
Kolmogorov-Smirnov 2-Sample Test ALL WOLF VS ALL DESM

```
K-S Test Statistic:              0.146
K-S Critical Value (Approx):     0.432
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



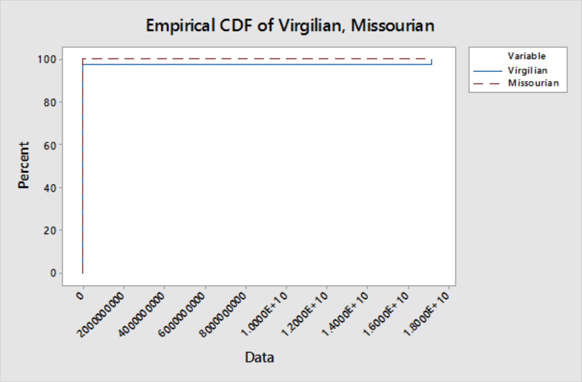
Kolmogorov-Smirnov 2-Sample Test ALL WOLF VS ALL ATOK

```
K-S Test Statistic:              0.133
K-S Critical Value (Approx):     0.515
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



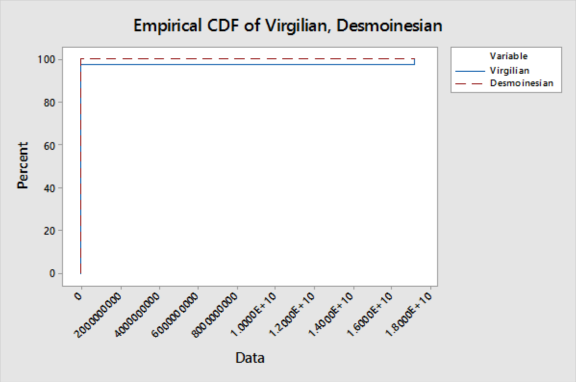
Kolmogorov-Smirnov 2-Sample Test ALL WOLF VS ALL MORR

```
K-S Test Statistic:              0.25
K-S Critical Value (Approx):     0.611
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```



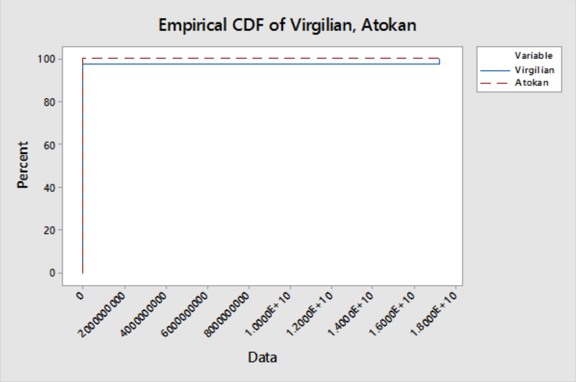
Kolmogorov-Smirnov 2-Sample Test ALL VIRG VS ALL MISS

```
K-S Test Statistic:               0.127
K-S Critical Value (Approx):      0.286
Alpha Level:                      0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



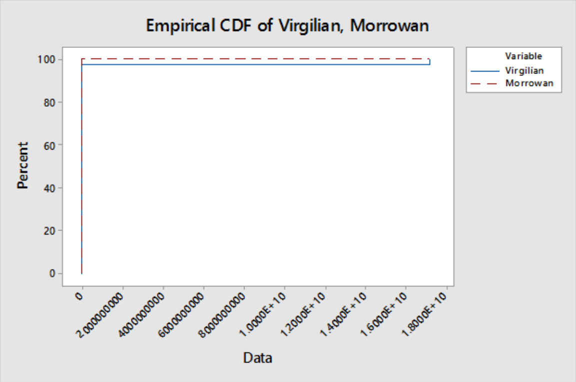
Kolmogorov-Smirnov 2-Sample Test ALL VIRG VS ALL DESM

```
K-S Test Statistic:               0.188
K-S Critical Value (Approx):      0.306
Alpha Level:                      0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



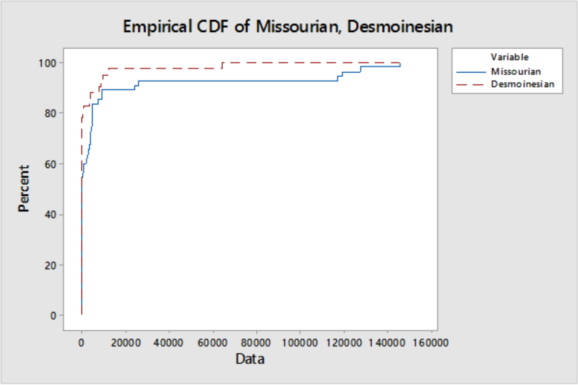
Kolmogorov-Smirnov 2-Sample Test ALL VIRG VS ALL ATOK

```
K-S Test Statistic:               0.261
K-S Critical Value (Approx):      0.414
Alpha Level:                      0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



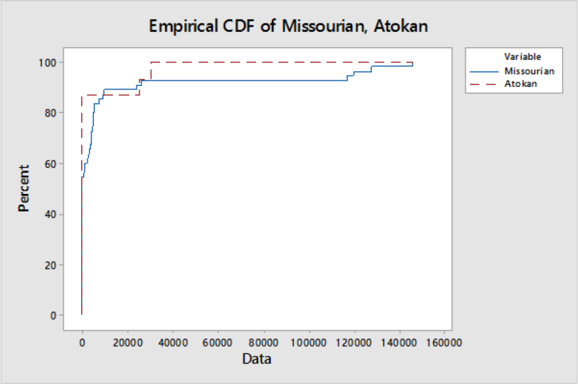
Kolmogorov-Smirnov 2-Sample Test ALL VIRG VS ALL MORR

```
K-S Test Statistic:               0.236
K-S Critical Value (Approx):      0.529
Alpha Level:                      0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```



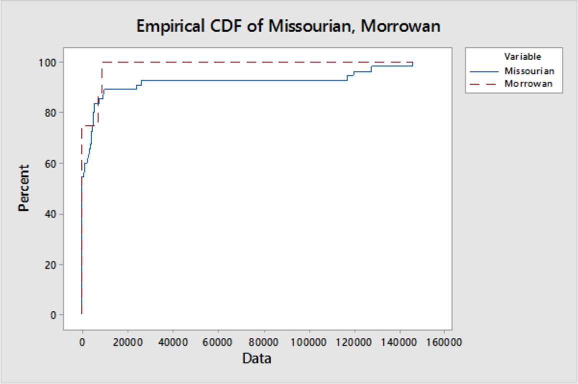
Kolmogorov-Smirnov 2-Sample Test ALL MISS VS ALL DESM

```
K-S Test Statistic:                0.247
K-S Critical Value (Approx):       0.280
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



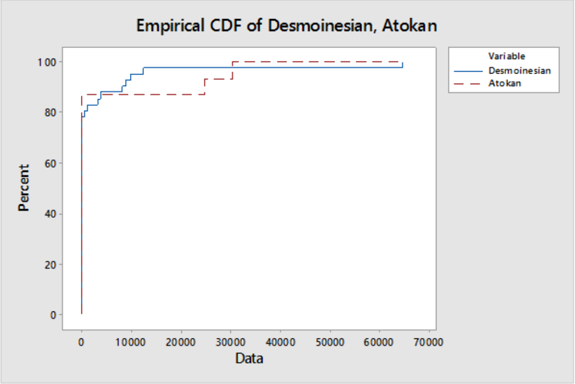
Kolmogorov-Smirnov 2-Sample Test ALL MISS VS ALL ATOK

```
K-S Test Statistic:                0.321
K-S Critical Value (Approx):       0.396
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



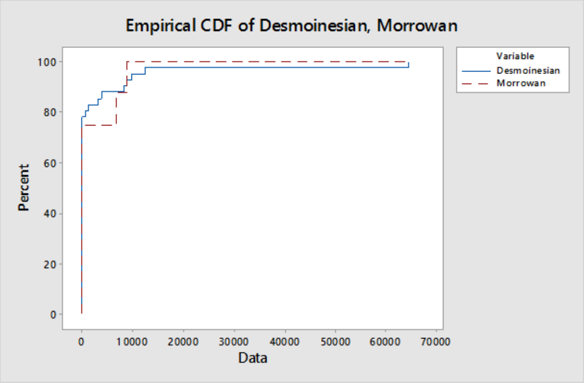
Kolmogorov-Smirnov 2-Sample Test ALL MISS VS ALL MORR

```
K-S Test Statistic:                0.204
K-S Critical Value (Approx):       0.514
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```



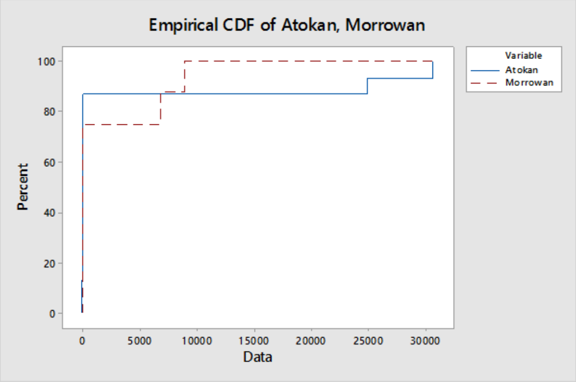
Kolmogorov-Smirnov 2-Sample Test ALL DESM VS ALL ATOK

```
K-S Test Statistic:                0.108
K-S Critical Value (Approx):       0.410
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test ALL DESM VS ALL MORR

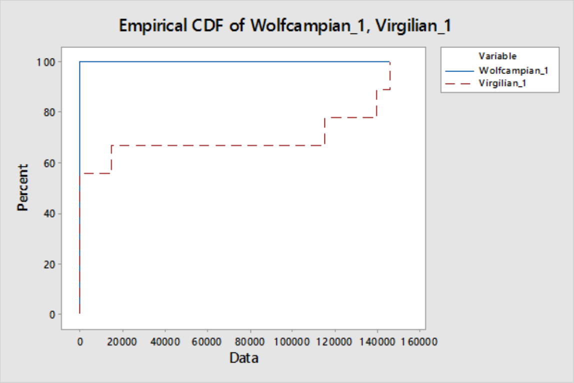
```
K-S Test Statistic:              0.170
K-S Critical Value (Approx):     0.525
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```



Kolmogorov-Smirnov 2-Sample Test: ALL ATOK VS ALL MORR

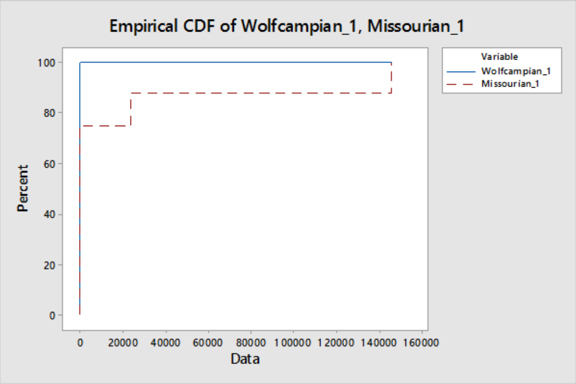
```
K-S Test Statistic:              0.133
K-S Critical Value (Approx):     0.595
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

Kolmogorov-Smirnov-Comparison of ammonoids groups:



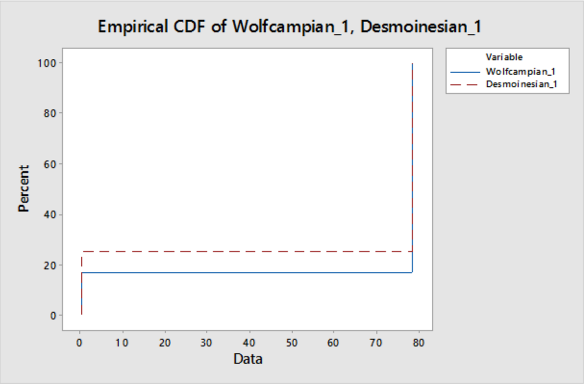
Kolmogorov-Smirnov 2-Sample Test: AM WOLF VS AM VIRG

```
K-S Test Statistic:              0.444
K-S Critical Value (Approx):     0.716
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



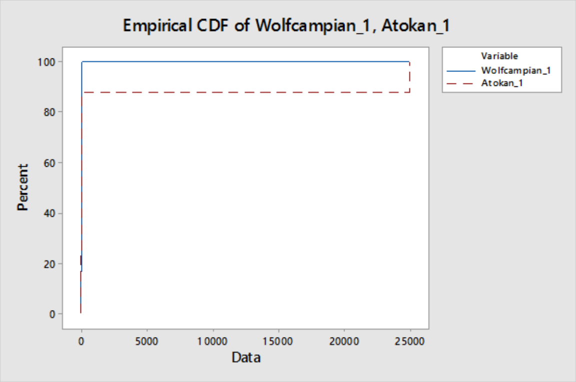
Kolmogorov-Smirnov 2-Sample Test: AM WOLF VS AM MISS

```
K-S Test Statistic:             0.25
K-S Critical Value (Approx):    0.734
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test AM WOLF VS AM DESM

```
K-S Test Statistic:             0.25
K-S Critical Value (Approx):    0.734
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```

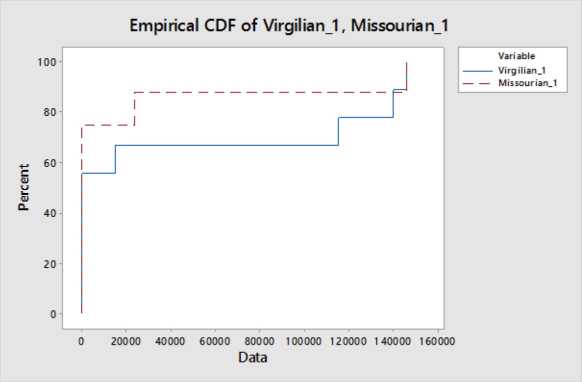


Kolmogorov-Smirnov 2-Sample Test: AM WOLF VS AM ATOK

```
K-S Test Statistic:             0.25
K-S Critical Value (Approx):    0.734
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

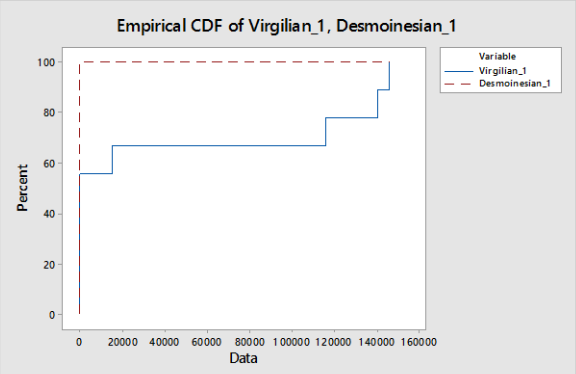
Kolmogorov-Smirnov 2-Sample Test: AM WOLF VS AM MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



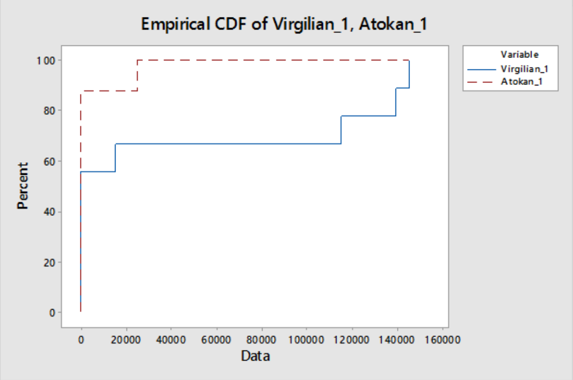
Kolmogorov-Smirnov 2-Sample Test AM VIRG VS AM MISS

```
K-S Test Statistic:              0.222
K-S Critical Value (Approx):     0.660
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test AM VIRG VS AM DESM

```
K-S Test Statistic:              0.444
K-S Critical Value (Approx):     0.660
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```

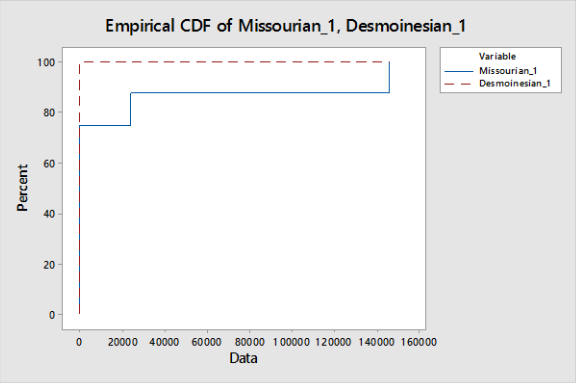


Kolmogorov-Smirnov 2-Sample Test AM VIRG VS AM ATOK

```
K-S Test Statistic:              0.333
K-S Critical Value (Approx):     0.660
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

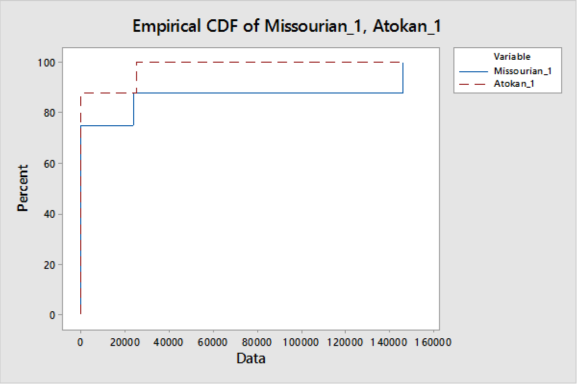
Kolmogorov-Smirnov 2-Sample Test: AM VIRG VS AM MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



Kolmogorov-Smirnov 2-Sample Test: AM MISS VS AM DESM

```
K-S Test Statistic:              0.25
K-S Critical Value (Approx):     0.68
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```

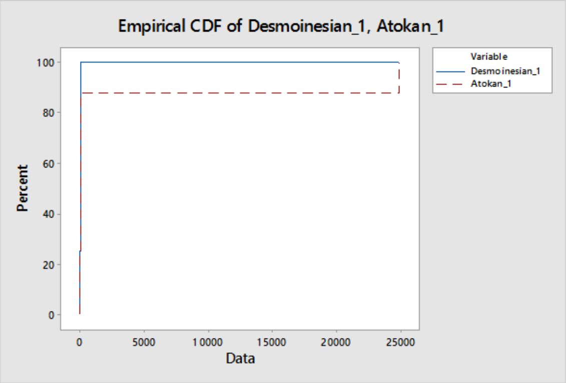


Kolmogorov-Smirnov 2-Sample Test: AM MISS VS AM ATOK

```
K-S Test Statistic:            0.25
K-S Critical Value (Approx):   0.68
Alpha Level:                   0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

Kolmogorov-Smirnov 2-Sample Test: AM MISS VS AM MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



Kolmogorov-Smirnov 2-Sample Test: AM DESM VS AM ATOK

```
K-S Test Statistic:            0.25
K-S Critical Value (Approx):   0.68
Alpha Level:                   0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

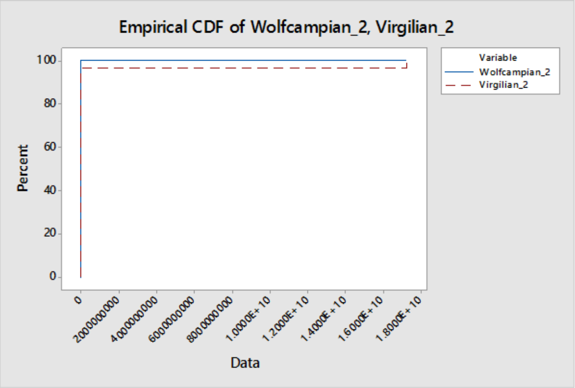
Kolmogorov-Smirnov 2-Sample Test: AM DESM VS AM MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```

Kolmogorov-Smirnov 2-Sample Test: AM ATOK VS AM MORR

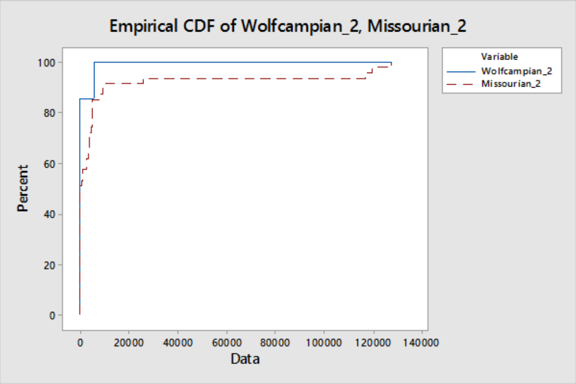
```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```

Kolmogorov-Smirnov-Comparison of nautiloid groups:



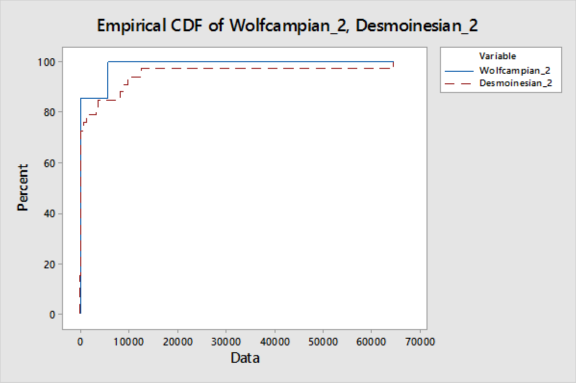
Kolmogorov-Smirnov 2-Sample Test: NAUT WOLF VS NAUT VIRG

```
K-S Test Statistic:            0.236
K-S Critical Value (Approx):   0.572
Alpha Level:                   0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



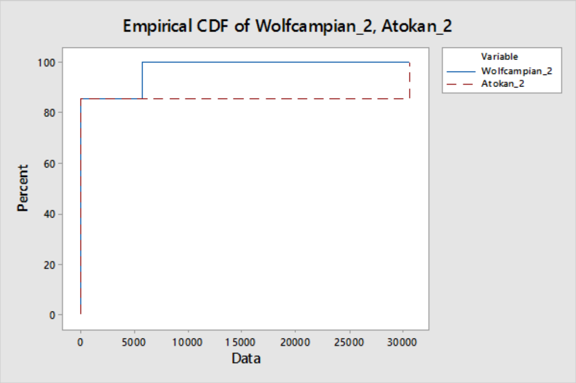
Kolmogorov-Smirnov 2-Sample Test NAUT WOLF VS NAUT MISS

```
K-S Test Statistic:                0.346
K-S Critical Value (Approx):       0.550
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test NAUT WOLF VS NAUT DESM

```
K-S Test Statistic:                0.151
K-S Critical Value (Approx):       0.565
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```

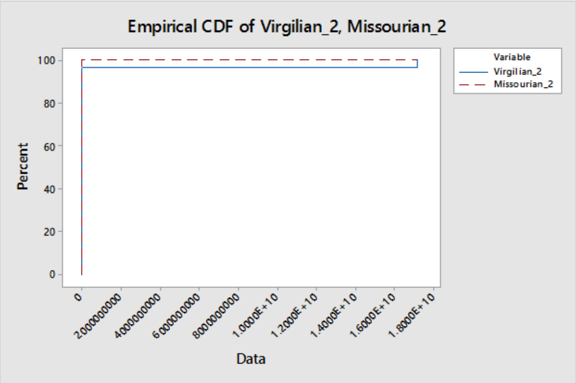


Kolmogorov-Smirnov 2-Sample Test NAUT WOLF VS NAUT ATOK

```
K-S Test Statistic:                0.142
K-S Critical Value (Approx):       0.726
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

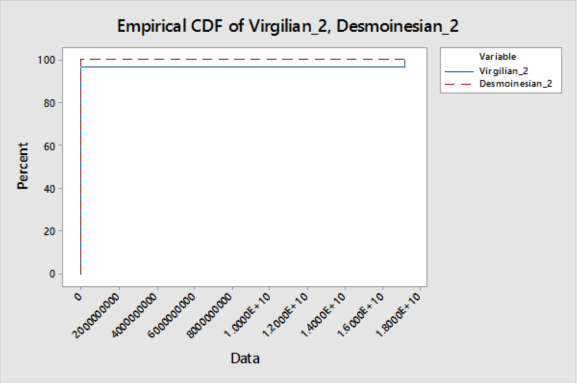
Kolmogorov-Smirnov 2-Sample Test NAUT WOLF VS NAUT MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



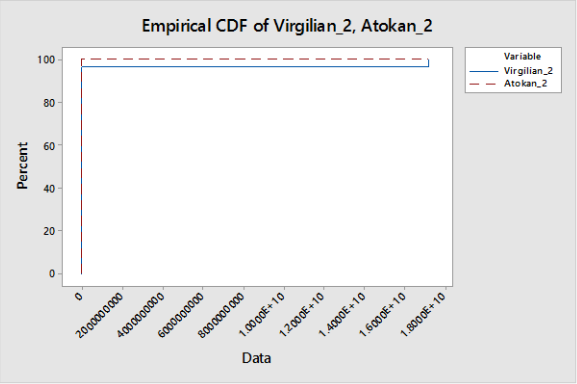
Kolmogorov-Smirnov 2-Sample Test NAUT VIRG VS NAUT MISS

```
K-S Test Statistic:                0.144
K-S Critical Value (Approx):       0.321
Alpha Level:                       0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test NAUT VIRG VS NAUT DESM

```
K-S Test Statistic:             0.111
K-S Critical Value (Approx):    0.346
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```

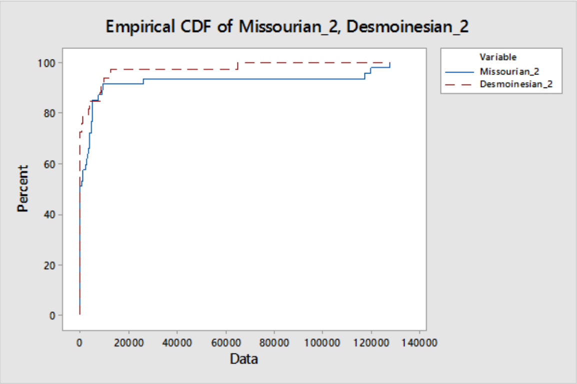


Kolmogorov-Smirnov 2-Sample Test NAUT VIRG VS NAUT ATOK

```
K-S Test Statistic:             0.236
K-S Critical Value (Approx):    0.572
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

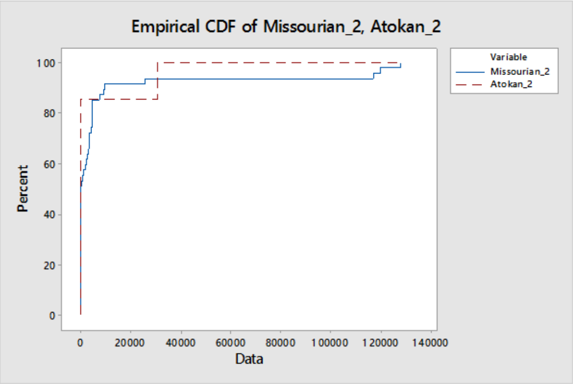
Kolmogorov-Smirnov 2-Sample Test NAUT VIRG VS NAUT MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



Kolmogorov-Smirnov 2-Sample Test NAUT MISS VS NAUT DESM

```
K-S Test Statistic:             0.234
K-S Critical Value (Approx):    0.308
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
Executing from file: KSTWO.MAC
```

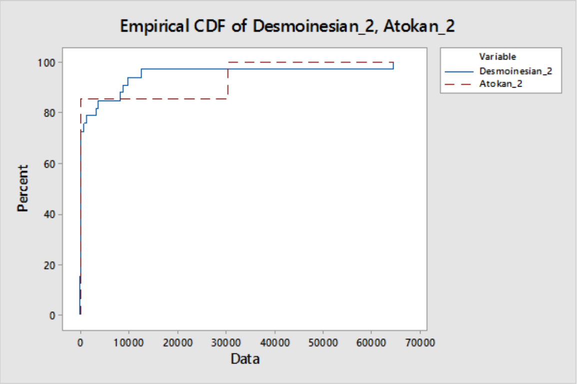


Kolmogorov-Smirnov 2-Sample Test NAUT MISS VS NAUT ATOK

```
K-S Test Statistic:             0.346
K-S Critical Value (Approx):    0.550
Alpha Level:                    0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

Kolmogorov-Smirnov 2-Sample Test NAUT MISS VS NAUT MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```



Kolmogorov-Smirnov 2-Sample Test NAUT DESM VS NAUT ATOK

```
K-S Test Statistic:              0.151
K-S Critical Value (Approx):     0.565
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

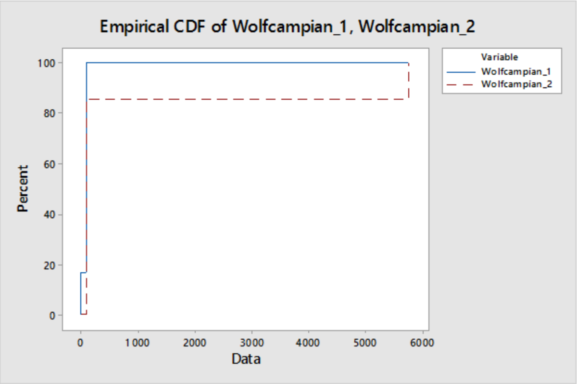
Kolmogorov-Smirnov 2-Sample Test NAUT DESM VS NAUT MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```

Kolmogorov-Smirnov 2-Sample Test NAUT ATOK VS NAUT MORR

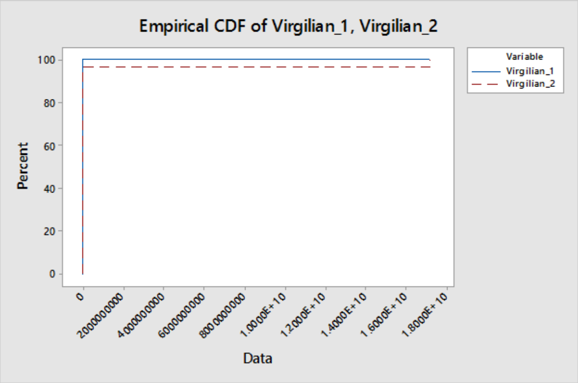
```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```

Kolmogorov-Smirnov-Comparison between nautiloids and ammonoids groups:



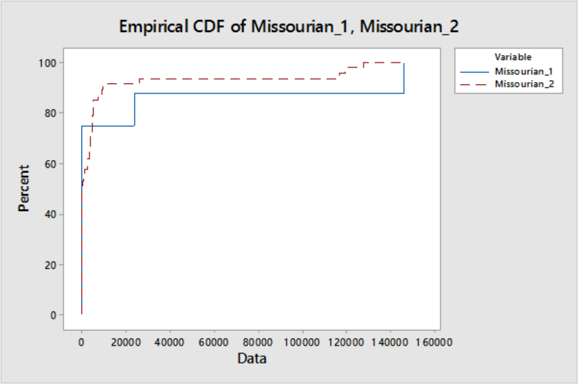
Kolmogorov-Smirnov 2-Sample Test AM WOLF VS NAUT WOLF

```
K-S Test Statistic:              0.166
K-S Critical Value (Approx):     0.756
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



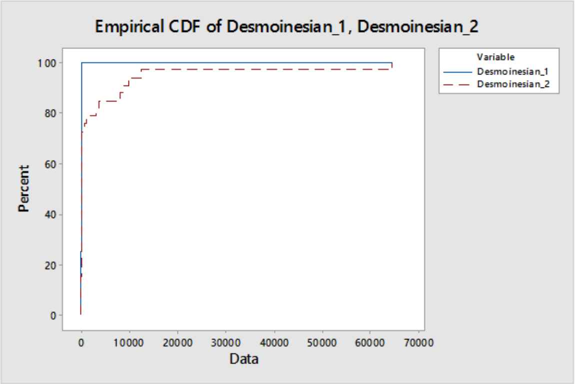
Kolmogorov-Smirnov 2-Sample Test AM VIRG VS NAUT VIRG

```
K-S Test Statistic:              0.340
K-S Critical Value (Approx):     0.518
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



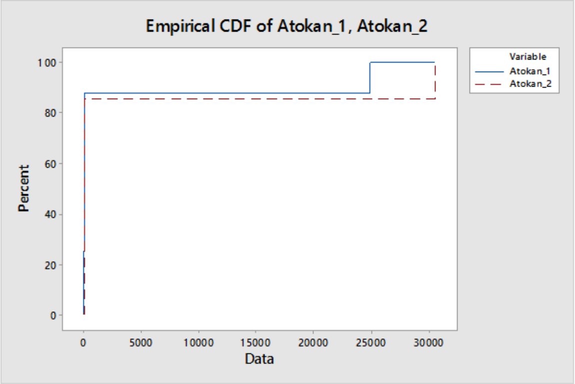
Kolmogorov-Smirnov 2-Sample Test AM MISS VS NAUT MISS

```
K-S Test Statistic:              0.239
K-S Critical Value (Approx):     0.520
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test AM DESM VS NAUT DESM

```
K-S Test Statistic:              0.272
K-S Critical Value (Approx):     0.535
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
Executing from file: KSTWO.MAC
```



Kolmogorov-Smirnov 2-Sample Test AM ATOK VS NAUT ATOK

```
K-S Test Statistic:              0.25
K-S Critical Value (Approx):     0.703
Alpha Level:                     0.05
The test statistic is less than the critical
value.
There is not sufficient evidence to conclude
that the underlying distributions are
different.
** WARNING ** With approximate critical
value, sample sizes > 12 are recommended
```

Kolmogorov-Smirnov 2-Sample Test AM MORR VS NAUT MORR

```
Executing from file: KSTWO.MAC
** Error ** Both sample sizes should be at least 6
```

Two-Sample T Test:

H_n: The means between the two groups are the same.

H_a: The means between the two groups are different.

The two Sample T Test was a parametric test utilized on transformed data to compare the means between temporal bins across all cephalopods and within ammonoid and nautiloid groups.

Two-Sample T Test-Comparison across all cephalopods:

Two-Sample T-Test and CI: Wolfcampian, Virgilian

```
Two-sample T for Wolfcampian vs Virgilian
              N  Mean  StDev  SE Mean
Wolfcampian  13  4.31   1.89     0.52
Virgilian    38  5.96   4.85     0.79
Difference = μ (Wolfcampian) - μ (Virgilian)
Estimate for difference:  -1.647
95% CI for difference:  (-3.547, 0.253)
T-Test of difference = 0 (vs ≠): T-Value = -1.74  P-Value = 0.088  DF = 47
```

Two-Sample T-Test and CI: Wolfcampian, Missourian

```
Two-sample T for Wolfcampian vs Missourian
              N  Mean  StDev  SE Mean
Wolfcampian  13  4.31   1.89     0.52
Missourian   55  5.65   3.62     0.49
Difference = μ (Wolfcampian) - μ (Missourian)
Estimate for difference:  -1.333
95% CI for difference:  (-2.786, 0.121)
T-Test of difference = 0 (vs ≠): T-Value = -1.86  P-Value = 0.071  DF = 35
```

Two-Sample T-Test and CI: Wolfcampian, Desmoinesian

```
Two-sample T for Wolfcampian vs Desmoinesian
               N  Mean  StDev  SE Mean
Wolfcampian   13  4.31   1.89     0.52
Desmoinesian  41  4.36   3.13     0.49
Difference = μ (Wolfcampian) - μ (Desmoinesian)
Estimate for difference:  -0.048
95% CI for difference:  (-1.506, 1.409)
T-Test of difference = 0 (vs ≠): T-Value = -0.07  P-Value = 0.947  DF = 34
```

Two-Sample T-Test and CI: Wolfcampian, Atokan

```
Two-sample T for Wolfcampian vs Atokan
              N  Mean  StDev  SE Mean
Wolfcampian  13  4.31   1.89     0.52
Atokan       15  4.05   3.96      1.0
Difference = μ (Wolfcampian) - μ (Atokan)
Estimate for difference:  0.27
95% CI for difference:  (-2.13, 2.67)
T-Test of difference = 0 (vs ≠): T-Value = 0.23  P-Value = 0.818  DF = 20
```

Two-Sample T-Test and CI: Wolfcampian, Morrowan

```
Two-sample T for Wolfcampian vs Morrowan
              N  Mean  StDev  SE Mean
Wolfcampian  13  4.31   1.89     0.52
Morrowan      8  5.51   2.13     0.75
Difference = μ (Wolfcampian) - μ (Morrowan)
Estimate for difference:  -1.199
95% CI for difference:  (-3.180, 0.782)
T-Test of difference = 0 (vs ≠): T-Value = -1.31  P-Value = 0.214  DF = 13
```

Two-Sample T-Test and CI: Virgilian, Missourian

```
Two-sample T for Virgilian vs Missourian
             N  Mean  StDev  SE Mean
Virgilian   38  5.96   4.85     0.79
Missourian  55  5.65   3.62     0.49
Difference = μ (Virgilian) - μ (Missourian)
Estimate for difference:  0.314
95% CI for difference:  (-1.534, 2.162)
T-Test of difference = 0 (vs ≠): T-Value = 0.34  P-Value = 0.735  DF = 64
```

Two-Sample T-Test and CI: Virgilian, Desmoinesian

```
Two-sample T for Virgilian vs Desmoinesian
```

```
              N  Mean  StDev  SE Mean
Virgilian     38  5.96   4.85     0.79
Desmoinesian  41  4.36   3.13     0.49
Difference = μ (Virgilian) - μ (Desmoinesian)
Estimate for difference:  1.599
95% CI for difference:  (-0.252, 3.449)
T-Test of difference = 0 (vs ≠): T-Value = 1.73  P-Value = 0.089  DF = 62
```

Two-Sample T-Test and CI: Virgilian, Atokan

```
Two-sample T for Virgilian vs Atokan
            N  Mean  StDev  SE Mean
Virgilian  38  5.96   4.85     0.79
Atokan     15  4.05   3.96      1.0
Difference = μ (Virgilian) - μ (Atokan)
Estimate for difference:  1.92
95% CI for difference:  (-0.72, 4.55)
T-Test of difference = 0 (vs ≠): T-Value = 1.48  P-Value = 0.148  DF = 31
```

Two-Sample T-Test and CI: Virgilian, Morrowan

```
Two-sample T for Virgilian vs Morrowan
            N  Mean  StDev  SE Mean
Virgilian  38  5.96   4.85     0.79
Morrowan    8  5.51   2.13     0.75
Difference = μ (Virgilian) - μ (Morrowan)
Estimate for difference:  0.45
95% CI for difference:  (-1.80, 2.69)
T-Test of difference = 0 (vs ≠): T-Value = 0.41  P-Value = 0.684  DF = 24
```

Two-Sample T-Test and CI: Missourian, Desmoinesian

```
Two-sample T for Missourian vs Desmoinesian
              N  Mean  StDev  SE Mean
Missourian    55  5.65   3.62     0.49
Desmoinesian  41  4.36   3.13     0.49
Difference = μ (Missourian) - μ (Desmoinesian)
Estimate for difference:  1.284
95% CI for difference:  (-0.088, 2.657)
T-Test of difference = 0 (vs ≠): T-Value = 1.86  P-Value = 0.066  DF = 91
```

Two-Sample T-Test and CI: Missourian, Atokan

```
Two-sample T for Missourian vs Atokan
             N  Mean  StDev  SE Mean
Missourian  55  5.65   3.62     0.49
Atokan      15  4.05   3.96      1.0
Difference = μ (Missourian) - μ (Atokan)
Estimate for difference:  1.60
95% CI for difference:  (-0.76, 3.97)
T-Test of difference = 0 (vs ≠): T-Value = 1.41  P-Value = 0.173  DF = 20
```

Two-Sample T-Test and CI: Missourian, Morrowan

```
Two-sample T for Missourian vs Morrowan
             N  Mean  StDev  SE Mean
Missourian  55  5.65   3.62     0.49
Morrowan     8  5.51   2.13     0.75
Difference = μ (Missourian) - μ (Morrowan)
Estimate for difference:  0.134
95% CI for difference:  (-1.804, 2.071)
T-Test of difference = 0 (vs ≠): T-Value = 0.15  P-Value = 0.884  DF = 13
```

Two-Sample T-Test and CI: Desmoinesian, Atokan

```
Two-sample T for Desmoinesian vs Atokan
              N  Mean  StDev  SE Mean
Desmoinesian  41  4.36   3.13     0.49
Atokan        15  4.05   3.96      1.0
Difference = μ (Desmoinesian) - μ (Atokan)
Estimate for difference:  0.32
95% CI for difference:  (-2.05, 2.68)
```

```
T-Test of difference = 0 (vs ≠): T-Value = 0.28  P-Value = 0.783  DF = 20
```

Two-Sample T-Test and CI: Desmoinesian, Morrowan

```
Two-sample T for Desmoinesian vs Morrowan
               N  Mean  StDev  SE Mean
Desmoinesian  41  4.36   3.13     0.49
Morrowan       8  5.51   2.13     0.75
Difference = μ (Desmoinesian) - μ (Morrowan)
Estimate for difference:  -1.151
95% CI for difference:  (-3.090, 0.789)
T-Test of difference = 0 (vs ≠): T-Value = -1.28  P-Value = 0.222  DF = 13
```

Two-Sample T-Test and CI: Atokan, Morrowan

```
Two-sample T for Atokan vs Morrowan
           N  Mean  StDev  SE Mean
Atokan    15  4.05   3.96      1.0
Morrowan   8  5.51   2.13     0.75
Difference = μ (Atokan) - μ (Morrowan)
Estimate for difference:  -1.47
95% CI for difference:  (-4.12, 1.18)
T-Test of difference = 0 (vs ≠): T-Value = -1.15  P-Value = 0.262  DF = 20
```

Two-Sample T Test-Comparison between ammonoid groups:

Two-Sample T-Test and CI: Wolfcampian_1, Virgilian_1

```
Two-sample T for Wolfcampian_1 vs Virgilian_1
               N  Mean  StDev  SE Mean
Wolfcampian_1  6  3.54   2.02     0.82
Virgilian_1    9  5.96   5.70      1.9
Difference = μ (Wolfcampian_1) - μ (Virgilian_1)
Estimate for difference:  -2.42
95% CI for difference:  (-7.03, 2.20)
T-Test of difference = 0 (vs ≠): T-Value = -1.17  P-Value = 0.270  DF = 10
```

Two-Sample T-Test and CI: Wolfcampian_1, Missourian_1

```
Two-sample T for Wolfcampian_1 vs Missourian_1
               N  Mean  StDev  SE Mean
Wolfcampian_1  6  3.54   2.02     0.82
Missourian_1   8  6.02   3.10      1.1
Difference = μ (Wolfcampian_1) - μ (Missourian_1)
Estimate for difference:  -2.48
95% CI for difference:  (-5.50, 0.54)
T-Test of difference = 0 (vs ≠): T-Value = -1.81  P-Value = 0.098  DF = 11
```

Two-Sample T-Test and CI: Wolfcampian_1, Desmoinesian_1

```
Two-sample T for Wolfcampian_1 vs Desmoinesian_1
                N  Mean  StDev  SE Mean
Wolfcampian_1   6  3.54   2.02     0.82
Desmoinesian_1  8  3.09   2.35     0.83
Difference = μ (Wolfcampian_1) - μ (Desmoinesian_1)
Estimate for difference:  0.45
95% CI for difference:  (-2.13, 3.03)
T-Test of difference = 0 (vs ≠): T-Value = 0.38  P-Value = 0.710  DF = 11
```

Two-Sample T-Test and CI: Wolfcampian_1, Atokan_1

```
Two-sample T for Wolfcampian_1 vs Atokan_1
               N  Mean  StDev  SE Mean
Wolfcampian_1  6  3.54   2.02     0.82
Atokan_1       8  3.02   4.95      1.8
Difference = μ (Wolfcampian_1) - μ (Atokan_1)
Estimate for difference:  0.52
95% CI for difference:  (-3.86, 4.89)
T-Test of difference = 0 (vs ≠): T-Value = 0.27  P-Value = 0.795  DF = 9
```

Two-Sample T-Test and CI: Wolfcampian_1, Morrowan_1

```
Two-sample T for Wolfcampian_1 vs Morrowan_1
               N  Mean  StDev  SE Mean
Wolfcampian_1  6  3.54   2.02     0.82
Morrowan_1     5  5.31   2.12     0.95
Difference = μ (Wolfcampian_1) - μ (Morrowan_1)
Estimate for difference:  -1.77
95% CI for difference:  (-4.66, 1.12)
T-Test of difference = 0 (vs ≠): T-Value = -1.41  P-Value = 0.196  DF = 8
```

Two-Sample T-Test and CI: Virgilian_1, Missourian_1

```
Two-sample T for Virgilian_1 vs Missourian_1
              N  Mean  StDev  SE Mean
Virgilian_1   9  5.96   5.70      1.9
Missourian_1  8  6.02   3.10      1.1
Difference = μ (Virgilian_1) - μ (Missourian_1)
Estimate for difference:  -0.06
95% CI for difference:  (-4.84, 4.72)
T-Test of difference = 0 (vs ≠): T-Value = -0.03  P-Value = 0.978  DF = 12
```

Two-Sample T-Test and CI: Virgilian_1, Desmoinesian_1

```
Two-sample T for Virgilian_1 vs Desmoinesian_1
                N  Mean  StDev  SE Mean
Virgilian_1     9  5.96   5.70      1.9
Desmoinesian_1  8  3.09   2.35     0.83
Difference = μ (Virgilian_1) - μ (Desmoinesian_1)
Estimate for difference:  2.86
95% CI for difference:  (-1.76, 7.49)
T-Test of difference = 0 (vs ≠): T-Value = 1.38  P-Value = 0.198  DF = 10
```

Two-Sample T-Test and CI: Virgilian_1, Atokan_1

```
Two-sample T for Virgilian_1 vs Atokan_1
             N  Mean  StDev  SE Mean
Virgilian_1  9  5.96   5.70      1.9
Atokan_1     8  3.02   4.95      1.8
Difference = μ (Virgilian_1) - μ (Atokan_1)
Estimate for difference:  2.93
95% CI for difference:  (-2.61, 8.48)
T-Test of difference = 0 (vs ≠): T-Value = 1.14  P-Value = 0.275  DF = 14
```

Two-Sample T-Test and CI: Virgilian_1, Morrowan_1

```
Two-sample T for Virgilian_1 vs Morrowan_1
             N  Mean  StDev  SE Mean
Virgilian_1  9  5.96   5.70      1.9
Morrowan_1   5  5.31   2.12     0.95
Difference = μ (Virgilian_1) - μ (Morrowan_1)
Estimate for difference:  0.65
95% CI for difference:  (-4.03, 5.32)
T-Test of difference = 0 (vs ≠): T-Value = 0.30  P-Value = 0.767  DF = 11
```

Two-Sample T-Test and CI: Virgilian_1, Morrowan_1

```
Two-sample T for Virgilian_1 vs Morrowan_1
             N  Mean  StDev  SE Mean
Virgilian_1  9  5.96   5.70      1.9
Morrowan_1   5  5.31   2.12     0.95

Difference = μ (Virgilian_1) - μ (Morrowan_1)
Estimate for difference:  0.65
95% CI for difference:  (-4.03, 5.32)
T-Test of difference = 0 (vs ≠): T-Value = 0.30  P-Value = 0.767  DF = 11
```

Two-Sample T-Test and CI: Missourian_1, Atokan_1

```
Two-sample T for Missourian_1 vs Atokan_1
              N  Mean  StDev  SE Mean
Missourian_1  8  6.02   3.10      1.1
Atokan_1      8  3.02   4.95      1.8
Difference = μ (Missourian_1) - μ (Atokan_1)
```

```
Estimate for difference:  3.00
95% CI for difference:  (-1.55, 7.54)
T-Test of difference = 0 (vs ≠): T-Value = 1.45  P-Value = 0.175  DF = 11
```

Two-Sample T-Test and CI: Missourian_1, Morrowan_1

```
Two-sample T for Missourian_1 vs Morrowan_1
              N  Mean  StDev  SE Mean
Missourian_1  8  6.02   3.10      1.1
Morrowan_1    5  5.31   2.12     0.95
Difference = μ (Missourian_1) - μ (Morrowan_1)
Estimate for difference:  0.71
95% CI for difference:  (-2.52, 3.94)
T-Test of difference = 0 (vs ≠): T-Value = 0.49  P-Value = 0.635  DF = 10
```

Two-Sample T-Test and CI: Desmoinesian_1, Atokan_1

```
Two-sample T for Desmoinesian_1 vs Atokan_1
                N  Mean  StDev  SE Mean
Desmoinesian_1  8  3.09   2.35     0.83
Atokan_1        8  3.02   4.95      1.8
Difference = μ (Desmoinesian_1) - μ (Atokan_1)
Estimate for difference:  0.07
95% CI for difference:  (-4.25, 4.39)
T-Test of difference = 0 (vs ≠): T-Value = 0.04  P-Value = 0.972  DF = 10
```

Two-Sample T-Test and CI: Desmoinesian_1, Morrowan_1

```
Two-sample T for Desmoinesian_1 vs Morrowan_1
                N  Mean  StDev  SE Mean
Desmoinesian_1  8  3.09   2.35     0.83
Morrowan_1      5  5.31   2.12     0.95
Difference = μ (Desmoinesian_1) - μ (Morrowan_1)
Estimate for difference:  -2.22
95% CI for difference:  (-5.07, 0.63)
T-Test of difference = 0 (vs ≠): T-Value = -1.76  P-Value = 0.112  DF = 9
```

Two-Sample T-Test and CI: Atokan_1, Morrowan_1

```
Two-sample T for Atokan_1 vs Morrowan_1
            N  Mean  StDev  SE Mean
Atokan_1    8  3.02   4.95      1.8
Morrowan_1  5  5.31   2.12     0.95
Difference = μ (Atokan_1) - μ (Morrowan_1)
Estimate for difference:  -2.29
95% CI for difference:  (-6.72, 2.14)
T-Test of difference = 0 (vs ≠): T-Value = -1.15  P-Value = 0.277  DF = 10
```

Two-Sample T Test-Comparison between nautiloid groups:

Two-Sample T-Test and CI: Wolfcampian_2, Virgilian_2

```
Two-sample T for Wolfcampian_2 vs Virgilian_2
                N  Mean  StDev  SE Mean
Wolfcampian_2   7  4.98   1.62     0.61
Virgilian_2    29  5.96   4.66     0.87
Difference = μ (Wolfcampian_2) - μ (Virgilian_2)
Estimate for difference:  -0.98
95% CI for difference:  (-3.15, 1.18)
T-Test of difference = 0 (vs ≠): T-Value = -0.93  P-Value = 0.361  DF = 29
```

Two-Sample T-Test and CI: Wolfcampian_2, Missourian_2

```
Two-sample T for Wolfcampian_2 vs Missourian_2
                N  Mean  StDev  SE Mean
Wolfcampian_2   7  4.98   1.62     0.61
Missourian_2   47  5.58   3.72     0.54
Difference = μ (Wolfcampian_2) - μ (Missourian_2)
Estimate for difference:  -0.606
```

```
95% CI for difference:  (-2.335, 1.123)
T-Test of difference = 0 (vs ≠): T-Value = -0.74  P-Value = 0.470  DF = 17
```

Two-Sample T-Test and CI: Wolfcampian_2, Desmoinesian_2

```
Two-sample T for Wolfcampian_2 vs Desmoinesian_2
                 N  Mean  StDev  SE Mean
Wolfcampian_2    7  4.98   1.62     0.61
Desmoinesian_2  33  4.67   3.25     0.57
Difference = μ (Wolfcampian_2) - μ (Desmoinesian_2)
Estimate for difference:  0.307
95% CI for difference:  (-1.446, 2.060)
T-Test of difference = 0 (vs ≠): T-Value = 0.37  P-Value = 0.717  DF = 18
```

Two-Sample T-Test and CI: Wolfcampian_2, Atokan_2

```
Two-sample T for Wolfcampian_2 vs Atokan_2
               N  Mean  StDev  SE Mean
Wolfcampian_2  7  4.98   1.62     0.61
Atokan_2       7  5.22   2.25     0.85
Difference = μ (Wolfcampian_2) - μ (Atokan_2)
Estimate for difference:  -0.24
95% CI for difference:  (-2.58, 2.10)
T-Test of difference = 0 (vs ≠): T-Value = -0.23  P-Value = 0.825  DF = 10
```

Two-Sample T-Test and CI: Wolfcampian_2, Morrowan_2

```
Two-sample T for Wolfcampian_2 vs Morrowan_2
               N  Mean  StDev  SE Mean
Wolfcampian_2  7  4.98   1.62     0.61
Morrowan_2     3  5.85   2.57      1.5
Difference = μ (Wolfcampian_2) - μ (Morrowan_2)
Estimate for difference:  -0.87
95% CI for difference:  (-7.79, 6.05)
T-Test of difference = 0 (vs ≠): T-Value = -0.54  P-Value = 0.641  DF = 2
```

Two-Sample T-Test and CI: Virgilian_2, Missourian_2

```
Two-sample T for Virgilian_2 vs Missourian_2
               N  Mean  StDev  SE Mean
Virgilian_2   29  5.96   4.66     0.87
Missourian_2  47  5.58   3.72     0.54
Difference = μ (Virgilian_2) - μ (Missourian_2)
Estimate for difference:  0.38
95% CI for difference:  (-1.67, 2.43)
T-Test of difference = 0 (vs ≠): T-Value = 0.37  P-Value = 0.712  DF = 49
```

Two-Sample T-Test and CI: Virgilian_2, Desmoinesian_2

```
Two-sample T for Virgilian_2 vs Desmoinesian_2
                 N  Mean  StDev  SE Mean
Virgilian_2     29  5.96   4.66     0.87
Desmoinesian_2  33  4.67   3.25     0.57
Difference = μ (Virgilian_2) - μ (Desmoinesian_2)
Estimate for difference:  1.29
95% CI for difference:  (-0.79, 3.37)
T-Test of difference = 0 (vs ≠): T-Value = 1.25  P-Value = 0.217  DF = 49
```

Two-Sample T-Test and CI: Virgilian_2, Atokan_2

```
Two-sample T for Virgilian_2 vs Atokan_2
              N  Mean  StDev  SE Mean
Virgilian_2  29  5.96   4.66     0.87
Atokan_2      7  5.22   2.25     0.85
Difference = μ (Virgilian_2) - μ (Atokan_2)
Estimate for difference:  0.75
95% CI for difference:  (-1.79, 3.28)
T-Test of difference = 0 (vs ≠): T-Value = 0.61  P-Value = 0.546  DF = 20
```

Two-Sample T-Test and CI: Virgilian_2, Morrowan_2

```
Two-sample T for Virgilian_2 vs Morrowan_2
```

```
              N  Mean  StDev  SE Mean
Virgilian_2  29  5.96   4.66     0.87
Morrowan_2    3  5.85   2.57      1.5
Difference = μ (Virgilian_2) - μ (Morrowan_2)
Estimate for difference:  0.11
95% CI for difference:  (-5.36, 5.59)
T-Test of difference = 0 (vs ≠): T-Value = 0.06  P-Value = 0.952  DF = 3
```

Two-Sample T-Test and CI: Missourian_2, Desmoinesian_2

```
Two-sample T for Missourian_2 vs Desmoinesian_2
                 N  Mean  StDev  SE Mean
Missourian_2    47  5.58   3.72     0.54
Desmoinesian_2  33  4.67   3.25     0.57
Difference = μ (Missourian_2) - μ (Desmoinesian_2)
Estimate for difference:  0.913
95% CI for difference:  (-0.650, 2.476)
T-Test of difference = 0 (vs ≠): T-Value = 1.16  P-Value = 0.248  DF = 74
```

Two-Sample T-Test and CI: Missourian_2, Atokan_2

```
Two-sample T for Missourian_2 vs Atokan_2
               N  Mean  StDev  SE Mean
Missourian_2  47  5.58   3.72     0.54
Atokan_2       7  5.22   2.25     0.85
Difference = μ (Missourian_2) - μ (Atokan_2)
Estimate for difference:  0.37
95% CI for difference:  (-1.86, 2.59)
T-Test of difference = 0 (vs ≠): T-Value = 0.36  P-Value = 0.723  DF = 11
```

Two-Sample T-Test and CI: Missourian_2, Morrowan_2

```
Two-sample T for Missourian_2 vs Morrowan_2
               N  Mean  StDev  SE Mean
Missourian_2  47  5.58   3.72     0.54
Morrowan_2     3  5.85   2.57      1.5
Difference = μ (Missourian_2) - μ (Morrowan_2)
Estimate for difference:  -0.27
95% CI for difference:  (-7.08, 6.54)
T-Test of difference = 0 (vs ≠): T-Value = -0.17  P-Value = 0.881  DF = 2
```

Two-Sample T-Test and CI: Desmoinesian_2, Atokan_2

```
Two-sample T for Desmoinesian_2 vs Atokan_2
                 N  Mean  StDev  SE Mean
Desmoinesian_2  33  4.67   3.25     0.57
Atokan_2         7  5.22   2.25     0.85
Difference = μ (Desmoinesian_2) - μ (Atokan_2)
Estimate for difference:  -0.55
95% CI for difference:  (-2.77, 1.68)
T-Test of difference = 0 (vs ≠): T-Value = -0.53  P-Value = 0.603  DF = 12
```

Two-Sample T-Test and CI: Desmoinesian_2, Morrowan_2

```
Two-sample T for Desmoinesian_2 vs Morrowan_2
                 N  Mean  StDev  SE Mean
Desmoinesian_2  33  4.67   3.25     0.57
Morrowan_2       3  5.85   2.57      1.5
Difference = μ (Desmoinesian_2) - μ (Morrowan_2)
Estimate for difference:  -1.18
95% CI for difference:  (-8.02, 5.66)
T-Test of difference = 0 (vs ≠): T-Value = -0.74  P-Value = 0.535  DF = 2
```

Two-Sample T-Test and CI: Atokan_2, Morrowan_2

```
Two-sample T for Atokan_2 vs Morrowan_2
            N  Mean  StDev  SE Mean
Atokan_2    7  5.22   2.25     0.85
Morrowan_2  3  5.85   2.57      1.5
Difference = μ (Atokan_2) - μ (Morrowan_2)
Estimate for difference:  -0.63
95% CI for difference:  (-6.09, 4.82)
```

```
T-Test of difference = 0 (vs ≠): T-Value = -0.37  P-Value = 0.736  DF = 3
```

Two-Sample T Test-Comparison between nautiloid and ammonoid groups:

Two-Sample T-Test and CI: Wolfcampian_1, Wolfcampian_2

```
Two-sample T for Wolfcampian_1 vs Wolfcampian_2
              N  Mean  StDev  SE Mean
Wolfcampian_1  6  3.54   2.02     0.82
Wolfcampian_2  7  4.98   1.62     0.61
Difference = μ (Wolfcampian_1) - μ (Wolfcampian_2)
Estimate for difference:  -1.44
95% CI for difference:  (-3.76, 0.89)
T-Test of difference = 0 (vs ≠): T-Value = -1.40  P-Value = 0.195  DF = 9
```

Two-Sample T-Test and CI: Virgilian_1, Virgilian_2

```
Two-sample T for Virgilian_1 vs Virgilian_2
              N  Mean  StDev  SE Mean
Virgilian_1   9  5.96   5.70      1.9
Virgilian_2  29  5.96   4.66     0.87
Difference = μ (Virgilian_1) - μ (Virgilian_2)
Estimate for difference:  -0.01
95% CI for difference:  (-4.60, 4.59)
T-Test of difference = 0 (vs ≠): T-Value = -0.00  P-Value = 0.998  DF = 11
```

Two-Sample T-Test and CI: Missourian_1, Missourian_2

```
Two-sample T for Missourian_1 vs Missourian_2
               N  Mean  StDev  SE Mean
Missourian_1   8  6.02   3.10      1.1
Missourian_2  47  5.58   3.72     0.54
Difference = μ (Missourian_1) - μ (Missourian_2)
Estimate for difference:  0.44
95% CI for difference:  (-2.29, 3.16)
T-Test of difference = 0 (vs ≠): T-Value = 0.36  P-Value = 0.729  DF = 10
```

Two-Sample T-Test and CI: Desmoinesian_1, Desmoinesian_2

```
Two-sample T for Desmoinesian_1 vs Desmoinesian_2
                 N  Mean  StDev  SE Mean
Desmoinesian_1   8  3.09   2.35     0.83
Desmoinesian_2  33  4.67   3.25     0.57
Difference = μ (Desmoinesian_1) - μ (Desmoinesian_2)
Estimate for difference:  -1.58
95% CI for difference:  (-3.74, 0.58)
T-Test of difference = 0 (vs ≠): T-Value = -1.57  P-Value = 0.139  DF = 14
```

Two-Sample T-Test and CI: Atokan_1, Atokan_2

```
Two-sample T for Atokan_1 vs Atokan_2
          N  Mean  StDev  SE Mean
Atokan_1  8  3.02   4.95      1.8
Atokan_2  7  5.22   2.25     0.85
Difference = μ (Atokan_1) - μ (Atokan_2)
Estimate for difference:  -2.19
95% CI for difference:  (-6.53, 2.14)
T-Test of difference = 0 (vs ≠): T-Value = -1.13  P-Value = 0.286  DF = 10
```

Two-Sample T-Test and CI: Morrowan_1, Morrowan_2

```
Two-sample T for Morrowan_1 vs Morrowan_2
            N  Mean  StDev  SE Mean
Morrowan_1  5  5.31   2.12     0.95
Morrowan_2  3  5.85   2.57      1.5
Difference = μ (Morrowan_1) - μ (Morrowan_2)
Estimate for difference:  -0.54
95% CI for difference:  (-6.15, 5.07)
T-Test of difference = 0 (vs ≠): T-Value = -0.31  P-Value = 0.779  DF = 3
```

ANOVA:

H_n: there is no difference in mean between levels

H_a: there is a difference in mean between levels

Assumptions:

(1) The values for each temporal bin follow a Normal

(2) The variances are the same for temporal bin

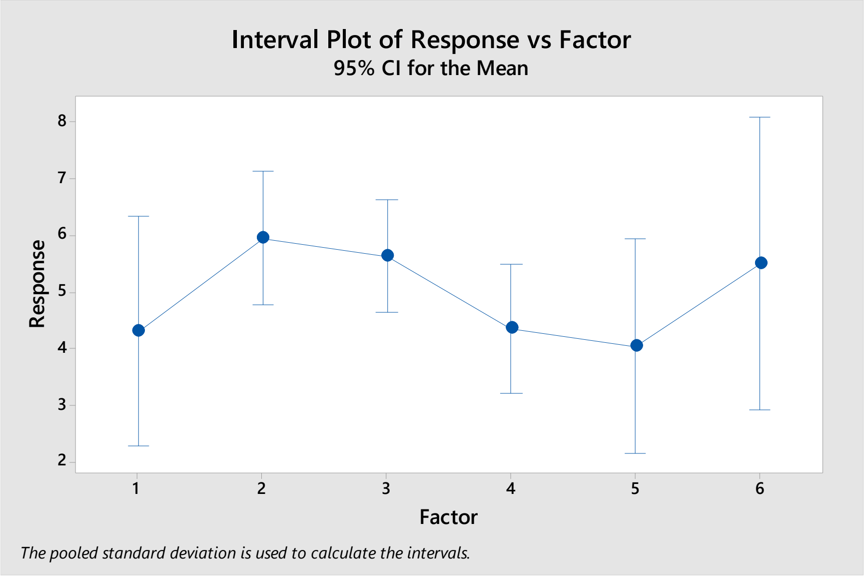
A One-Way ANOVA was a parametric test utilized on transformed data to detect differences in means between groups and to test the effect of temporal bin on geographic range. These analyses were performed separately with the assumption of equal variance and without the assumption of equal variance. A Tukey Cramer Comparison test used with the One-Way ANOVA to create confidence intervals for all pairwise differences between level means while controlling the error. Further, I decided to try a GLM to cope with the unbalanced nature of my data and the results of these analyses are presented below. The test is significant at $p \leq 0.05$.

ANOVA-Comparison across all cephalopods:

One-way ANOVA: Response versus Factor

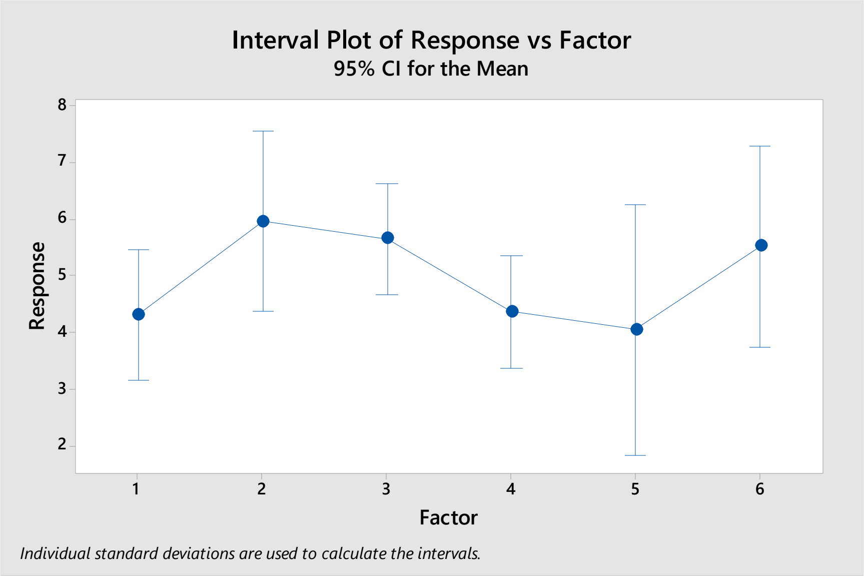
```
Method
Null hypothesis         All means are equal
Alternative hypothesis At least one mean is different
Significance level      α = 0.05
Rows unused             304
Equal variances were assumed for the analysis.
Factor Information

Factor  Levels  Values
Factor       6  1, 2, 3, 4, 5, 6
Analysis of Variance
Source   DF   Adj SS  Adj MS  F-Value  P-Value
Factor    5    92.41   18.48     1.34    0.250
Error   164  2263.03   13.80
Total   169  2355.44

Model Summary
      S   R-sq  R-sq(adj)  R-sq(pred)
3.71469  3.92%      0.99%       0.00%
Means
Factor   N   Mean  StDev       95% CI
1       13  4.313  1.890  (2.279, 6.348)
2       38  5.960  4.845  (4.771, 7.150)
3       55  5.646  3.618  (4.657, 6.635)
4       41  4.362  3.134  (3.216, 5.507)
```

```
5        15   4.05   3.96  ( 2.15,  5.94)
6         8  5.513  2.129  (2.919, 8.106)
Pooled StDev = 3.71469
```



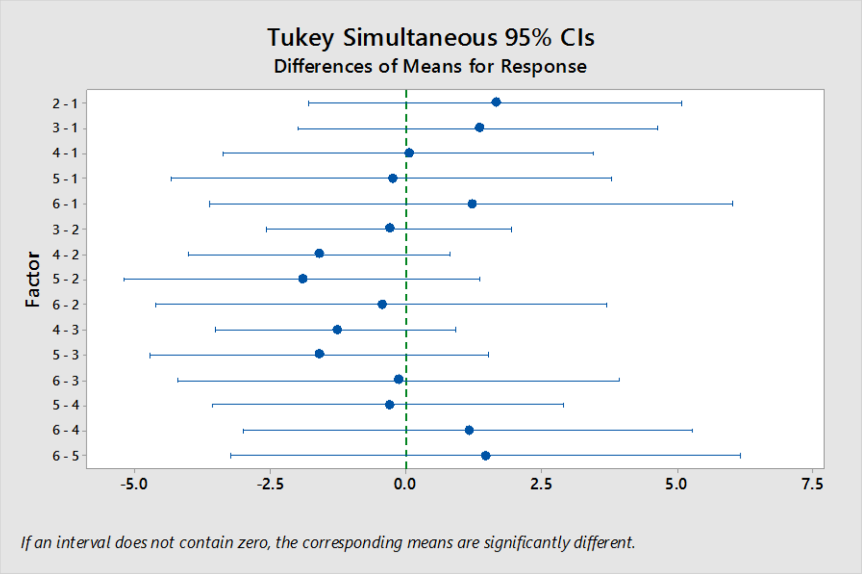
One-way ANOVA: Response versus Factor

```
Method
Null hypothesis           All means are equal
Alternative hypothesis    At least one mean is different
Significance level        α = 0.05
Rows unused               304
Equal variances were not assumed for the analysis.
Factor Information
Factor  Levels  Values
Factor       6  1, 2, 3, 4, 5, 6
Welch’s Test
         DF
Source  Num   DF Den  F-Value  P-Value
Factor    5  42.6711     1.50    0.211
Model Summary
 R-sq  R-sq(adj)  R-sq(pred)
3.92%      0.99%       0.00%
Means
Factor   N   Mean  StDev       95% CI
1       13  4.313  1.890  (3.172, 5.455)
2       38  5.960  4.845  (4.368, 7.553)
3       55  5.646  3.618  (4.668, 6.624)
4       41  4.362  3.134  (3.373, 5.351)
5       15   4.05   3.96  ( 1.85,  6.24)
6        8  5.513  2.129  (3.733, 7.292)
```



Tukey Pairwise Comparisons: Response = Response, Term = Factor

```
Grouping Information Using the Tukey Method and 95% Confidence
Factor   N     Mean  Grouping
2       38  5.96041  A
3       55  5.64627  A
6        8  5.51259  A
4       41  4.36190  A
1       13  4.31344  A
5       15  4.04534  A

Means that do not share a letter are significantly different.
Tukey Simultaneous Tests for Differences of Means
Difference
of Factor   Difference      SE of    Simultaneous            Adjusted
Levels        of Means  Difference       95% CI      T-Value  P-Value
2 - 1             1.65        1.19  ( -1.80,  5.09)     1.38    0.739
3 - 1             1.33        1.15  ( -1.97,  4.64)     1.16    0.853
4 - 1             0.05        1.18  ( -3.36,  3.46)     0.04    1.000
5 - 1            -0.27        1.41  ( -4.33,  3.79)    -0.19    1.000
6 - 1             1.20        1.67  ( -3.62,  6.01)     0.72    0.979
3 - 2           -0.314       0.784  (-2.575, 1.947)    -0.40    0.999
4 - 2           -1.599       0.836  (-4.012, 0.815)    -1.91    0.399
5 - 2            -1.92        1.13  ( -5.18,  1.35)    -1.69    0.540
6 - 2            -0.45        1.44  ( -4.62,  3.72)    -0.31    1.000
4 - 3           -1.284       0.766  (-3.496, 0.927)    -1.68    0.550
5 - 3            -1.60        1.08  ( -4.72,  1.52)    -1.48    0.678
6 - 3            -0.13        1.41  ( -4.19,  3.92)    -0.10    1.000
5 - 4            -0.32        1.12  ( -3.55,  2.92)    -0.28    1.000
6 - 4             1.15        1.44  ( -2.99,  5.29)     0.80    0.967
6 - 5             1.47        1.63  ( -3.22,  6.16)     0.90    0.945
Individual confidence level = 99.56%
```

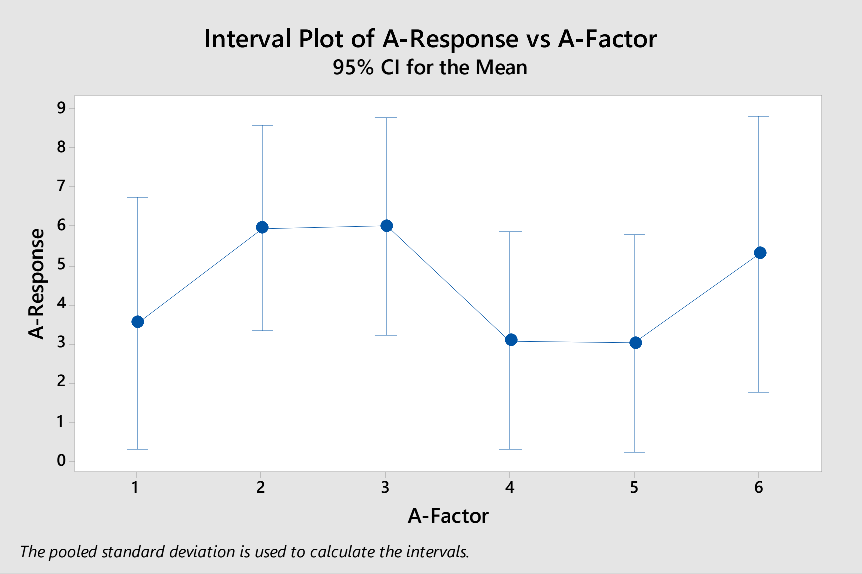


If an interval does not contain zero, the corresponding means are significantly different.

ANOVA-Comparison across ammonoid groups:

One-way ANOVA: A-Response versus A-Factor

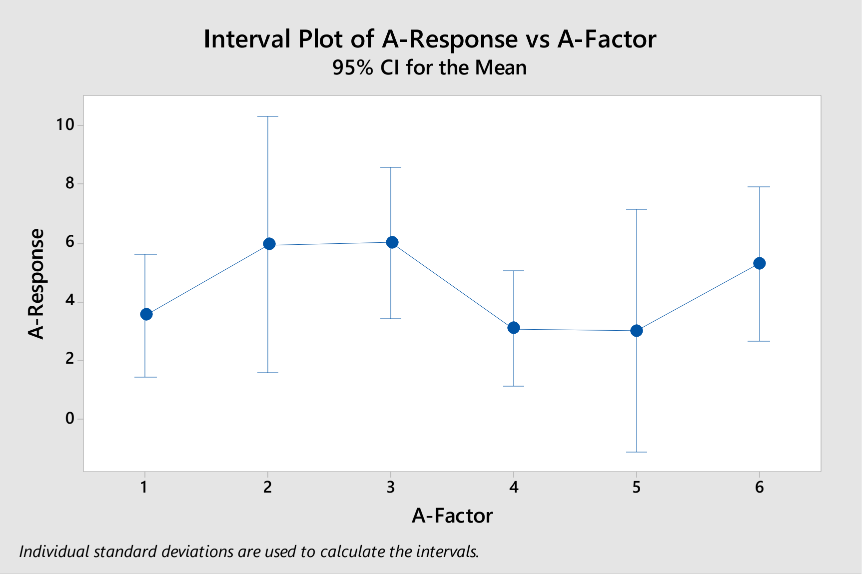
```
Method
Null hypothesis          All means are equal
Alternative hypothesis   At least one mean is different
Significance level       α = 0.05
Rows unused              88
Equal variances were assumed for the analysis.
Factor Information
Factor     Levels  Values
A-Factor        6  1, 2, 3, 4, 5, 6
Analysis of Variance
Source     DF  Adj SS   Adj MS  F-Value  P-Value
A-Factor    5   79.71    15.94     1.05    0.402
Error      38  576.19    15.16
Total      43  655.90
Model Summary
      S    R-sq  R-sq(adj)  R-sq(pred)
3.89397  12.15%      0.59%       0.00%
Means
A-Factor   N   Mean  StDev       95% CI
1          6  3.539  2.019  (0.321, 6.758)
2          9   5.96   5.70  ( 3.33,  8.58)
3          8   6.02   3.10  ( 3.23,  8.81)
4          8  3.092  2.355  (0.305, 5.879)
5          8   3.02   4.95  ( 0.23,  5.81)
6          5  5.310  2.116  (1.785, 8.835)

Pooled StDev = 3.89397
```



The pooled standard deviation is used to calculate the intervals.

One-way ANOVA: A-Response versus A-Factor

```
Method
Null hypothesis         All means are equal
Alternative hypothesis  At least one mean is different
Significance level      α = 0.05
Rows unused             88
Equal variances were not assumed for the analysis.
Factor Information
Factor    Levels  Values
A-Factor       6  1, 2, 3, 4, 5, 6
Welch’s Test
           DF
Source     Num   DF Den  F-Value  P-Value
A-Factor     5  17.0530     1.35    0.290
Model Summary
  R-sq  R-sq(adj)  R-sq(pred)
12.15%      0.59%       0.00%
Means
A-Factor  N   Mean  StDev       95% CI
1         6  3.539  2.019  (1.421, 5.658)
2         9   5.96   5.70  ( 1.57, 10.34)
3         8   6.02   3.10  ( 3.42,  8.61)
4         8  3.092  2.355  (1.124, 5.060)
5         8   3.02   4.95  (-1.12,  7.16)
6         5  5.310  2.116  (2.682, 7.938)
```


Interval Plot of A-Response vs A-Factor

95% CI for the Mean

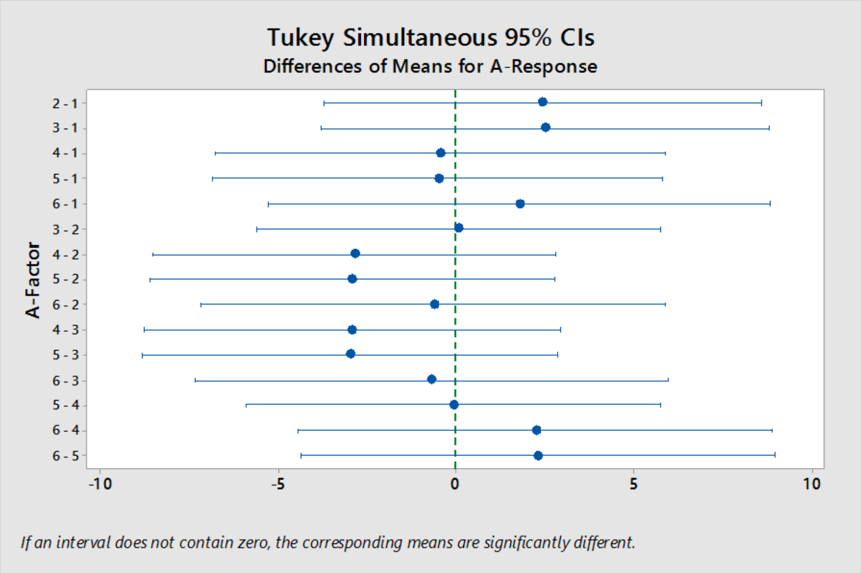
Individual standard deviations are used to calculate the intervals.

General Linear Model: A-Response versus A-Factor

```
Method
Factor coding  (-1, 0, +1)
Rows unused    88

Factor Information
Factor     Type   Levels  Values
A-Factor   Fixed       6  1, 2, 3, 4, 5, 6

Analysis of Variance
Source       DF  Adj SS  Adj MS  F-Value  P-Value
  A-Factor    5   79.71   15.94     1.05    0.402
Error        38  576.19   15.16
Total        43  655.90

Model Summary
      S    R-sq  R-sq(adj)  R-sq(pred)
3.89397  12.15%      0.59%       0.00%

Coefficients
Term        Coef  SE Coef  T-Value  P-Value   VIF
Constant   4.490    0.599     7.49    0.000
A-Factor
  1        -0.95     1.43    -0.66    0.510  1.48
  2         1.47     1.22     1.20    0.236  1.33
  3         1.53     1.27     1.20    0.237  1.37
  4        -1.40     1.27    -1.10    0.279  1.37
  5        -1.47     1.27    -1.15    0.256  1.37

Regression Equation
A-Response = 4.490 - 0.95 A-Factor_1 + 1.47 A-Factor_2 + 1.53 A-Factor_3 - 1.40 A-
Factor_4
             - 1.47 A-Factor_5 + 0.82 A-Factor_6
Fits and Diagnostics for Unusual Observations
Obs  A-Response   Fit  Resid  Std Resid
 44       -3.22  5.96  -9.17      -2.50  R
 95       -6.77  3.02  -9.79      -2.69  R
R  Large residual
```

Tukey Pairwise Comparisons: Response = A-Response, Term = A-Factor

```
Grouping Information Using the Tukey Method and 95% Confidence
A-Factor  N     Mean  Grouping
3         8  6.01913  A
2         9  5.95618  A
6         5  5.31001  A
1         6  3.53948  A
4         8  3.09208  A
5         8  3.02121  A
Means that do not share a letter are significantly different.

Tukey Simultaneous Tests for Differences of Means
Difference
of A-Factor  Difference       SE of   Simultaneous           Adjusted
Levels         of Means  Difference      95% CI      T-Value  P-Value
2 - 1              2.42        2.05  (-3.74,  8.57)     1.18    0.845
3 - 1              2.48        2.10  (-3.83,  8.78)     1.18    0.844
4 - 1             -0.45        2.10  (-6.75,  5.86)    -0.21    1.000
5 - 1             -0.52        2.10  (-6.82,  5.79)    -0.25    1.000
6 - 1              1.77        2.36  (-5.30,  8.84)     0.75    0.974
3 - 2              0.06        1.89  (-5.61,  5.74)     0.03    1.000
4 - 2             -2.86        1.89  (-8.54,  2.81)    -1.51    0.658
5 - 2             -2.93        1.89  (-8.61,  2.74)    -1.55    0.634
6 - 2             -0.65        2.17  (-7.16,  5.87)    -0.30    1.000
4 - 3             -2.93        1.95  (-8.76,  2.91)    -1.50    0.664
5 - 3             -3.00        1.95  (-8.84,  2.84)    -1.54    0.642
6 - 3             -0.71        2.22  (-7.36,  5.95)    -0.32    1.000
5 - 4             -0.07        1.95  (-5.91,  5.77)    -0.04    1.000
6 - 4              2.22        2.22  (-4.44,  8.87)     1.00    0.915
6 - 5              2.29        2.22  (-4.37,  8.94)     1.03    0.904
Individual confidence level = 99.52%
```



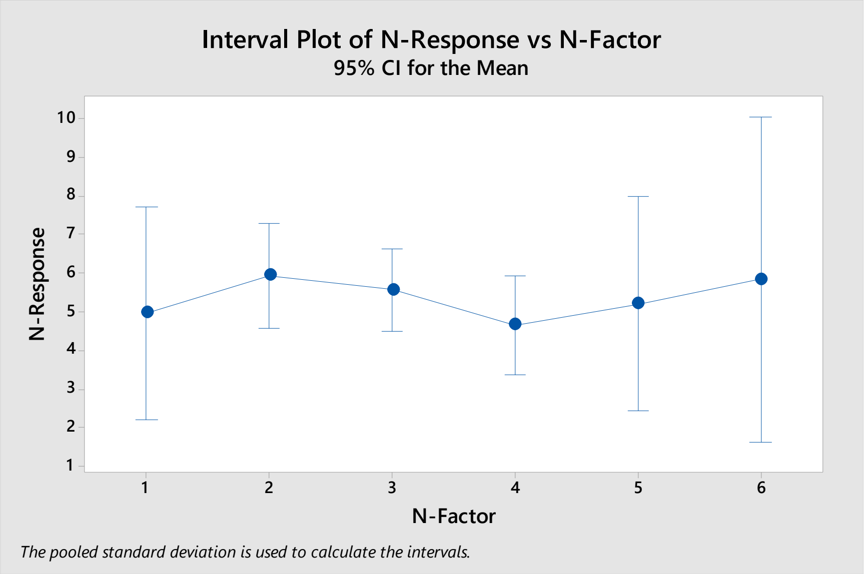
If an interval does not contain zero, the corresponding means are significantly different.

ANOVA-Comparison of nautiloid groups:

One-way ANOVA: N-Response versus N-Factor

```
Method
Null hypothesis         All means are equal
Alternative hypothesis  At least one mean is different
Significance level      α = 0.05
/Rows unused             216
```

```
Equal variances were assumed for the analysis.
Factor Information
Factor    Levels  Values
N-Factor       6  1, 2, 3, 4, 5, 6
Analysis of Variance
Source     DF  Adj SS  Adj MS  F-Value  P-Value
N-Factor    5    30.38   6.077     0.44    0.817
Error     120  1644.30  13.703
Total     125  1674.69
Model Summary
      S   R-sq  R-sq(adj)  R-sq(pred)
3.70169  1.81%      0.00%       0.00%
Means
N-Factor   N   Mean  StDev       95% CI
1          7  4.977  1.622  (2.207, 7.747)
2         29  5.962  4.661  (4.601, 7.323)
3         47  5.583  3.725  (4.514, 6.652)
4         33  4.670  3.250  (3.394, 5.946)
5          7  5.216  2.255  (2.446, 7.986)
6          3   5.85   2.57  ( 1.62, 10.08)
Pooled StDev = 3.70169
```

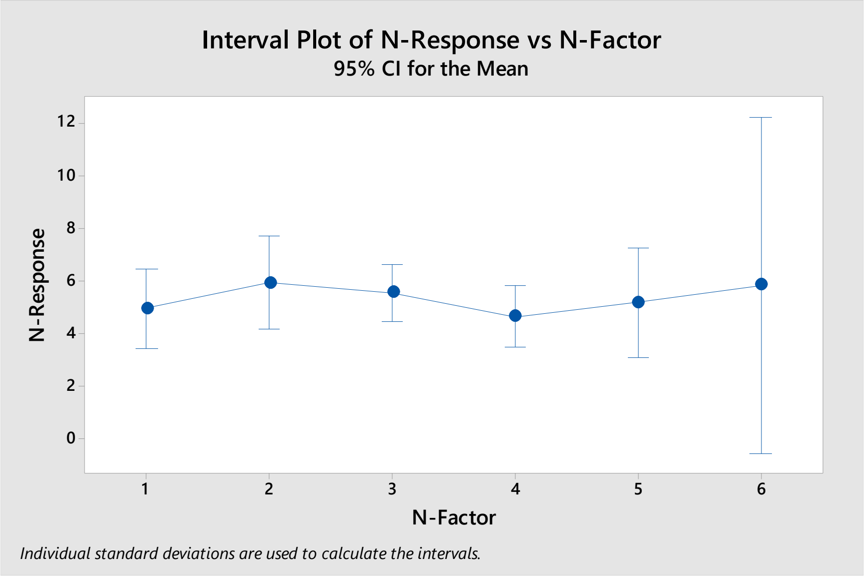


The pooled standard deviation is used to calculate the intervals.

One-way ANOVA: N-Response versus N-Factor

```
Method
Null hypothesis         All means are equal
Alternative hypothesis  At least one mean is different
Significance level      α = 0.05
Rows unused             216
Equal variances were not assumed for the analysis.
Factor Information
Factor    Levels  Values
N-Factor       6  1, 2, 3, 4, 5, 6
Welch's Test
           DF
Source    Num   DF Den  F-Value  P-Value
N-Factor    5  15.4457     0.42    0.828
Model Summary
 R-sq  R-sq(adj)  R-sq(pred)
1.81%      0.00%       0.00%
Means
N-Factor   N   Mean  StDev       95% CI
```

```
1          7  4.977  1.622  (3.476, 6.477)
2         29  5.962  4.661  (4.189, 7.735)
3         47  5.583  3.725  (4.489, 6.677)
4         33  4.670  3.250  (3.517, 5.822)
5          7  5.216  2.255  (3.131, 7.301)
6          3   5.85   2.57  (-0.55, 12.25)
```



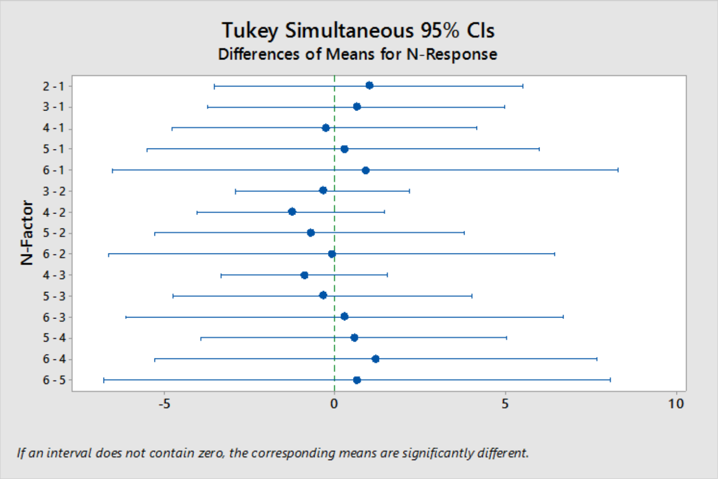
General Linear Model: N-Response versus N-Factor

```
Method
Factor coding  (-1, 0, +1)
Rows unused    216
Factor Information
Factor     Type   Levels  Values
N-Factor  Fixed        6  1, 2, 3, 4, 5, 6
Analysis of Variance
Source        DF   Adj SS  Adj MS  F-Value  P-Value
  N-Factor     5    30.38   6.077     0.44    0.817
Error        120  1644.30  13.703
Total        125  1674.69
Model Summary
      S    R-sq  R-sq(adj)  R-sq(pred)
3.70169  1.81%      0.00%       0.00%
Coefficients
Term         Coef  SE Coef  T-Value  P-Value   VIF
Constant    5.376    0.518    10.38    0.000
N-Factor
  1         -0.40     1.25    -0.32    0.751  1.13
  2         0.586    0.764     0.77    0.445  1.13
  3         0.207    0.680     0.30    0.762  1.17
  4        -0.706    0.738    -0.96    0.341  1.15
  5         -0.16     1.25    -0.13    0.898  1.13
Regression Equation
N-Response = 5.376 - 0.40 N-Factor_1 + 0.586 N-Factor_2 + 0.207 N-Factor_3 - 0.706 N-
Factor_4
             - 0.16 N-Factor_5 + 0.47 N-Factor_6
Fits and Diagnostics for Unusual Observations
Obs  N-Response   Fit  Resid  Std Resid
101       23.57  5.96  17.61       4.84  R
112       -2.27  5.96  -8.23      -2.26  R
131       -1.90  5.58  -7.48      -2.04  R
140       -2.28  5.58  -7.87      -2.15  R
```

```
233         4.36  5.22  -0.85       -0.25     X
247         4.36  5.22  -0.85       -0.25     X
248         4.36  5.22  -0.85       -0.25     X
264         4.36  5.22  -0.85       -0.25     X
267         4.36  5.22  -0.85       -0.25     X
276        10.33  5.22   5.11        1.49     X
284         4.36  5.22  -0.85       -0.25     X
304         8.82  5.85   2.97        0.98     X
324         4.36  5.85  -1.49       -0.49     X
341         4.36  5.85  -1.49       -0.49     X
R  Large residual
X  Unusual X
```

Tukey Pairwise Comparisons: Response = N-Response, Term = N-Factor

```
Grouping Information Using the Tukey Method and 95% Confidence
N-Factor   N     Mean  Grouping
2         29  5.96172  A
6          3  5.85022  A
3         47  5.58281  A
5          7  5.21577  A
1          7  4.97684  A
4         33  4.66974  A
Means that do not share a letter are significantly different.
Tukey Simultaneous Tests for Differences of Means
Difference
of N-Factor  Difference       SE of    Simultaneous              Adjusted
Levels         of Means  Difference        95% CI       T-Value   P-Value
2 - 1              0.98        1.56  ( -3.53,  5.50)       0.63     0.988
3 - 1              0.61        1.50  ( -3.74,  4.95)       0.40     0.999
4 - 1             -0.31        1.54  ( -4.77,  4.16)      -0.20     1.000
5 - 1              0.24        1.98  ( -5.50,  5.98)       0.12     1.000
6 - 1              0.87        2.55  ( -6.53,  8.28)       0.34     0.999
3 - 2            -0.379       0.874  (-2.913, 2.155)      -0.43     0.998
4 - 2            -1.292       0.942  (-4.024, 1.440)      -1.37     0.744
5 - 2             -0.75        1.56  ( -5.27,  3.77)      -0.48     0.997
6 - 2             -0.11        2.24  ( -6.62,  6.40)      -0.05     1.000
4 - 3            -0.913       0.841  (-3.350, 1.524)      -1.09     0.886
5 - 3             -0.37        1.50  ( -4.71,  3.98)      -0.24     1.000
6 - 3              0.27        2.20  ( -6.12,  6.66)       0.12     1.000
5 - 4              0.55        1.54  ( -3.92,  5.01)       0.35     0.999
6 - 4              1.18        2.23  ( -5.29,  7.65)       0.53     0.995
6 - 5              0.63        2.55  ( -6.77,  8.04)       0.25     1.000
Individual confidence level = 99.55%
```



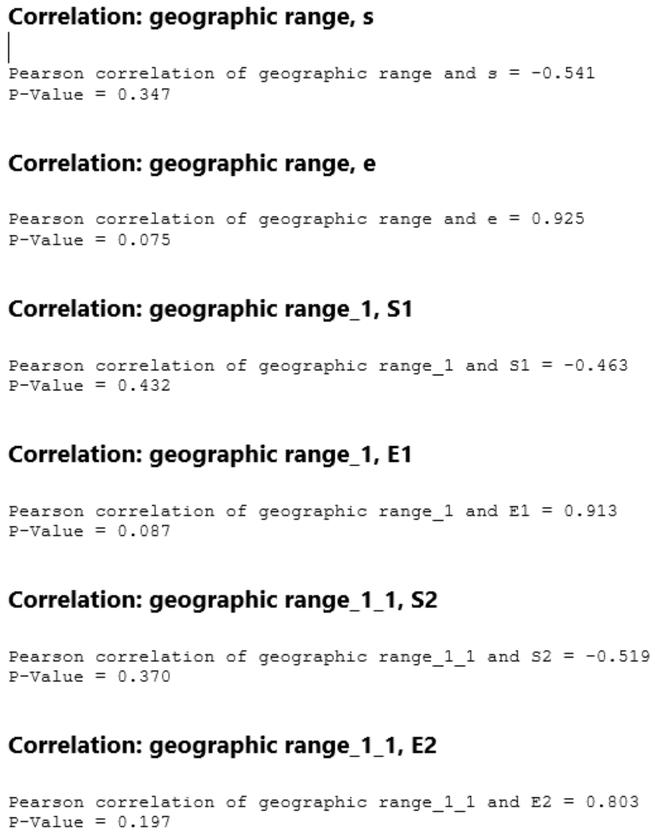
Speciation & Extinction Rate Calculations:

W/ sing	Cephalopod	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/ sing	Cephalopod	Wolfcampian	13	7	6	7	13	14	#VALUE!	0.044217086	#VALUE!
W/ sing	Cephalopod	Virgilian	38	32	6	32	38	5	-0.303965151	0.034370051	0.338335
W/ sing	Cephalopod	Missourian	55	33	22	33	55	3	-0.01025722	0.170275208	0.180532
W/ sing	Cephalopod	Desmoinesian	41	12	29	12	41	3	0.337200304	0.409555139	0.072355
W/ sing	Cephalopod	Atokan	15	7	8	7	15	2	0.26949825	0.381070026	0.111572
W/ sing	Cephalopod	Morrowan	8	0	8	0	8	6	#NUM!	#NUM!	#NUM!
W/ sing	Ammonoid	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/ sing	Ammonoid	Wolfcampian	6	1	5	1	6	14	#VALUE!	0.127982819	#VALUE!
W/ sing	Ammonoid	Virgilian	10	6	4	6	10	5	-0.358351894	0.102165125	0.460517
W/ sing	Ammonoid	Missourian	8	6	2	6	8	3	0	0.095894024	0.095894
W/ sing	Ammonoid	Desmoinesian	8	5	3	5	8	3	0.060773852	0.156667876	0.095894
W/ sing	Ammonoid	Atokan	8	4	4	4	8	2	0.111571776	0.34657359	0.235002
W/ sing	Ammonoid	Morrowan	5	0	5	0	5	6	#NUM!	#NUM!	#NUM!
W/ sing	Nautiloid	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/ sing	Nautiloid	Wolfcampian	7	6	1	6	7	14	#VALUE!	0.011010763	#VALUE!
W/ sing	Nautiloid	Virgilian	28	26	2	26	28	5	-0.293267414	0.014821594	0.308089
W/ sing	Nautiloid	Missourian	47	27	20	27	47	3	-0.012580109	0.184770245	0.19735
W/ sing	Nautiloid	Desmoinesian	33	7	26	7	33	3	0.449975572	0.516865804	0.06689
W/ sing	Nautiloid	Atokan	7	3	4	3	7	2	0.42364893	0.42364893	0
W/ sing	Nautiloid	Morrowan	3	0	3	0	3	6	#NUM!	#NUM!	#NUM!
W/O	Cephalopod	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/O	Cephalopod	Wolfcampian	7	7	0	7	7	14	#VALUE!	0	#VALUE!
W/O	Cephalopod	Virgilian	33	32	1	32	33	5	-0.303965151	0.006154332	0.310119
W/O	Cephalopod	Missourian	40	33	7	33	40	3	-0.01025722	0.064123964	0.074381
W/O	Cephalopod	Desmoinesian	35	12	23	12	35	3	0.337200304	0.356813804	0.019614
W/O	Cephalopod	Atokan	14	7	7	7	14	2	0.26949825	0.34657359	0.077075
W/O	Cephalopod	Morrowan	7	0	7	0	7	6	#NUM!	#NUM!	#NUM!
W/O	Ammonoid	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/O	Ammonoid	Wolfcampian	1	1	0	1	1	14	#VALUE!	0	#VALUE!
W/O	Ammonoid	Virgilian	7	6	1	6	7	5	-0.358351894	0.030830136	0.389182
W/O	Ammonoid	Missourian	6	6	0	6	6	3	0	0	0
W/O	Ammonoid	Desmoinesian	7	5	2	5	7	3	0.060773852	0.112157412	0.051384
W/O	Ammonoid	Atokan	7	4	3	4	7	2	0.111571776	0.279807894	0.168236
W/O	Ammonoid	Morrowan	4	0	4	0	4	6	#NUM!	#NUM!	#NUM!
W/O	Nautiloid	stage	Species Richness	species carry over	"new species"	N_o	N_f	Duration	R	S	E
W/O	Nautiloid	Wolfcampian	6	6	0	6	6	14	#VALUE!	0	#VALUE!
W/O	Nautiloid	Virgilian	26	26	0	26	26	5	0.293267414	0	-0.29327
W/O	Nautiloid	Missourian	34	27	7	27	34	3	0.012580109	0.07684122	0.064261
W/O	Nautiloid	Desmoinesian	28	7	21	7	28	3	-0.449975572	0.46209812	0.912074
W/O	Nautiloid	Atokan	7	3	4	3	7	2	-0.42364893	0.42364893	0.847298
W/O	Nautiloid	Morrowan	3	0	3	0	3	6	#NUM!	#NUM!	#NUM!

Correlation Analyses:

The Pearson product moment correlation test were utilized upon non-transformed data to evaluate the relationship between two variables. The relationship is ‘correlated’ when a change in one variable is associated with a proportional change in the other variable. The test is significant at $p \leq 0.05$.

Correlation between mean geographic range size and speciation (s) and extinction (e) rates:



Correlation: geographic range, s

```
Pearson correlation of geographic range and s = -0.541
P-Value = 0.347
```

Correlation: geographic range, e

```
Pearson correlation of geographic range and e = 0.925
P-Value = 0.075
```

Correlation: geographic range_1, S1

```
Pearson correlation of geographic range_1 and S1 = -0.463
P-Value = 0.432
```

Correlation: geographic range_1, E1

```
Pearson correlation of geographic range_1 and E1 = 0.913
P-Value = 0.087
```

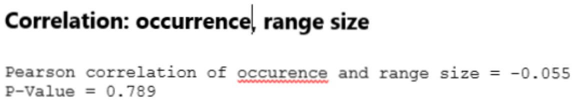
Correlation: geographic range_1_1, S2

```
Pearson correlation of geographic range_1_1 and S2 = -0.519
P-Value = 0.370
```

Correlation: geographic range_1_1, E2

```
Pearson correlation of geographic range_1_1 and E2 = 0.803
P-Value = 0.197
```

Correlation between genera occurrence data and geographic range size:



Correlation: occurrence, range size

```
Pearson correlation of occurence and range size = -0.055
P-Value = 0.789
```

Correlation Analysis between species richness and speciation and extinction rates:

Correlation: Richness, speciation

```
Pearson correlation of Richness and speciation = 0.005
P-Value = 0.993
```

Correlation: Richness, extinction

```
Pearson correlation of Richness and extinction = 0.214
P-Value = 0.786
```

Analysis of Bias:

Outcrop Area vs. Species Range Area Test:

A percent coverage table of the range size of species overlaid against temporal outcrop availability was created using GIS mapping and *Excel* software. A low percentage of overlap between range size and outcrop area would suggest that species distributions reflect 'real' biogeographic patterns while a high percentage would suggest that the presence or absence of outcrop was significantly influencing our results

STAGE:	Wolfcampian	1518052.708	PERCENT
Metacoceras	dubium	5745.847979	0.0037850
Domatoceras	umbilicatum	78.539816	0.0000517
Domatoceras	williamsi	78.539816	0.0000517
Mescalites	discoidalis	78.539816	0.0000517
Metacoceras	angulatum	78.539816	0.0000517

STAGE:	Virgilian	1665938.874	PERCENT
Orthoceras	kansasense	17195700000	10321.92733
Schistoceras	missouriense	145678.1478	0.087445074
Schistoceras	hildrethi	139876	0.083962264
Gonioloboceras	welleri	115412	0.069277452
Metacoceras	cornutum	85771	0.051485082

STAGE:	Missourian	1737036.164	PERCENT

Schistoceras	missouriense	145678.1478	0.083865927
Ephippioceras	ferratum	127692	0.073511423
Liroceras	liratum	119598	0.068851762
Domatoceras	moorei	117036	0.067376836
Solenochilius	brammeri	25888.01539	0.014903556

STAGE:	Desmoinesian	1835450.827	PERCENT
Pseudorthoceras	knoxense	64660	0.035228402
Domatoceras	umbilicatum	12489.5771	0.006804637
Solenochilius	springeri	9839.21795	0.005360655
Brachcycloceras	normale	8757	0.004771035
Mooreoceras	normale	8202	0.004468657

STAGE:	Atokan	934292.2165	PERCENT
Pseudorthoceras	knoxense	30599	0.032750995
Phaneroceras	compressum	24924	0.026676879
Brachcycloceras	normale	78.539816	8.406E-05
Liroceras	liratum	78.539816	8.406E-05
Liroceras	milleri	78.539816	8.406E-05

STAGE:	Morrowan	900649.1324	PERCENT
Pseudopronorites	arkansasensis	8916.063243	0.009899597
Liroceras	liratum	6791.691877	0.007540885
Mooreoceras	normale	78.539816	8.72036E-05
Phaneroceras	compressum	78.539816	8.72036E-05
Megapronorites	baconi	78.539816	8.72036E-05

Jackknife Analysis:

The second test used to analyze to what extent the fossil record might be biasing results was an “n-1” jack-knifing analysis. This procedure sub-sampled species range size within each temporal bin to test the resilience of data to outliers. Mean range size estimations were generated for each temporal bin that were input into a one-way ANOVA to compare jackknife estimates and the ‘real’ geographic range size as an estimation of bias.

R version 3.4.0 (2017-04-21) -- "You Stupid Darkness"

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Platform: x86_64-w64-mingw32/x64 (64-bit)

```
Wolfcampian
$jack.values
 [1] 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802
84.74802 83.74109 83.74109 84.74802 84.74802
[14] 84.74802 83.74109 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802
84.74802 84.74802 84.74802 84.74802 84.74802
[27] 83.74109 84.74802 84.74802 84.74802 84.74802 11.08330 84.74802 84.74802
84.74802 84.74802 83.74109 84.74802 84.74802
[40] 83.74109 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802 84.74802
84.74802 84.74802 84.74802 84.74802 84.74802
[53] 84.74802 84.74802 84.74802 84.74802 83.74109 84.74802 84.74802 84.74802
84.74802 84.74085 83.74109 83.74109 84.74802
[66] 83.74109 84.74802 84.74802 83.74109 84.74802 84.74802 84.74802 84.74802
84.74802 84.74802 84.74802 84.74802 84.74802
[79] 84.74802

   Min. 1st Qu.  Median    Mean 3rd Qu.    Max. 
  11.08   84.75   84.75   83.68   84.75   84.75 
   aov(formula = Mean ~ WOLF, data = wolf1)

> aov1 <-aov(Mean~WOLF,data=wolf1)
> summary(aov1)
             Df   Sum Sq Mean Sq F value Pr(>F)
WOLF          1        0       0       0      1
Residuals   156 32534847  208557               

Virgilain
$jack.values
[1] 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.20466
0e+08 2.204660e+08 2.204660e+08 2.204660e+08
[10] 2.204659e+08 2.204660e+08 2.204660e+08 2.204659e+08 2.204660e+08 2.2046
60e+08 2.204660e+08 2.204658e+08 2.204660e+08
[19] 2.204645e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204658e+08
[28] 2.204660e+08 2.204660e+08 2.204660e+08 2.204649e+08 2.204660e+08 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204660e+08
[37] 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.204659e+08 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204660e+08
[46] 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 7.949273e+03 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204660e+08
[55] 2.204660e+08 2.204660e+08 2.204651e+08 2.204660e+08 2.204660e+08 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204660e+08
[64] 2.204660e+08 2.204642e+08 2.204641e+08 2.204660e+08 2.204660e+08 2.2046
60e+08 2.204660e+08 2.204660e+08 2.204660e+08
[73] 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.204660e+08 2.2046
60e+08 2.204660e+08
     Min.   1st Qu.    Median      Mean   3rd Qu.      Max. 
     7949 220466010 220466011 217675302 220466011 220466011 
> summary(aov2)
             Df   Sum Sq   Mean Sq F value Pr(>F)
VIRG          1 0.00e+00 0.000e+00       0      1
Residuals   156 2.92e+20 1.872e+18               

Missourian
$jack.values
```

```
[1] 8227.561 8227.561 8227.561 8227.561 8227.561 8227.561 8228.565 6728.106
8227.561 8184.465 8228.558 6591.491 8179.504
[14] 8227.561 8228.568 8228.568 8227.561 8228.568 8227.561 8215.455 8227.561
8227.561 8228.566 8228.568 6695.260 8167.914
[27] 8107.305 8228.568 8110.215 8228.559 8228.557 8228.566 8227.561 8200.183
8228.561 8164.696 8168.657 8228.557 8227.561
[40] 8228.568 8165.555 8181.439 8171.298 8228.568 8164.734 8198.580 8227.561
8180.387 8227.561 8220.747 8227.561 8227.561
[53] 8228.568 8228.568 8228.568 8228.568 8131.427 8228.568 8228.568 8227.561
8227.561 8228.568 8228.568 8228.568 7921.965
[66] 6360.899 8227.561 8228.568 8228.568 8228.568 7896.670 8189.247 8227.561
8211.627 8228.568 8228.568 8228.568 8228.568
[79] 8228.568
> summary(col3)#summary of col1
   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
   6361    8194    8228    8124    8229    8229
> summary(aov3)
             Df    Sum Sq   Mean Sq F value Pr(>F)
MISS          1 0.000e+00         0       0      1

Desmoinesian
$jack.values
[1] 1471.6926 1456.6097 1470.6889 1471.6852 1359.4266 1471.6959 1470.6889 14
70.6889 1470.6889 1311.5731 1423.4651
[12] 1429.7856 1470.6889 1471.6959 1471.6959 1471.6899 1470.6889 1471.6959 1
470.6889 1471.6959 1471.6959 1471.6959
[23] 1471.6959 1470.6889 1470.6889 1470.6889 1471.6942 1470.6889 1471.6959 1
470.6889 1463.0985 1471.6959 1471.6959
[34] 1471.6959 1471.6959 1471.6936 1470.6889 1471.6959 1471.6959 1471.6959 1
471.6959 1470.6889 1470.6889 1471.6959
[45] 1366.5420 1471.6959 1471.6959 1471.6959 1470.6889 1470.6889 1470.6889 1
470.6889 1471.6918 1471.6894 1471.6959
[56] 1471.6959  642.7215 1471.6959 1471.6959 1471.6959 1470.6889 1471.6959 1
471.6959 1471.6959 1470.6889 1470.6889
[67] 1470.6889 1471.6959 1471.6959 1471.6959 1471.6959 1471.6959 1471.6959 1
471.6959 1471.6959 1470.6889 1471.6959
[78] 1345.5520 1470.6889
> summary(col4)#summary of col1
   Min. 1st Qu.  Median    Mean 3rd Qu.    Max.
  642.7  1470.7  1471.7  1453.1  1471.7  1471.7
> summary(aov4)
             Df    Sum Sq  Mean Sq F value Pr(>F)
DESM          1 0.000e+00        0       0      1
Residuals   156 4.438e+09 28451470

Atokan
$jack.values
[1] 722.9142 722.9142 722.9142 722.9142 721.9073 722.9142 722.9142 722.9142
722.9142 722.9142 722.9142 722.9142 722.9142
[14] 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142
722.9142 722.9142 722.9142 721.9073 721.9073
[27] 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142
722.9142 722.9142 722.9142 722.9142 722.9142
[40] 722.9142 722.9142 721.9073 722.9142 722.9142 721.9073 722.9142 722.9142
722.9142 722.9142 722.9142 722.9142 722.9142
[53] 722.9142 722.9142 403.3757 722.9095 330.6193 722.9142 721.9073 722.9142
721.9073 722.9142 722.9142 722.9142 721.9073
[66] 721.9073 721.9073 722.9142 722.9142 722.9142 722.9142 722.9142 722.9142
722.9142 722.9142 722.9142 722.9142 721.9073
[79] 722.9142
> summary(aov5)
             Df    Sum Sq Mean Sq F value Pr(>F)
ATOK          1 0.000e+00       0       0      1
Residuals   156 1.518e+09 9728043
```

```
Morrowan
$jack.values
[1] 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230
207.4230 207.4230 207.4230 207.4230 207.4230
[14] 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230
207.4230 207.4230 207.4230 120.3500 207.4230
[27] 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230
207.4230 207.4230 207.4230 207.4230 207.4230
[40] 207.4230 207.4230 207.4230 207.4230 207.4230 206.4161 207.4230 207.4230
207.4230 207.4230 207.4230 207.4230 207.4230
[53] 207.4230 207.4230 206.4161 207.4230 207.4230  93.1145 206.4161 207.4230
206.4161 207.4230 207.4230 207.4230 206.4161
[66] 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230 207.4230
207.4230 207.4230 207.4230 207.4230 206.4161
[79] 207.4230
> summary(aov6)
             Df    Sum Sq Mean Sq F value Pr(>F)
MORR          1         0       0       0      1
Residuals   156 122366967  784404
```

Appendix 2: Reconstructed Range Values

Geographic Information Systems (GIS) provide a valuable tool for biogeographic range reconstruction in both modern and paleo- ecological studies. *ArcGIS v. 10.3* software allows for both the mapping of fossil geographic ranges through the *PaleoWeb* extension (The Rothwell Group LP, 2016) and calculation of range area throughout temporal bins. In this way, it is possible to use GIS to understand biogeographic changes through geologic time and infer evolutionary dynamics. Methods for paleo-range reconstruction of Pennsylvanian-Early Permian cephalopods were taken from Rode & Lieberman (2004 & 2005), Stigall & Lieberman (2006), Myers & Lieberman (2011) and M. Casey (personal communication, 2016).

After specimen occurrence data were georeferenced and assigned to temporal bins, *Excel* CSV files were created for the occurrence points of all specimens within species. CSV files were imported into *ArcGIS* and layers were created using geographic coordinate system ‘WGS 1984’ and projected coordinate system ‘WGS 1984 World Mercator’. These layers were input into *PaleoWeb* to rotate coordinates into continental configuration and geographic position of the Midcontinent Region during the Pennsylvanian-Early Permian (see Chapter 1 for further information) and to minimize any error in species range reconstruction (Myers & Lieberman, 2011). Paleo-coordinates were generated for each specimen occurrence point in each species layer using *PaleoWeb*. These paleo-coordinate layers were then re-projected into *ArcMap*.

Ranges were reconstructed using minimum bounding geometry; convex hulls or buffers were given to every specimen occurrence point in each species and these shapefiles were re-projected in ‘South America-Albers Equal Area Conic’. This model was used to accommodate the rotation of species occurrence coordinates into the southern hemisphere during the Late Paleozoic. Species with three or more occurrence points were given a convex hull that spanned the entire area between occurrences. In this way, multiple occurrence points were combined to recreate the geographic range of a single species. Species with only one occurrence point were given a 10km^2 buffer, while species with two occurrence points were each given a 10km^2 buffer and combined using map geometry. This ‘buffering’ method gives an area to species with only one or two occurrence points and allows for incorporation of these species into biogeographic analysis. After this step, it was possible to calculate range area for each species using map geometry. Please find a complete list of species range values through geologic time. Species are first organized by alphabetically by genus and then by species.

Species Geographic Range Values:

Genus	species	Wolfcampian	Virgilian	Missourian	Desmoinesian	Atokan	Morrowan
Brachycycloceras	***bransoni***	0.00000000	78.53981600	78.53981600	0.25079800	0.00000000	0.00000000
Brachycycloceras	***crebrincinctum***	0.00000000	0.52379800	78.53981600	1176.71847600	0.00000000	0.00000000
Brachycycloceras	***curtum***	0.00000000	377.41226100	78.53981600	78.53981600	0.00000000	0.00000000
Brachycycloceras	***longulum***	0.00000000	1065.65468300	78.53981600	0.83369700	0.00000000	0.00000000
Brachcycloceras	***normale***	0.00000000	0.49404300	78.53981600	8757.00000000	78.53981600	0.00000000
Domatoceras	***bradyi***	0.00000000	78.53981600	78.53981600	0.00000000	0.00000000	0.00000000
Domatoceras	***kleihegei***	0.00000000	0.00000000	0.22033800	78.53981600	0.00000000	0.00000000
Domatoceras	***moorei***	0.00000000	0.00000000	117036.00000000	78.53981600	0.00000000	0.00000000
Domatoceras	***sculptile***	0.00000000	78.53981600	78.53981600	78.53981600	0.00000000	0.00000000
Domatoceras	***umbilicatum***	78.53981600	12010.00000000	3440.00000000	12489.57710400	0.00000000	0.00000000
Domatoceras	***williamsi***	78.53981600	78.53981600	0.72978900	3762.00000000	0.00000000	0.00000000
Ephippioceras	***ferratum***	0.00000000	2810.00000000	127692.00000000	3269.00000000	0.00000000	0.00000000
Euloxoceras	***greenei***	0.00000000	7594.00000000	3827.00000000	78.53981600	0.00000000	0.00000000
Gonioloboceras	***bridgeportensis***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000
Mescalites	***discoidalis***	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Gonioloboceratoides	***elaisi***	0.00000000	0.00000000	0.00000000	0.46606900	0.00000000	0.00000000
Gonioloboceras	***goniolobum***	0.00000000	15174.00000000	78.53981600	78.53981600	0.00000000	0.00000000
Gonioloboceras	***gracellenae***	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000
Gonioloboceras	***welleri***	0.00000000	115412.00000000	78.53981600	78.53981600	0.00000000	0.00000000
Millkoninckioceras	***elaisi***	0.00000000	0.00000000	1022.81549300	0.00000000	0.00000000	0.00000000
Millkoninckioceras	***jewetti***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000
Millkoninckioceras	***wyandottense***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000

Knightoceras	***abundum***	0.00000000	0.00000000	0.14947500	0.00000000	0.00000000	0.00000000
Knightoceras	***missouriense***	0.00000000	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000
Liroceras	***liratum***	0.00000000	0.00000000	119598.00000000	78.53981600	78.53981600	6791.69187700
Liroceras	***milleri***	0.00000000	0.00000000	4731.00000000	78.53981600	78.53981600	0.00000000
Metacoceras	***angulatum***	78.53981600	13702.44863200	9458.49073400	0.13077300	0.00000000	0.00000000
Metacoceras	***bituberculatum***	0.00000000	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000
Metacoceras	***bowmani***	0.00000000	0.00000000	9231.47599300	0.00000000	0.00000000	0.00000000
Metacoceras	***cheneyi***	0.00000000	78.53981600	0.63981000	78.53981600	0.00000000	0.00000000
Metacoceras	***cornutum***	0.00000000	85771.00000000	0.79348600	670.59274300	0.00000000	0.00000000
Metacoceras	***dubium***	5745.84797900	78.53981600	0.10184300	0.00000000	0.00000000	0.00000000
Metacoceras	***inconspicuim***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000
Metacoceras	***jacksonense***	0.00000000	78.53981600	2214.00000000	0.00000000	0.00000000	0.00000000
Metacoceras	***knighti***	0.00000000	0.00000000	0.49733300	0.00000000	0.00000000	0.00000000
Metacoceras	***mutabile***	0.00000000	0.00000000	4982.00000000	0.17545000	0.00000000	0.00000000
Metacoceras	***nodosum***	78.53981600	78.53981600	4673.00000000	78.53981600	0.00000000	0.00000000
Metacoceras	***perelegans***	0.00000000	0.00000000	0.79348600	0.00000000	0.00000000	0.00000000
Metacoceras	***sulciferum***	0.00000000	78.53981600	78.53981600	0.00000000	0.00000000	0.00000000
Metacoceras	***sublaeve***	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Mooreoceras	***bakeri***	0.00000000	4981.34920000	4915.00000000	0.00000000	0.00000000	0.00000000
Mooreoceras	***condrai***	0.00000000	78.53981600	3676.00000000	78.53981600	78.53981600	0.00000000
Mooreoceras	***conicum***	0.00000000	0.00000000	4467.00000000	78.53981600	0.00000000	0.00000000
Mooreoceras	***giganteum***	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000
Mooreoceras	***normale***	0.00000000	0.00000000	4979.00000000	8202.00000000	78.53981600	78.53981600
Mooreoceras	***ovale***	0.00000000	78.53981600	2339.00000000	0.00000000	0.00000000	0.00000000
Mooreoceras	***tuba***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000
Mooreoceras	***wedingtonianum***	0.00000000	0.00000000	3758.11373900	0.00000000	0.00000000	0.00000000
Orthoceras	***dunbari***	0.00000000	0.00000000	78.53981600	78.53981600	0.00000000	0.00000000
Orthoceras	***kansasense***	0.00000000	17195728778.00000000	610.05091400	78.53981600	0.00000000	0.00000000
Orthoceras	***longissimicameratum***	0.00000000	78.53981600	78.53981600	78.53981600	0.00000000	0.00000000
Orthoceras	***occidentale***	0.00000000	78.53981600	78.53981600	78.53981600	0.00000000	0.00000000
Hebetorthoceras	***unicamera***	0.00000000	0.00000000	0.00000000	0.31208500	0.00000000	0.00000000
Pseudoparalegoceras	***brazoense***	0.00000000	0.00000000	0.00000000	0.50582500	0.00114400	0.00000000
Phaneroceras	***compressum***	0.00000000	0.00000000	0.00000000	0.00000000	24924.00000000	78.53981600
Phaneroceras	***kesslerense***	0.00000000	0.00000000	0.00000000	0.00000000	0.36836800	0.00000000
Pseudorthoceras	***knoxense***	78.53981600	71899.00000000	7577.00000000	64660.00000000	30599.00000000	0.00000000
Pseudopronorites	***arkansasensis***	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000	8916.06324300

Megapronorites	***baconi***	0.00000000	0.00000000	0.00000000	0.00000000	78.53981600	78.53981600
Pseudopronorites	***kansasensis***	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000
Pronorites	***pseudotimorensis***	0.00000000	78.53981600	78.53981600	78.53981600	78.53981600	78.53981600
Properrinites	***boesei***	0.55926200	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Properrinites	***cumminsi***	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Properrinites	***plummeri***	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Schistoceras	***hildrethi***	0.00000000	139876.00000000	23915.00000000	78.53981600	78.53981600	78.53981600
Schistoceras	***missouriense***	78.53981600	145678.14775800	145678.14775800	78.53981600	78.53981600	0.00000000
Schistoceras	***unicum***	0.00000000	0.27535300	78.53981600	78.53981600	78.53981600	0.00000000
Parashumardites	***senex***	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000
Vidrioceras	***uddeni***	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000	0.00000000
Shumarites	***cuyleri***	0.00000000	0.04008400	0.00000000	0.00000000	0.00000000	0.00000000
Solenochilius	***brammeri***	0.00000000	0.00000000	25888.01538900	0.00000000	0.00000000	0.00000000
Solenochilius	***kempae***	0.00000000	0.00000000	3067.00000000	0.00000000	0.00000000	0.00000000
Solenochilius	***kerefordensis***	0.00000000	2277.10978100	78.53981600	0.00000000	0.00000000	0.00000000
Solenochilius	***missouriense***	0.00000000	0.00000000	1321.36647600	0.00000000	0.00000000	0.00000000
Solenochilius	***newloni***	0.00000000	78.53981600	0.00000000	0.00000000	0.00000000	0.00000000
Solenochilius	***peculiare***	0.00000000	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000
Shumarites	***simondsi***	0.00000000	0.10367800	0.00000000	0.00000000	0.00000000	0.00000000
Solenochilius	***springeri***	0.00000000	0.00000000	0.00000000	9839.21795000	78.53981600	78.53981600
Solenochilius	***syracusense***	0.00000000	0.00000000	0.00000000	78.53981600	0.00000000	0.00000000