Using GIS to Examine Biogeographic and Macroevolutionary patterns in Late Paleozoic Cephalopods from the North American Midcontinent Sea

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Abstract

Geographic range is an important macroevolutionary parameter frequently considered in paleontological studies as species' distributions and range sizes determined by a variety of biotic and abiotic factors well known to affect the differential birth and death of species. Thus, considering how distributions and range sizes fluctuate over time can provide important insight into evolutionary dynamics. This study uses Geographic Information Systems (GIS) and analyses of evolutionary rates to examine how in the Cephalopoda, an important pelagic clade, geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and early Permian in the North American Midcontinent Sea. This period is particularly interesting for biogeographic and evolutionary studies because it is characterized by repetitive interglacial-glacial cycles, a global transition from an icehouse to a greenhouse climate during the Late Paleozoic Ice Age, and decelerated macroevolutionary dynamics, i.e. low speciation and extinction rates.

The analyses presented herein indicate that cephalopod species diversity was not completely static and actually fluctuated throughout the Pennsylvanian and early Permian, matching findings from other studies. However, contrary to some other studies, the mean geographic ranges of cephalopod species did not change significantly through time, despite numerous climate oscillations; further, geographic range size did not correlate with rates of speciation and extinction. These results suggest that pelagic organisms may have responded differently to late Paleozoic climate changes than benthic organisms, although additional consideration of this issue is needed. Finally, these results indicate that, at least in the case of cephalopods, macroevolution

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during the late Paleozoic was more dynamic than previously characterized, and patterns may have varied across different clades during this interval.

Introduction

Much work has focused on the relationship between geographic range size and rates of speciation and extinction (e.g., Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Lieberman, 2000; Jablonski & Roy, 2003; Rode & Lieberman, 2004, 2005; Kiessling & Aberhan, 2007; Liow, 2007; Payne & Finnegan, 2007; Abe & Lieberman, 2009; Stigall, 2010; Myers & Saupe, 2013; Myers, MacKenzie, & Lieberman, 2013; Dunhill & Wills, 2015; Jablonski & Hunt, 2015; Orzechowski et al., 2015; Saupe et al., 2015; Castiglione et al., 2017; Pie & Meyer, 2017; Simões et al., 2016; Lam, Stigall, & Matzke, 2018; Schneider, 2018). Furthermore, the use of Geographic Information Systems (GIS) has greatly facilitated investigations into this macroevolutionary relationship (Stigall & Lieberman, 2006; Hendricks, Lieberman, & Stigall, 2008; Dunhill, 2012; Myers, MacKenzie, & Lieberman, 2013; Dunhill & Wills, 2015; Lieberman & Kimmig, 2018). Here, we focus on how geographic range size and rates of speciation and extinction changed throughout the Pennsylvanian and early Permian in the North American Midcontinent Sea in the Cephalopoda, an important clade of pelagic invertebrates (Landman, Tanabe, & Davis, 1996; Monnet, De Baets, & C. Klug, 2011; Korn et al., 2015), using GIS. This time interval is particularly interesting for biogeographic and evolutionary analysis because it is characterized by repetitive glacial-interglacial cycles, a global transition from an icehouse to greenhouse climate during the Late Paleozoic Ice Age (LPIA) (Montañez & Poulsen, 2013). Further, it is generally considered a time of sluggish macroevolutionary dynamics, i.e. low speciation and extinction rates and low degrees of faunal

47 turnover, that have been demonstrated in studies of other marine invertebrate taxa (Sepkoski,
48 1998; Stanley & Powell, 2003; Bonelli & Patzkowsky, 2011). However, Balseiro (2016) did
49 document the existence of some profound evolutionary turnover in bivalves and brachiopods
50 over the course of this interval in regions closer to the ice sheets, such as present-day western
51 Argentina. Furthermore, recently Segessenman & Kammer (2018) showed that advanced cladid
52 crinoids do display elevated rates of evolution and turnover during this time interval (although
53 three other subclasses of crinoids do show subdued evolutionary rates), and fusulinid
54 foraminifera also fit the pattern shown in the advanced cladids (Groves & Lee, 2008; Groves &
55 Yue, 2009; Segessenman & Kammer, 2018).
56
57 There have been a variety of hypotheses proposed for the postulated decelerated
58 macroevolutionary dynamics of the LPIA. Some studies contend that this pattern is a result of
59 environmental changes linked to glacial cycling while others point to tectonic activity (Stanley
60 and Powell, 2003; Powell, 2005; Fielding, Frank, & Isbell, 2008; DiMichele et al., 2009; Falcon-
61 Lang & DiMichele, 2010; Bonelli and Patzkowsky, 2011; Cecil, DiMichele, & Elrick, 2014;
62 Segessenman & Kammer, 2018). To date, many of the studies focusing on the
63 macroevolutionary dynamics of the LPIA have concentrated on benthic marine invertebrates
64 (e.g., Stanley & Powell, 2003; Powell, 2007; Bonelli & Patzkowsky, 2011; Balseiro, 2016;
65 Segessenman & Kammer, 2018) as they are highly diverse and very abundant. However, it is
66 valuable to explicitly investigate evolutionary patterns in pelagic marine invertebrates as these
67 are also diverse and abundant organisms in late Paleozoic marine ecosystems (Landman, Tanabe,
68 & Davis,1996; Monnet, De Baets, & Klug, 2011; Korn et al., 2015). In particular, given the
69 significant role that geographic factors play in speciation (Mayr, 1942; Eldredge & Gould, 1972;

Jablonski, 1986; Brooks & McLennan, 1991; Wiley & Lieberman, 2011; Jablonski & Hunt, 2015; Pie & Meyer, 2017), we might expect that pelagic organisms, because of their innately greater dispersal ability (at least as adults), might show different patterns relative to taxa that were benthic (Rojas et al., 2017; Yacobucci, 2017). This greater dispersal ability might allow pelagic organisms to more fully occupy potentially available habitats than benthic organisms, which could lead to larger geographic ranges and also less change in geographic ranges through time. It also could potentially influence patterns of speciation and extinction by dampening opportunities for geographic isolation and creating larger effective population sizes.

This study focuses on cephalopods from the Pennsylvanian-early Permian (Morrowan, Atokan, Desmoinesian, Missourian, Virgilian, and Wolfcampian) in the Midcontinent Sea of the United States as knowledge of the systematic affinities, geographic distribution and overall diversity of cephalopods during this interval is relatively well understood (Miller, Dunbar, & Condra,1933; Newell, 1936; Plummer & Scott, 1937; Miller & Youngquist, 1949; Nassichuk, 1975; Landman, Tanabe, & Davis, 1996; Kröger, 2005; Korn et al., 2015), the stratigraphy of the region is well constrained (Heckel, 2008, 2013), and there are extensive exposures of fossiliferous units in the region. Moreover, at this time the Midcontinent Sea was bordered by the Antler Orogeny to the north, the Ancestral Rocky Mountain Orogeny to the west/northwest and the Ouachita Mountain belt to the south/southeast (as well as various structural arches), such that it constituted a distinct biogeographic region for marine invertebrates (Wells et al., 2007; Nelson & Lucas, 2011; Joachimski & Lambert, 2015).

The Late Paleozoic Ice Age (LPIA) was the longest lived glacial period of the Phanerozoic and is relatively well understood due to numerous stratigraphic, sedimentologic, paleontologic, and isotopic studies (e.g., Mii, Grossman, & Yancey,1999; Isbell, 2003; Stanley & Powell, 2003; Raymond & Metz, 2004; Montañez, 2007; Powell, 2007; Tabor & Poulsen, 2007; Fielding, Frank, & Isbell, 2008; Heckel, 2008; DiMichele et al., 2009; Bonelli & Patzkowsky, 2011; Montañez & Poulsen, 2013; Balseiro, 2016; Roark et al., 2017; Segessenman & Kammer, 2018). Glacial cycling in the midcontinent region has received much study (e.g., Isbell, 2003; Heckel, 2008, 2013). Modern synthesis of the glacial history 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 (Montañez & Poulsen, 2013). 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; Montañez, 2007; Tabor, 2007; Heckel, 2008; Cecil, DiMichele, & Elrick, 2014). The sea-level and temperature changes were likely to have had an important influence on species distribution and geographic range size during this time (Waterhouse & Shi, 2010). Though perhaps pelagic taxa would be less influenced by glacial sea-level cycles than benthic taxa, as these cycles are also known to cause variation in seafloor ventilation, with concomitant dysoxia/anoxia that is more severe for benthic taxa (A. Dunhill, pers. comm., 2018).

Comentario [GP1]: Yes, maybe, dysoxia-anoxia can be verified in hypersaline stratified estuarine or delta conditions, where soft body organisms predominate but have a lower preservational potential. So, you must be specific here and leave clear that you are talking just for cephalopods, do you? If not, you may have a taphonomic bias affecting the real stability of the benthic communities that is not being taken into account.

Materials and methods

Taxa considered, stratigraphic correlation, specimens examined, and georeferencing: 79 species belonging to 26 genera (13 nautiloids and 13 ammonoids) of cephalopods in the Pennsylvanian-Permian North American Midcontinent Sea were considered (Table S1). These represent the most abundant, well preserved, and taxonomically well understood species. Range reconstructions relied on the occurrence records of specimens derived from a comprehensive consideration of the entire taxonomic literature on the taxa studied. In particular, the following publications were utilized: Cox (1857), Swallow (1858), McChesney (1860), Meek & Worthen (1860, 1870), White & St. John (1867), White (1889), Hyatt (1891, 1893), Keyes (1894), Miller (1892), Smith (1896, 1903), Girty (1911, 1915), Mather (1915) Böse (1919, 1920), Miller (1930), Sayre (1930), Miller, Dunbar, & Condra (1933), Miller & Cline (1934), Miller & Owen (1934, 1937, 1939), Foerste (1936), Miller & Thomas (1936), Newell (1936), Plummer & Scott (1937), Elias (1938a, b), Miller & Moore (1938), Smith (1938), Miller & Furnish (1940a, b, 1957), Teichert (1940), Clifton (1942), Miller & Unklesbay (1942), Young (1942), Sturgeon (1946), Miller, Lane, & Unklesbay (1947), Miller & Downs (1948, 1950), Miller & Youngquist (1947, 1949), Miller, Youngquist, & Nielsen (1952), Kummel (1953, 1963), Ruzhentsev & Shimanskiy (1954), Unklesbay (1954), Arkell et al. (1957), Unklesbay & Palmer (1958), Hoare (1961), Furnish, Glenister, & Hansman (1962), McCaleb (1963), Gordon (1964), Miller & Breed (1964), Teichert et al. (1964), Furnish & Glennister (1971), Ruzhentsev & Bogoslovskaya (1971), Nassichuk (1975), Sturgeon et al. (1982), Hewitt et al. (1989), Boardman et al. (1994), Kues (1995), White & Skorina (1999), Kröger & Mapes (2005), Furnish et al. (2009), and Niko & Mapes (2009) as well as from examination of all specimens, including types, housed in: 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). These institutions house the most complete repository of cephalopod diversity from this region and time as well as contain many of the type specimens of the species examined. Moreover, all specimens used in the analysis were personally examined and taxonomically-vetted via consideration of the literature, relevant type specimens, and other material, with species assignments and determinations made by the first author. Over 1,100 specimens were identified to species level in this study (Kolis, 2017). We chose to focus on the particular species considered, rather than downloading data from the Paleobiology Data Base (PBDB), as we wanted to be able to personally validate the taxonomic identity of specimens using collections data in conjunction with the literature in order to present more rigorously corroborated hypotheses about the geographic distributions of species. We consider this approach to be complementary to those approaches that utilize the PBDB in paleobiogeographic studies. On the one hand, our approach did limit the number of species we were able to consider. On the other hand, we believe it is quite important to evaluate hypotheses about systematic affinities of fossil specimens, the actual data of the fossil record themselves, in detail and thereby accurately define the taxonomic units considered. Given that species represent key macroevolutionary units in nature (Eldredge, 1989; Wiley & Lieberman, 2011; Hendricks et al., 2014), correctly characterizing them taxonomically, and thus validating the scope of their geographic distributions, is critical. Moreover, it has recently been shown by Marshall et al. (2018) that incorporating museum specimen data in the manner that our study has can greatly expand, enhance, and improve knowledge of geographic distributions of fossil species, relative to studies that only utilize data from the PBDB.

Specimens were assigned to the Virgilian, Missourian, Desmoinesian, Atokan, Morrowan, or Wolfcampian stages using the USGS National Geologic Map Database (U.S. Geological Survey, 2017), Sawin et al. (2006, 2008, 2009), Zeller (1968), Pope (2012), and Heckel (2013). The temporal boundaries of stages were derived from Davydov, Korn, & Schmitz (2012) (Table S2). All specimen localities were georeferenced during the course of the study. *GEOLocate* (Rios and Bart, 2018) and the *MaNIS Georeferencing Calculator* (Wieczorek, 2015) were used to obtain coordinates and uncertainty radii. All points were calculated in decimal degrees within the WGS84 model in the *GEOLocate* (Rios & Bart, 2018) world topo layer to ensure consistency and accuracy in determinations. Most uncertainty radii were less than 10 kms. Any specimens with questionable locality information were excluded from analyses, as were specimens with an uncertainty radius larger than the county they were contained within. This left 950 specimens (Table S1) to use in range reconstruction and statistical analysis of geographic range through geologic time. All statistical analyses were performed using Minitab® Statistical Software *Minitab v. 17* (Minitab, 2016) and *R-Studio Version 3.4.0* (2017).

Range reconstruction using GIS: Methods for range reconstruction follow Rode & Lieberman (2004, 2005), Stigall & Lieberman (2006), Hendricks, Lieberman, & Stigall (2008), Myers & Lieberman (2011), Myers, MacKenzie, and Lieberman (2013), and Dunhill & Wills (2015). In particular, after specimen occurrence data were georeferenced and assigned to temporal bins, *Excel* CSV files were compiled for the occurrence points for all specimens within species. CSV files were imported into *ArcGIS v. 10.3* (ESRI, 2014) and layers were created using geographic coordinate system 'WGS 1984' and projected coordinate system 'WGS 1984 World Mercator' (Fig. 1). These layers were input into *PaleoWeb* (The Rothwell Group LP, 2016) to rotate coordinates into continental configuration and geographic position of the midcontinent region

during the Pennsylvanian-early Permian (Fig. 2). These paleo-coordinate layers were then re-projected into *ArcMap* (ESRI, 2014).

Geographic range values were calculated for each species (Table S3), using minimum bounding geometry. This method has been shown to provide the most accurate procedure for reconstructing changes in geographic range, especially for fossil taxa (Darroch & Saupe, 2018). 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; species with just two occurrence points were given a 10km^2 wide buffer which was used, in conjunction with their distance, to derive an area value (following Rode & Lieberman [2004, 2005], Hendricks, Lieberman, & Stigall [2008], Myers & Lieberman [2011], and Myers, MacKenzie, and Lieberman [2013]).

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Comentario [GP2]: Why you use Late here and "late" in other parts of the text?

Con formato: Resaltar

Assessing fossil record bias: A common concern when studying the fossil record is that there might be biases that could lead to inaccurate or artifactual 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 aware of the fact that the fossil record is incomplete, it is worth recognizing that there is a large body of research that demonstrates that many of the biogeographic patterns preserved in the fossil record, particularly in marine settings, represent real biological phenomena, rather than taphonomic artifacts (Myers & Lieberman,

2011; Rook, Heim, & Marcot, 2013; Dunhill & Wills, 2015). Further, it is also prudent to realize that sampling bias is a common issue 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 (Lieberman, 2002; Carrasco, 2003).

The possibility that biases in the fossil record might lead to artifactual results was assessed in a few different ways. First, the relationship between outcrop availability and the geographic range of Pennsylvanian and Permian cephalopods was determined (see Myers & Lieberman, 2011). A percent coverage table of the range size of species overlaid against temporal outcrop availability was created using *ArcGIS v. 10.3* (ESRI, 2014). A low percentage of overlap between range size and outcrop area would suggest species distributions are more likely to reflect 'real' biogeographic patterns while a high percentage of overlap would suggest the presence or absence of outcrops was significantly influencing results (Myers & Lieberman, 2011; Myers, MacKenzie, & Lieberman, 2013; however, see also Dunhill, 2012 for an alternative viewpoint). The second test used was an "n-1" jackknifing 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; these were input into a one-way ANOVA to compare jackknife estimates with the initial geographic range size estimates (Myers & Lieberman, 2011; Myers, MacKenzie, & Lieberman, 2013). Finally, a Pearson rank correlation test was performed to test the association of occurrence points and geographic range size; a close correlation would indicate that reconstructed ranges were very much dependent on sampling and suggest that reconstructed biogeographic patterns might be an artifact of a biased fossil record (Myers, MacKenzie, & Lieberman, 2013).

Comentario [GP3]: Yes, it is possible, but see my previous comment for this particular study.

Comentario [GP4]: Sampling bias is a problem when part of the original community was not preserved, but you are right that the problem exists even in studies of recent biotas.

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Comentario [GP5]: It is as 2013 in the references list. Please check

Speciation and extinction rate calculations: Speciation and extinction rates were calculated in order to consider macroevolutionary dynamics in cephalopods from the Late Paleozoic Midcontinent Sea. Macroevolutionary rates were calculated using the following equation, presented in Foote (2000) and Rode & Lieberman (2005):

$$N_f = N_0 e^{rt}$$

where 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. The temporal bins used were North American stages (Table S2). 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. For example, $r_{Atokan} = (\ln N_{0\text{-}Desmoinesian} - \ln N_{0\text{-}Atokan}) / t_{Atokan}$. 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).

Results

Paleobiogeographic patterns: Geographic range data were analyzed separately across all cephalopods and individually for both nautiloids and ammonoids. Species geographic range size data were tested for normality within each temporal stage using the Anderson-Darling normality test. Range size data within each temporal stage were not normally distributed for any data

combination ($P < 0.005$). Instead, distributions were left skewed across all temporal stages for every data grouping. Data were subsequently log-transformed to normalize data, and statistical analyses were performed on both original and transformed data.

In general, geographic range size (either mean of transformed data or median of original) of ammonoids and nautiloids increases during the Missourian and Virgilian stages (Fig. 3), which was a time of sea-level rise due to warming during an interglacial (Isbell, 2003; Montañez & Poulsen, 2013), such that there may be an association between the sea-level rise and the increase in geographic range. Another possibility is that there was some change in taphonomic conditions that occurred during the Virgilian that made it easier to discern the actual biogeographic distributions of species at this time, relative to other time intervals (G. Piñeiro, pers. comm., 2018). However, none of the changes in geographic range were statistically significant, so it is not possible to infer strong correlation between the sea-level rise, or possible taphonomic factors, and the range expansion. For instance, Mann-Whitney U tests found no statistically significant changes (at $P \leq 0.05$) in median geographic range size for any temporal stages separately across all cephalopods, as well as individually for nautiloids and ammonoids, even prior to correction for multiple comparisons. This is because with the Mann-Whitney U test median range values are considered, and for all cephalopods the median range values are constant through time ($79 km^2$).

The same was true for two-sample t-tests performed on log-transformed data which again found no statistically significant changes (at $P \leq 0.05$) in mean geographic range size though time, even prior to correction for multiple comparisons. Again, recall that *mean* range size data are shown

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Comentario [GP6]: This is confusing to me, sorry. You applied the Mann-Whitney U test in your cephalopod sample to test the median range value, right? On the other hand you calculated the median of range size for all cephalopods and according to your figure 3 it is not constant through time. Please, explain a little better the results shown in figure 3.

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Comentario [GP7]: Do you have any figure to refer here?

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in Figure 3, and the differences among log-transformed data through time are far less substantial (and ultimately not significant). Furthermore, a one-way ANOVA, either with or without the assumption of equal variance, failed to find any significant differences (at $P \leq 0.05$) between stages for log-transformed mean geographic range size across all cephalopods as well as individually for nautiloids and ammonoids.

Comentario [GP8]: But the peak shown in figure 3 corresponding to the Virgilian period should mean something!

Comentario [GP9]: Ok again, but the peak shown in figure 3 corresponding to the Virgilian period should mean something! Maybe it would be good to say that even though the lack of any significant differences suggested by the tests used, there is a peak in the Virgilian that could suggest that a change existed but it is not as relevant as to be detected statistically. Because the peak exists and casually you have the highest extinction rate also in the Virgilian and continued so in the Wolfcampian (your figure 4)!

Analysis of macroevolutionary rates: Speciation rate (S) and extinction rate (E) were calculated for the Atokan, Desmoinesian, Missourian, and Virgilian stages across all cephalopods and within nautiloids and ammonoids, respectively. The S and E presented across all cephalopods are comprised of two calculations; one calculation included taxa that only occurred in a single temporal stage (Table 1; Fig. 4), while the other calculation excluded taxa that occurred in a single temporal stage (Table S4). S and E was also calculated for ammonoids and for nautiloids including (Tables S5, S6) and excluding taxa that occurred in a single stage (Tables S7, S8). Note, due to the dependence of calculations on diversity metrics from both adjacent stages, it is not possible to accurately calculate the rate of biodiversity change (R), or S and E for the first stage considered, the Morrowan, nor R or E for the last stage considered, the Wolfcampian (these are thus left blank in Table 1 and Tables S4-S8). While it might have been possible to infer S and E using other methods, to do so would exaggerate the significance of edge effects and thus be problematic (Foote, 2000).

Across all cephalopods, S was high in the Atokan and Desmoinesian, fell in the Missourian, and reached very low levels in the Virgilian and Wolfcampian (Fig. 4). By contrast, E was low in the Atokan and Desmoinesian, began to rise in the Missourian, and reached even higher levels in the

303 Virgilian (Fig. 4). Essentially, across all cephalopods examined, when S is high, E is low, and
304 when S is low, E is high. This is potentially contrary to the pattern expected with an ecological
305 opportunity model of speciation (Simões et al., 2016), although the specific processes driving the
306 diversification could not be determined at this time. However, it is possible that when S was
307 high there may have been many short-lived species that could not be sampled that were actually
308 going extinct, and this phenomenon would artificially depress E.
309
310 As expected, S and E are lower when singletons are excluded (see Tables 1, S4). (See
311 Segesseman & Kammer [2018] for a recent discussion of how singletons can affect manifest
312 patterns in these types of studies.) Notably though, S and E patterns diverge somewhat between
313 ammonoids and nautiloids when considered individually. For instance, in nautiloids S is high in
314 the Atokan and Desmoinesian, then declines to moderate in the Missourian, and is at its lowest in
315 the Missourian and Wolfcampian (Table S6), whereas in ammonoids S is only high in the
316 Atokan, declines to moderate in the Desmoinesian, declines somewhat more in the Missourian
317 and then remains essentially constant through the Wolfcampian (Table S5). In addition, E is low
318 in ammonoids during the Desmoinesian and Missourian but high in the Atokan and
319 Wolfcampian (Table S5), whereas in nautiloids there are no observed extinctions during the
320 Atokan; values remain quite low for nautiloids in the Desmoinesian, rise somewhat in the
321 Missourian, and then rise again in the Virgilian (Table S6).
322
323 An important caveat regarding the calculation of S is that many of the species analyzed belong to
324 genera that were widely distributed beyond the Midcontinent Sea during the Late Paleozoic.
325 Thus, although none of the species considered in these analyses occurred outside of the

Comentario [GP10]: Interesting that in ammonoids S and E are high in the Atokan, a pattern that is not seen in the study for all cephalopods. It seems that the pattern for nautiloids is prevalent.

Midcontinent Sea, their close relatives did. It is conceivable that while speciation events and rates by necessity are herein treated as occurring *in situ*, this might not always have been the case. Instead, some speciation events could have occurred outside of the Midcontinent Sea with subsequent invasion events into that region. These invasions would appear as *in situ* speciation events in this analysis, although they actually were not. In the absence of phylogenetic hypotheses for the genera considered it is not currently possible to consider how much of the pattern pertaining to speciation rate shown in Fig. 4 is due to invasion instead of speciation. Further, a related phenomenon could affect the calculation of E: at times what were treated as extinction events might have simply been local extinctions in the Midcontinent Sea which could have included emigration to other regions. As mentioned previously, it does not appear that any of the species considered occur outside of the Midcontinent Sea, but a phylogenetic hypothesis for these groups would be valuable for considering this issue in greater detail.

Relationship between biogeography and macroevolutionary rates: Mean geographic range size increased during the Missourian and Virgilian and declined in the Wolfcampian (Fig. 3); speciation rates were high in the Atokan and Desmoinesian and fell in the Virgilian (Fig. 4); extinction rates were low in the Atokan and Desmoinesian and rose in the Virgilian (Fig. 4). The Pearson correlation test in *Minitab 17* (Minitab, 2016) was used to examine the association between geographic range and either speciation rate extinction rate in greater detail. No significant (at $P \leq 0.05$) correlation between speciation or extinction rate and range size was found across all cephalopods or within ammonoids or nautiloids individually (Table 2). However, in cases the values approach P = 0.05 for instance, the association between

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Comentario [GP11]: Perhaps it is what the individual patterns are suggesting?

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Comentario [GP12]: Except for ammonoids?

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decreasing geographic range size and increasing extinction for all cephalopods and for ammonoids alone. Notably, an association between decreasing geographic range size and increasing extinction has been documented by numerous studies (e.g. Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Jablonski & Roy, 2003; Rode & Lieberman, 2004, 2005; Kiessling & Aberhan, 2007; Payne & Finnegan, 2007; Stigall, 2010; Dunhill & Wills, 2015; Jablonski & Hunt, 2015; Orzechowski et al., 2015; Saupe et al., 2015; Castiglione et al., 2017; Pie & Meyer, 2017; Lam, Stigall, & Matzke, 2018; Schneider, 2018) and thus is a very robust phenomenon in general and likely to be operating to some extent herein. However, over this time interval and for this particular group of species the association is not statistically significant (Table 2), probably because sample sizes are not large, and further this is likely because many taxa were culled by the late Mississippian extinction (M. Powell, pers. comm., 2018).

Analysis of fossil record bias: The low percentage of overlap between cephalopod species geographic ranges and available outcrops, less than 1% in 29 out of 30 species (Table S9; the one species with a larger percentage value, *Orthoceras kansasense*, occurs throughout the Midcontinent Sea), suggests the results are not simply an artifact of an incomplete fossil record, at least pertaining to outcrop availability. The "n-1" jackknifing analysis also supports the robustness of the reconstructed ranges, as no statistically significant differences were found between the mean of the reconstructed and subsampled range values for any time interval (all P-values > 0.9), suggesting that one or a few occurrence records are not having a major influence on biogeographic patterns. Similar results were found in other taxa and time periods by Hunt, Roy, & Jablonski (2005), Myers & Lieberman (2011), and Myers, MacKenzie, & Lieberman (2013), although Dunhill, Hannisdal, & Be dysoxia/anoxia is more severe for benthic taxa

Comentario [GP13]: Sentence needs revision. It seems something is missing or maybe it is wrong formulated or it is closely related to the following sentence?

Con formato: Resaltar

Comentario [GP14]: Thus, this same problem can be affecting the results that suggest a constant geographic range size for cephalopods through time

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nton (2014) did find some association between outcrop area and diversity in the case of the marine fossil record of Great Britain. Finally, the Pearson correlation test shows no correlation (-0.055, P-Value = 0.789) between the number of occurrence points and geographic range size; this provides further evidence that the biogeographic signatures of Late Paleozoic cephalopods are unlikely to be simply an artifact of the fossil record.

Diversity patterns: Across all cephalopods, species richness increased from the Morrowan to the Atokan, peaked in the Desmoinesian, and decreased through the Wolfcampian (Fig. S1). A similar pattern is seen in the nautiloids (Fig. S2). However, the ammonoids (Fig. S3) demonstrate an earlier peak in the Atokan, followed by a Desmoinesian to Virgilian plateau, with a decrease in the Wolfcampian. Notably, previous studies of Late Paleozoic brachiopod communities in Bolivia showed a consistent trend between diversity and glacial cycling with increased diversity during glacial periods and decreased diversity during inter-glacial periods (Badyrka, Clapham, & Lopez, 2013). However, there seems to be less consistency between species richness trends and glacial cycling in the Midcontinent Sea. For instance, there is an increase in cephalopod species richness throughout the Morrowan to Desmoinesian associated with localized glaciation, and an interglacial period with generally minor glaciation is associated with a decrease in cephalopod species richness from the Desmoinesian to Virgilian, yet by contrast widespread glaciation is associated with a decrease in species richness from the Virgilian to the Wolfcampian. An important point, however, is that these are just raw diversity patterns and sample standardized diversity patterns show a different result (M. Powell, pers. comm., 2018).

Discussion

Comentario [GP15]: Yes, it is clear that the pattern for all cephalopods is influenced by nautiloids.

Comentario [GP16]: You have not selected lower case for this? Why?

Con formato: Resaltar

Comentario [GP17]: Also, it should be taken into account that brachiopods and cephalopods can show different behavior in response to climatic changes and the conditions associated to them.

Geographic range shifts through time are one of the pervasive phenomena in the history of life; these are manifest both within species and higher-level clades, occur at a number of different time scales, and are frequently linked to climatic change (Wiley & Lieberman, 2011). Specific examples do come from the Late Paleozoic, a time of extensive climate change including profound glaciation along with numerous glacial and interglacial cycles (Montañez and Poulsen, 2013). Those changes impacted patterns of geographic range in both terrestrial plant (e.g., DiMichele et al., 2009; Falcon-Lang & DiMichele, 2010) and marine invertebrate ecosystems (e.g., Leighton, 2005; Powell, 2007; Waterhouse & Shi, 2010). When it comes to marine invertebrates from this time interval, most of the focus has been on the highly diverse benthic faunas (e.g., Stanely & Powell, 2003; Powell, 2007; Bonelli & Patzkowsky, 2011; Balseiro, 2016; Segessenman & Kammer, 2018); however, taxa that have a pelagic life style (as adults) are also worth examining. Herein, 79 pelagic species of cephalopods were examined for patterns of range size change using GIS and although in general these species exhibit some evidence for changes in geographic range size (Fig. 3), those changes were not statistically significant nor can they be directly tied to climate change. In a similar vein, many paleontological studies have demonstrated that species with larger geographic ranges tend to have lower extinction rates than species with narrower geographic range sizes (e.g., Vrba, 1980; Jablonski, 1986; Eldredge, 1989; Stanley, 1990; Rode & Lieberman, 2004; Stigall & Lieberman, 2006; Payne & Finnegan, 2007; Stigall, 2010; Hopkins, 2011; Dunhill & Wills, 2015). Again, this phenomenon was not found to be statistically significant in the case of the Late Paleozoic cephalopod species considered herein (Table 2).

Con formato: Resaltar

Comentario [GP18]: However, the peak in figure 3 for an increased geographic range is associated to a widespread glaciation.

Con formato: Resaltar

Comentario [GP19]: To be consistent with all the results you got, I would say that the same phenomenon can be detected in the Late Paleozoic cephalopod species considered herein, but it resulted statistically not significant, probably because the small samples size.

There may be a few different explanations for these findings. First, it may be that cephalopod species were not significantly affected by the glacial-interglacial climatic cycles transpiring within the Late Paleozoic Midcontinent Sea. A second possible explanation, perhaps coupled to the first, is that since cephalopods are highly mobile relative to benthic marine invertebrates such as gastropods, bivalves, brachiopods, etc., they can more easily occupy a greater portion of their potential range (at least as adults). Further, perhaps the available potential range of cephalopod species does not change much in glacial relative to interglacial regimes. This may seem unlikely given the vast fluctuations in sea level occurring at the time, but pelagic marine organisms, because of their ease of dispersal, may more easily maintain consistent geographic ranges relative to benthic counterparts. Another possible explanation for the pattern retrieved is that, given the limits of stratigraphic correlation, sample size, and the completeness of the fossil record, it was necessary for the analyses of species distribution conducted herein to focus on the time scale of geological stages, whereas in actuality there were climatic changes occurring within stages (Heckel, 2008, 2013); these probably did cause fluctuations in species' geographic ranges within stages, but simply could not be observed in the present study. A final set of explanations are related to the issue of sampling. For instance, 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. 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, and although it is not entirely obviated by the results presented regarding the apparent quality of the fossil record suggested by the various tests presented, it does become harder to invoke as a specific, primary reason for results retrieved.

Comentario [GP20]: Removed redundant text

Eliminado: relative to taxa that are benthic

Eliminado:), such as brachiopods

Another finding perhaps contrary to what might typically be expected for the Late Paleozoic is that there was at least some evolutionary diversification and turnover within cephalopods, such that species diversity did fluctuate throughout the Pennsylvanian and early Permian. Pennsylvanian rates of macrevolution are typically classified as 'sluggish' or 'stolid' across all marine animals, and Sepkoski (1998) formalized the notion that there was a marked decline in evolutionary rates of Carboniferous and Permian marine faunas. Stanley & Powell (2003) reiterated this result and identified low mean macroevolutionary rates for marine invertebrate taxa. Bonelli & Patzkowsky (2011) also documented a pattern of low turnover in the face of major episodes of sea-level rise and fall due to climatic change. The results from the analyses presented herein could indicate that macroevolutionary rate, at least in the case of Late Paleozoic cephalopods, was more dynamic than often thought. One possible reason for this result is that cephalopods are a fairly evolutionarily volatile group (Lieberman & Melott, 2013) relative to many other marine invertebrate groups and have relatively high rates of diversification (Stanley, 1979; Jacobs et al., 1994; Landman, Tanabe, & Davis,1996; Monnet, De Baets, & Klug, 2011; Korn, Klug, & Walton, 2015; Korn et al., 2015); thus, they would generally be expected to have higher rates of speciation and extinction than typical. However, this may not be the entire explanation, as other groups also seem to show elevated rates of speciation and extinction during this time interval. For instance, Balseiro (2016) did document evolutionary turnover at high latitudes, and elevated evolutionary rates have also been found in fusulinid foraminifera (Groves & Lee, 2008; Groves & Yue, 2009) and advanced cladid crinoids (Segessenman & Kammer, 2018). Ultimately, we support the contention raised by Segessenman & Kammer (2018) that patterns from a few individual groups do not refute the general pattern of sluggish macroevolution postulated for this time period in the history of life. The results may lend

Comentario [GP21]: I do not understand. If you use "late" instead "Late" you should be consistent.

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Comentario [GP22]: Both are benthic taxa

credence to the notion that macroevolutionary patterns across all marine animals are rarely unitary for any one time period in the history of life, and instead often tend to be variegated.

Conclusions

Patterns of range size change in late Paleozoic cephalopods from the North American Midcontinent Sea were investigated using GIS. These species do exhibit some evidence for changes in geographic range size through time, but the changes were not statistically significant nor could they be directly tied to climate change. Further, in contradistinction to what is usually found in the fossil record, cephalopod species with larger geographic ranges were not found to have lower extinction rates than species with narrower geographic ranges. These distinctive patterns may perhaps be related to the fact that cephalopods are pelagic and highly mobile, at least relative to many benthic marine invertebrates. Finally, the group shows more evolutionary diversification and turnover during the Pennsylvanian and early Permian than is typical of other marine invertebrate groups and this could be related to the fact that cephalopods are an evolutionarily volatile group.

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References

Abe FR, Lieberman BS. 2009. The nature of evolutionary radiations: a case study involving Devonian trilobites. *Evolutionary Biology* **36**:225-234.

Arkell WJ, Furnish WM, Kummel B, Miller AK, Moore RC, Schindewolf OH, Sylvester-Brady PC, Wright CW. 1957. Part L. Mollusca Cephalopoda Ammonoidea. *Treatise on Invertebrate Palaeontology.* Lawrence, Kansas: Geological Society of America.

Badyrka K, Clapham ME, Lopez S. 2013. Paleoecology of brachiopod communities during the late Paleozoic ice age in Bolivia (Copacabana Formation, Pennsylvanian-Early Permian). *Palaeogeography, Palaeoclimatology, Palaeoecology* **387**:56-65.

Balseiro D. 2016. Compositional turnover and ecological changes related to the waxing and waning of glaciers during the Late Paleozoic ice age in ice-proximal regions (Pennsylvanian, western Argentina). *Paleobiology* **42**:335-357.

Boardman DR II, Work DM, Mapes RH, Barrick JE. 1994. Biostratigraphy of middle and late Pennsylvanian (Desmoinesian-Virgilian) ammonoids. *Kansas Geological Survey Bulletin*

232:1-121.

Bonelli JR, Patzkowsky ME. 2011. Taxonomic and ecologic persistence across the onset of the Late Paleozoic Ice Age: evidence from the upper Mississippian (Chesterian series), Illinois basin, United States. *Palaios* **26**:5-17.

Böse E. 1919. The Permo-Carbonioferous ammonoids of the Glass Mountains, West Texas, and their stratigraphical significance. *University of Texas Bulletin* **1762**:1-241.

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**:51-60.

Brooks DR, McLennan DA. 1991. *Phylogeny, Ecology, and Behavior: a Research Program in Comparative Biology*. Chicago: University of Chicago Press.

Carrasco MA. 2013. The impact of taxonomic bias when comparing past and present species diversity. *Palaeogeography, Palaeoclimatology, Palaeoecology* **372**:130–137.

Castiglione S, Mondanaro A, Melchionna M, Serio C, Di Febbraro M, Carotenuto F, Raia P. 2017. Diversification rates and the evolution of species range size frequency distribution. *Frontiers in Ecology and Evolution* **5**:147, 1-10.

Cecil CB, DiMichele WA, Elrick SD. 2014. Middle and Late Pennsylvanian cyclothems, American Midcontinent: Ice-Age environmental changes and terrestrial biotic dynamics. *Comptes Rendus Geoscience* **346**:159-168.

Clifton RL. 1942. Invertebrate faunas from the Blaine and the Dog Creek formations of the Permian Leonard Series. *Journal of Paleontology* **16**:685-699.

Cox DD. 1857. First report of a geological reconnoissance of the northern countries of Arkansas, made during the years 1857 and 1858. *Arkansas Geological Survey*.

Darroch SAF, Saupe EE. 2018. Reconstructing geographic range-size dynamics from fossil data. *Paleobiology* **44**:25-39.

Davydov VI, Körn D, Schmitz MD. 2012. Chapter 23 - The Carboniferous Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM, eds. *The Geologic Time Scale*. Amsterdam: Elsevier, 603 - 651.

DiMichele WA, Montañez IP, Poulsen CJ, Tabor NJ. 2009. Climate and vegetational regime shifts in the late Paleozoic ice age earth. *Geobiology* **7**:200-226.

Dunhill AM. 2012. Problems with using rock outcrop area as a paleontological sampling proxy: rock outcrop and exposure area compared with coastal proximity, topography, land use, and lithology. *Paleobiology* **38**:126-143.

Dunhill AM, Wills MA. 2015. Geographic range did not confer resilience to extinction in terrestrial vertebrates at the end-Triassic crisis. *Nature Communications* **6**:7980.

Dunhill AM, Hannisdal B, Benton MJ. 2014. Disentangling rock record bias and common-cause from redundancy in the British fossil record. *Nature Communications* **5**:4818.

Eldredge N. 1989. *Macroevolutionary Dynamics: Species, Niches, and Adaptive Peaks.* New York: McGraw-Hill.

Eldredge N, Gould SJ. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: Schopf TJM, ed. *Models in Paleobiology*. San Francisco: Freeman, Cooper, 82-115.

Elias MK. 1938a. *Properrinites plummeri* Elias, n. gen and sp., from late Paleozoic rocks of Kansas. *Journal of Paleontology* **12**:101-105.

561 **Elias MK. 1938b**. Revision of *Gonioloboceras* from late Paleozoic rocks of the midcontinent region.
562 *Journal of Paleontology* **12**:91100.

563 **ESRI. 2014.** *ArcGIS Desktop: Release 10.3*. Redlands, CA: Environmental Systems Research
564 Institute.

565 **Falcon-Lang HJ, DiMichele WA.** 2010. What happened to the coal forests during
566 Pennsylvanian glacial phases? *Palaios* **25**:611-617.

567 **Fielding CR, Frank TD, Isbell JL. 2008.** The Late Paleozoic Ice Age: a review of current
568 understanding and synthesis of global climate patterns. *Geological Society of America*
569 *Special Paper* **441**:343-354.

570 **Foerste AF. 1936.** Silurian cephalopods of the Port Daniel area on Gaspé Peninsula, in eastern
571 Canada. *Bulletin of Denison University, Journal of the Scientific Laboratories* **31**:21-92.

572 **Foote M. 2000.** Origination and extinction components of taxonomic diversity: general
573 problems. *Paleobiology* **26**:74-102.

574 **Furnish WM, Glenister BF. 1971**. Permian Gonioloboceratidae (Ammonoidea). *Smithsonian*
575 *Contributions to Paleobiology* **3**:301-312.

576 **Furnish WM, Glenister BF, Hansman RH. 1962.** Brachycycloceratidae, novum, deciduous
577 Pennsylvanian nautiloids. *Journal of Paleontology* **36**:1341-1356.

578 **Furnish WM, Glenister BF, Kullmann J, Zhou Z. 2009.** Part L. Mollusca 4, Revised, Vol. 2:
579 Carboniferous and Permian Ammonoidea (Goniatitida and Prolecanitida), pg. 136-144.
580 *Treatise on Invertebrate Palaeontology*. Lawrence: The University of Kansas Paleontological
581 Institute.

582 **Girty GH. 1911.** On some new genera and species of Pennsylvanian fossils from the Wewoka
583 Formation of Oklahoma. *Annals of the New York Academy of Sciences* **21**:119-156.

584 **Girty GH. 1915.** Fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey*
585 *Bulletin* **544**:1-353.

586 **Gordon M. 1964.** Carboniferous cephalopods of Arkansas. *United States Geological Survey*
587 *Professional Paper* **460**:1-322.

588 **Groves JR, Lee A.** 2008. Accelerated rates of foraminiferal origination and extinction during the
589 late Paleozoic ice age. *Journal of Foraminiferal Research* **38**:74-84.

590 **Groves JR, Yue W. 2009.** Foraminiferal diversification during the late Paleozoic ice age.
591 *Paleobiology* **35**:367-392.

592 **Heckel PH. 1986.** Sea-level curve for Pennsylvanian eustatic marine transgressive-regressive
593 depositional cycles along midcontinent outcrop belt, North America. *Geology* **14**:330-
594 334.

595 **Heckel PH. 2008.** Pennsylvanian cyclothems in midcontinent North America as far-field effects
596 of waxing and waning of Gondwana ice sheets. *Geological Society of America Special*
597 *Paper* **441**:275-289.

598 **Heckel PH. 2013.** Pennsylvanian cyclothems of northern midcontinent shelf and biostratigraphic
599 correlation of cyclothems. *Stratigraphy* **10**:3-40.

600 **Hendricks JR, Lieberman BS, Stigall AL. 2008.** Using GIS to study palaeobiogeographic and
601 macroevolutionary patterns in soft-bodied Cambrian arthropods. *Palaeogeography,*
602 *Palaeoclimatology, Palaeoecology* **264**:163-175.

603 **Hendricks JR, Saupe EE, Myers CE, Hermsen EJ, Allmon WD. 2014**. The generification of
604 the fossil record. *Paleobiology* **40**:511-528.
605 **Hewitt RA, Dokainish MA, El Aghoury M, Westermann GE. 1989.** Bathymetric limits of a
606 Carboniferous orthoconic nautiloid deduced by finite element analysis. *Palaios* **4**:157-167.
607 **Hoare RD. 1961.** Desmoinesian Brachiopoda and Mollusca from southwest Missouri. *Missouri*
608 *University Studies* **36**:1-262.
609 **Hopkins MJ. 2011.** How species longevity, intraspecific morphological variation, and
610 geographic range size are related: a comparison using Late Cambrian trilobites.
611 *Evolution* **65**:3253-3273.
612 **Hunt G, Roy K, Jablonski D. 2005.** Species-level heritability reaffirmed: a comment on 'on the
613 heritability of geographic range sizes'. *American Naturalist* **166**:129-135.
614 **Hyatt A. 1891.** Carboniferous cephalopods. *Geological Survey of Texas Annual Report* **2**:329-356.
615 **Hyatt A. 1893.** Carboniferous cephalopods: Second paper. *Geological Survey of Texas Annual*
616 *Report* **4**:377-474.
617 **Isbell JL. 2003.** Timing of the late Paleozoic glaciation in Gondwana: was glaciation responsible
618 for the development of northern hemisphere cyclothems? *Geological Society of America*
619 *Special Paper* **370**:5-24.
620 **Jablonski D. 1986.** Larval ecology and macroevolution in marine invertebrates. *Bulletin of*
621 *Marine Science* **39**:565-587.
622 **Jablonski D, Hunt G. 2015.** Larval ecology, geographic range, and species survivorship in
623 Cretaceous mollusks: organismic versus species-level explanations. *American Naturalist*
624 **168**:556-564.

Jablonski D, Roy K. 2003. Geographical range and speciation in fossil and living molluscs. *Proceedings of the Royal Society of London, Series B* **270**:401-406.

Joachimski MM, Lambert LL. 2015. Salinity contrast in the US Midcontinent Sea during Pennsylvanian glacio-eustatic highstands: evidence from conodont apatite δ18 O. *Palaeogeography, Palaeoclimatology, Palaeoecology* **433**:71-80.

Keyes CR. 1894. Paleontology of Missouri. *Missouri Geological Survey* **4**:1-226.

Kiessling W, Aberhan M. 2007. Geographical distribution and extinction risk: lessons from Triassic-Jurassic marine benthic organisms. *Journal of Biogeography* **34**:1473-1489.

Klug C, Korn D, De Baets K, Kruta I, Mapes RH, **eds**. 2015. *Ammonoid Paleobiology: from Macroevolution to Paleogeography*. Berlin: Springer.

Kolis K. 2017. 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. Master's Thesis, Department of Ecology & Evolutionary Biology, University of Kansas.

Korn D, Klug C, Walton SA. 2015. Taxonomic diversity and morphological disparity of Paleozoic ammonoids. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH, eds. *Ammonoid Paleobiology: from Macroevolution to Paleogeography*. Berlin: Springer, 231-264.

Kröger B. 2005. Adaptive evolution in Paleozoic coiled cephalopods. *Paleobiology* **31**:253-268.

Kröger B, Mapes RH. 2005. Revision of some common Carboniferous genera of North American orthocerid nautiloids. *Journal of Paleontology* **79**:1002-1011.

Kues BS. 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.

Kummel B. 1953. American Triassic coiled nautiloids. *U. S. Geological Survey Professional Paper* **250**:1-149.

Kummel B. 1963. Miscellaneous nautilid type species of Alpheus Hyatt. *Bulletin of the Museum of Comparative Zoology* **128**:325-368.

Lam AR, Stigall AL, Matzke N. 2018. Dispersal in the Ordovician: speciation patterns and paleobiogeographic analyses of brachiopods and trilobites. *Palaeogeography, Palaeoclimatology, Palaeoecology* **489**:147-165.

Landman N, Tanabe K, Davis RA, eds. 1996. Ammonoid Paleobiology. New York: Plenum.

Leighton LR. 2005. The latitudinal diversity gradient through deep time: testing the "Age of Tropics" hypothesis using Carboniferous productidine brachiopods. *Evolutionary Ecology* **19**:563-581.

Liow LH. 2007. Does versatility as measured by geographic range, bathymetric range and morphological variability contribute to taxon longevity? *Global Ecology and Biogeography* **16**:117-128.

Lieberman BS. 2000. *Paleobiogeography: Using Fossils to Study Global Change, Plate Tectonics, and Evolution.* New York: Kluwer Academic/Plenum.

Lieberman BS. 2002. Biogeography with and without the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* **178**:39-52.

Lieberman BS, Kimmig J. 2018. Museums, paleontology, and a biodiversity science based approach. In: Rosenberg GD, Clary RM, eds. *Museums at the Forefront of the History of Geology: History Made, History in the Making*. *Geological Society of America Special*

Paper **535**. In press. https://doi.org/10.1130/2018.2535(22)

Lieberman BS, Melott AL. 2013. Declining volatility, a general property of disparate systems: from fossils, to stocks, to the stars. *Palaeontology* **56**:1297-1304.

Marshall CR, Finnegan S, Clites EC, Holroyd PA, Bonuso N, Cortez C, Davis E, Dietl GP, Druckenmiller PS, Eng RC, Garcia C, Estes-Smargiassi K, Hendy A, Hollis KA, Little H, Nesbitt EA, Roopnarine P, Skibinski L, Vendetti J, White LD. 2018. Quantifying the dark data in museum fossil collections as palaeontology undergoes a second digital revolution. *Biology Letters* **14**:20180431.

Mather KF. 1915. The fauna of the Morrow group of Arkansas and Oklahoma. *Bulletin of Science Laboratories of Denison University* **18**:59-284.

Mayr E. 1942. *Systematics and the Origin of Species*. Cambridge: Harvard University Press.

McCaleb JA. 1963. The goniatite fauna from the Pennsylvanian Winslow Formation of northwest Arkansas. *Journal of Paleontology* **37**:110-115.

McChesney AM. 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.

Meek FB, Worthen AH. 1860. Descriptions of new Carboniferous fossils from Illinois and other western states. *Proceeding of the Academy of Natural Sciences of Philadelphia* **4**:447–472.

Meek FB, Worthen AH. 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***:22-56.*

Mii HS, Grossman EL, Yancey TE. 1999. Carboniferous isotope stratigraphies of North

America: implications for Carbonifeous paleoceanography and Mississippian glaciation. *Geological Socity of America Bulletin* **111**:960-973.

Miller AK. 1930. A new ammonoid fauna of Late Paleozoic age from western Texas. *Journal of Paleontology* **4**:383-412.

Miller AK, Cline LM. 1934. The cephalopod fauna of the Pennsylvanian Nellie Bly Formation of Oklahoma. *Journal of Paleontology* **8**:171-185.

Miller AK, Downs R. 1948. A cephalopod fauna from the type section of the Pennsylvanian "Winslow Formation" of Arkansas. *Journal of Paleontology* **22**:672-680.

Miller AK, Downs RH. 1950. Ammonoids of the Pennsylvanian Finis Shale of Texas. *Journal of Paleontology* **24**:185-218.

Miller AK, Furnish WM. 1940a. Permian Ammonoids of the Guadalupe Mountain region and adjacent areas. *Geological Society of America, Special Papers* **26**:1-238.

Miller AK, Furnish WM. 1940b. Studies of Carboniferous Ammonoids, Parts 5-7. *Journal of Paleontology* **14**:521-543.

Miller AK, Furnish WM. 1957. Introduction to Ammonoidea. Pp. L1-L6 in W. J. Arkell et al., *Part L Mollusca 4 Cephalopoda Ammonoidea. Treatise on Invertebrate Paleontology*. Lawrence, Kansas: Geological Society of America.

Miller AK, Moore A, 1938. Cephalopods from the Carboniferous Morrow group of northern Arkansas and Oklahoma. *Journal of Paleontology* **22**:341-354.

Miller AK, Owen JB. 1937. A new Pennsylvanian cephalopod fauna from Oklahoma. *Journal of Paleontology* **11**:403-422.

Miller AK, Owen JB. 1939. An ammonoid fauna from the lower Pennsylvanian Cherokee Formation of Missouri. *Journal of Paleontology* **13**:141-162.

Miller AK, Thomas HD. 1936. The Casper Formation (Pennsylvanian) of Wyoming and its cephalopod fauna. *Journal of Paleontology* **10**:715-738.

Miller AK, Unklesbay AG. 1942. Permian nautiloids from western United States. *Journal of Paleontology* **16**:719-738.

Miller AK, Youngquist W. 1947. Lower Permian Cephalopods from the Texas Colorado River Valley. *The University of Kansas Paleontological Contributions* **2**:1-15.

Miller AK, Youngquist WL. 1949. American Permian nautiloids. *Geological Society of America Memoir* **41**:1-217.

Miller AK, Dunbar CO, Condra GE. 1933. The nautiloid cephalopods of the Pennsylvanian System in the Mid-continent region. *Nebraska Geological Survey Bulletin* **9**:1-240.

Miller AK, Lane JH, Unklesbay AG. 1947. A nautiloid cephalopod fauna from the Pennsylvanian Winterset Limestone of Jackson Country, Missouri. *University of Kansas Paleontological Contributions* **2**:1-11.

Miller AK, Youngquist W, Nielsen ML. 1952. Mississippian cephalopods from western Utah. *Journal of Paleontology* **26**:148-161.

Miller HW, Breed WJ. 1964. *Metacoceras bowmani*, a new species of nautiloid from the Toroweap Formation (Permian) of Arizona. *Journal of Paleontology* **38**:877-880.

Miller SA. 1892. Palaeontology. *Geological Survey of Indiana Annual Report Advance Sheets* **18**.

Minitab 17 Statistical Software. 2016. State College, PA: Minitab, Inc.

733 **Monnet C, De Baets K, Klug C.** 2011. Parallel evolution controlled by adaptation and
734 covariation in ammonoid cephalopods. *BMC Evolutionary Biology* **11**:115, 1-21.
735 **Montañez IP. 2007.** CO_2-forced climate and vegetational instability during Late Paleozoic
736 deglaciation. *Science* **315**:87-91.
737 **Montañez IP, Poulsen CJ. 2013.** The late Paleozoic Ice Age: an evolving paradigm. *Annual*
738 *Review of Earth Planet Science* **41**:629-656.
739 **Myers CE, Lieberman BS. 2011.** Sharks that pass in the night: using Geographical Information
740 Systems to investigate competition in the Cretaceous Interior Seaway. *Proceedings of the*
741 *Royal Society of London, Series B* **278**:681-689.
742 **Myers CE, Saupe EE. 2013.** A macroevolutionary expansion of the modern synthesis and the
743 importance of extrinsic abiotic factors. *Palaeontology* **56**:1179-1198.
744 **Myers CE, MacKenzie RA, Lieberman BS. 2013.** Greenhouse biogeography: the relationship
745 of geographic range to invasion and extinction in the Western Interior Seaway.
746 *Paleobiology* **39**:135-148.
747 **Nassichuk WW. 1975.** Carboniferous ammonoids and stratigraphy in the Canadian Arctic
748 archipelago. *Geological Survey of Canada Bulletin* **237**:1-240.
749 **Nelson WJ, Lucas SG. 2011.** Carboniferous geologic history of the Rocky Mountain region.
750 *New Mexico Museum of Natural History and Science Bulletin* **53**:115-142.
751 **Newell ND. 1936.** Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma: III.
752 Cephalopoda. *Journal of Paleontology* **10**:481-489.

Niko S, Mapes RH. 2009. Redescription and new information on the Carboniferous cephalopod *Brachycycloceras normale* Miller, Dunbar and Condra, 1933. *Paleontological Research* **13**:337-343.

Orzechowski EA, Lockwood R, Byrnes JEK, Anderson SC, Finnegan S, Finkel ZV, Harnik PG, Lindberg DR, Liow LH, Lotze HK, McClain CR, McGuire JL, O'Dea A, Pandolfi JM, Simpson C, Tittensor D. 2015. Marine extinction risk shaped by trait-environment interactions over 500 million years. *Global Change Biology* **21**:3595-3607.

Payne JL, Finnegan S. 2007. The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences, USA* **104**:10506-10511.

Pie MR, Meyer ALS. 2017. The evolution of range sizes in mammals and squamates: heritability and differential evolutionary rates for low- and high-latitude limits. *Evolutionary Biology* **44**:347-355.

Plummer FB, Scott G. 1937. Upper Paleozoic ammonites of Texas: the geology of Texas. *University of Texas Bulletin* **3701, vol 3, part 1**:1-516.

Pope JP. 2012. Description of Pennsylvanian units, revision of stratigraphic nomenclature and reclassification of the Morrowan, Atokan, Desmoinesian, Missourian, and Virgilian stages in Iowa. *Iowa Department of Natural Resources Special Report Series* **5**:1-140.

Powell MG. 2005. Climatic basis for sluggish macroevolution during the late Paleozoic ice age. *Geology* **33**:381-384.

Powell MG. 2007. Latitudinal diversity gradients for brachiopod genera during late Paleozoic

time: links between climate, biogeography and evolutionary rates. *Global Ecology and Biogeography* **16**:519-528.

R version 3.4.0. 2017. *You Stupid Darkness.* Vienna, Austria: R foundation for statistical computing.

Raymond A, Metz C. 2004. Ice and its consequences: glaciation in the Late Ordovician, Late Devonian, Pennsylvanian-Permian and Cenozoic compared. *Journal of Geology* **112**:655-670.

Rios NE, Bart HL Jr. 2018. GEOlocate: a platform for georeferencing natural history collections data. https://www.geo-locate.org .

Roark A, Flake R, Grossman EL, Olszewski T, Lebold J, Thomas D, Marcantonio F, Miller B, Raymond A, Yancey T. 2017. Brachiopod geochemical records from across the Carboniferous seas of North America: evidence for salinity gradients, stratification, and circulation patterns. *Palaeogeography, Palaeoclimatology Palaeoecology* **485**:136-153.

Rode AL, Lieberman BS. 2004. Using GIS to unlock the interactions between biogeography, environment, and evolution in Middle and Late Devonian brachiopods and bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* **211**:345-359.

Rode AL, Lieberman BS. 2005. Intergrating evolution and biogeography: a case study involving Devonian crustaceans. *Journal of Paleontology* **79**:267-276.

Rojas A, Patarroyo P, Mao L, Bengtson P, Kowalewski M. 2017. Global biogeography of Albian ammonoids: a network-based approach. *Geology* **45**:659-662.

Rook DL, Heim NA, Marcot J. 2013. Contrasting patterns and connections of rock and biotic

diversity in the marine and non-marine fossil records of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **372**:123-129.

Rothwell Group LP. 2016. *PaleoWeb: Free Plate Tectonics Software*. Lakewood, CO.

Ruzhentsev VE, Bogoslovskaya MF. 1971. Namurskiy etap v evolyutsii ammonoidey. Rannenamyurskie ammonoidei. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta* **133**:1-382.

Ruzhentsev VE, Shimanskiy VN. 1954. Nizhnepermskie svernutye i sognutye Nautiloidei yuzhnogo Urala. *Akademiya Nauk SSSR, Trudy Paleontologicheskogo Instituta* **50**:1-150.

Saupe EE, Qiao H, Hendricks JR, Portell RW, Hunter SJ, Soberón J, Lieberman BS. 2015. Niche breadth and geographic range size as determinants of species survival on geological time scales. *Global Ecology and Biogeography* **24**:1159-1169.

Sawin RS, West RR, Franseen EK, Watney WL, McCauley JR. 2006. Carboniferous-Permian boundary in Kansas, midcontinent, USA: current research in earth sciences. *Kansas Geological Survey, Bulletin* **252, Part 2**:1-13.

Sawin RS, Franseen EK, West RR, Ludvigson GA, Watney WL. 2008. Clarification and changes in Permian stratigraphic nomenclature in Kansas: current research in earth sciences. *Kansas Geological Survey, Bulletin* **254, Part 2**:1-4.

Sawin RS, Franseen EK, Watney WL, West RR, Ludvigson GA. 2009. New stratigraphic rank for the Carboniferous, Mississippian, and Pennsylvanian in Kansas: current research in earth sciences. *Kansas Geological Survey, Bulletin* **256, Part 1**:1-4.

Sayre AN. 1930. The fauna of the Drum Limestone of Kansas and western Missouri. *University of Kansas Science Bulletin* **19**:1-203

Schneider CL. 2018. Marine refugia past, present, and future: lessons from ancient geologic crises for modern marine ecosystem conservation. In: Tyler CL, Schneider CL, eds.. *Marine Conservation Paleobiology*. Berlin: Springer, 163-208.

Segessenman DC, Kammer TW. 2018. Testing evolutionary rates during the late Paleozoic ice age using the crinoid fossil record. *Lethaia* **51**:330-343.

Sepkoski JJ Jr. 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society of London* **353**:315-326.

Simões M, Breitkreuz L, Alvarado M, Baca S, Cooper JC, Heins L, Herzog K, Lieberman BS. 2016. The evolving theory of evolutionary radiations. *Trends in Ecology and Evolution (TREE)* **31**:27-34.

Smith HJ. 1938. *The Cephalopod Fauna of the Buckhorn Asphalt.* Chicago: University of Chicago Libraries.

Smith JP. 1896. Marine fossils from the Coal Measures of Arkansas. *Proceedings of the American Philosophical Society* **35**:213-285.

Smith JP. 1903. The Carboniferous Ammonoids of America. *Monographs of the United States Geological Survey* **52**:1-211.

Stanley SM. 1979. *Macroevolution*. San Francisco: W. H. Freeman.

Stanley SM. 1990. The general correlation between rate of speciation and rate of extinction: fortuitous causal linkages. In: Ross RM, Allmon WD, eds. *Causes of Evolution: a Paleontological Perspective*. Chicago: University of Chicago Press, 103-127.

Stanley SM, Powell MG. 2003. Depressed rates of origination and extinction during the late

Paleozoic ice age: a new state for the global marine ecosystem. *Geology* **31**:877-880.

Stigall AL. 2010. Using GIS to assess the biogeographic impact of species invasions on native brachiopods during the Richmondian Invasion in the type-Cincinnatian (Late Ordovician, Cincinnati region). *Palaeontologia Electronica* **13(1), 5A**:1-19.

Stigall AL, Lieberman BS. 2006. Quantatative palaeobiogeography: GIS, phylogenetic biogeographical analysis and conservation insights. *Journal of Biogeography* **33**:2051-2060.

Sturgeon MT. 1946. Allegheny fossil invertebrates from eastern Ohio-Nautiloidea. *Journal of Paleontology* **20**:8-37.

Sturgeon MT, Windle DL, Mapes RH, Hoare RD. 1982. New and revised taxa of Pennsylvanian cephalopods in Ohio and West Virginia. *Journal of Paleontology* **56**:1453-1479.

Swallow GC. 1858. Rocks of Kansas with descriptions of new Permian fossils. *Transactions of the Academy of Sciences St. Louis* **1**:1-27.

Tabor NJ. 2007. Permo-Pennsylvanian palaeotemperatures from Fe-Oxide and phyllosilicate δO18 values. *Earth and Planetary Science Letters* **253**:159-171.

Tabor NJ, Poulsen CJ. 2007. Paleoclimate across the late Pennsylvanian-early Permian tropical paleolatitudes: a review of climate indicators, their distribution, and relation to palaeophysiographic climate factors. *Palaeogeography, Palaeoclimatology, Palaeoecology* **268**:293-310.

Teichert C. 1940. Contributions to nautiloid nomenclature. *Journal of Paleontology* **14**:590-597.

Teichert C, Kummel B, Sweet WC, Stenzel HB, Furnish WM, Glenister BF, Erben HK, Moore

RC, Zeller D. 1964. *Part K Mollusca 3 Cephalopoda—General Features, Endoceratoidea—Actinoceratoidea–Nautiloidea—Bactritoidea. Treatise on Invertebrate Paleontology.* Lawrence, Kansas: The Geological Society of America.

Unklesbay AG. 1954. Distribution of American Pennsylvanian cephalopods. *Journal of Paleontology* **28**:84-95.

Unklesbay AG, Palmer EJ. 1958. Cephalopods from the Burgner Formation in Missouri. *Journal of Paleontology* **32**:1071-1076.

US Geological Survey. 2017. U.S. Geologic Names Lexicon ("Geolex"). Retrieved from the National Geologic Map Database: https://ngmdb.usgs.gov/Geolex/search .

Vrba ES. 1980. Evolution, species, and fossils: how does life evolve? *South African Journal of Science* **76**:61-84.

Waterhouse JB, Shi GR. 2010. Late Palaeozoic global changes affecting high-latitude environments and biotas: an introduction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **298**:1-16.

Wells MR, Allison PA, Piggott MD, Gorman GJ, Hampson GJ, Pain CC, Fang F. 2007. Numerical modeling of tides in the late Pennsylvanian Midcontinent Seaway of North America with implications for hydrography and sedimentation. *Journal of Sedimentary Research* **77**:843-865.

White CA. 1889. On the Permian formation of Texas. *The American Naturalist* **23**:109-128.

White CA, St. John OH. 1867. 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.

White RD, Skorina LK. 1999. A type catalog of fossil invertebrates (Mollusca: Actinoceratoiclea, Bactritoidea, Endoceratoidea, and Nautiloidea) in the Yale Peabody Museum. *Postilla* **219**:1-39.

Wieczorek C, Wieczorek J. 2015. Georeferencing calculator (version 20160920). Museum of Vertebrate Zoology, University of California, Berkeley. http://manisnet.org/gci2.html .

Wiley EO, Lieberman BS. 2011. *Phylogenetics, 2nd edition*. New York: J. Wiley & Sons.

Yacobucci MM. 2017. Marine life in a greenhouse world: cephalopod biodiversity and biogeography during the early Late Cretaceous. *Paleobiology* **43**:587-619.

Young JA. 1942. Pennsylvanian Scaphopoda and Cephalopoda from New Mexico. *Journal of Paleontology* **16**:120-125.

Zeller DE, ed. 1968. The stratigraphic succession in Kansas. *Kansas Geological Survey, Bulletin* **189**:1-81.

Figure Captions

Figure 1: Distribution of Pennsylvanian and early Permian cephalopods.

A) Distribution of Pennsylvanian nautiloid and ammonoid data points (red) and B) early Permian nautiloid and ammonoid data points (blue) across the midcontinent region of North America. Plotted using *ArcGIS v. 10.3* (ESRI, 2014) software at 1: 20,000,000.

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Figure 2: Occurrence points of *Metacoceras* sp. and *Mooreoceras* sp.

For the Virgilian, shown on possible paleogeography of that stage, at 1:1,000,000,000 scale; plotted using *PaleoWeb* (The Rothwell Group LP, 2016).

Figure 3: **Mean geographic range size in km^2 of cephalopods through time.**

Nautiloid species (A) and ammonoid species (B) range changes occur but are not statistically significant when analyzed using non-parametric tests (note, median range size data not graphed but for all cephalopods they are 79km^2 for all time intervals, for ammonoids they are 78.5km^2 for the Desmoinesian and Wolfcampian and 79km^2 for all other time intervals, and for nautiloids they are 79km^2 for all time intervals) or when log transformed data are analyzed using parametric tests (note log transformed data not graphed but mean transformed values for all cephalopods are 5.51 [standard error 0.75] for the Morrowan, 4.05 [standard error 1.02] for the Atokan, 4.36 [standard error 0.49] for the Desmoinesian, 5.65 [standard error 0.49] for the Missourian, 5.96 [standard error 0.79] for the Virgilian, and 4.31 [standard error 0.52] for the Wolfcampian).

Figure 4: **Speciation and extinction rates through time.**

Values given in per Myr and derived from Table 1.

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Con formato: Superíndice