Population Paleoecology of *Neochonetes granulifer* in the Foraker Formation, Hughes Creek Shale Member (Carboniferous), Richardson County, Nebraska.

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Abstract

The chonetid brachiopod, *Neochonetes granulifer*, is an abundant member of the fauna from the Carboniferous Foraker Formation, Hughes Creek Shale (HCS) Member (Carboniferous, Gzhelian – 303-299 million years old) throughout midcontinent North America. Three localities of the Member in southeastern Nebraska were sampled for *N. granulifer* for population characteristics in order to infer paleoecology. Taphonomic conditions of the specimens (articulation and pedicle valve percentages) suggest that the original living populations have been altered by pre-burial removal and destruction of shell material, a potential bias for interpreting original ecologies. Statistical comparison of length measures of *N. granulifer* from three localities reveal that one locality is significantly different from the other two. Potential explanations for this difference include: 1) different paleo-environments related to water depth and paleo-latitude and, 2) different stratigraphic levels (= different time intervals) within the HCS. Differentiating the two explanations is made difficult due to the spotty nature of preserved outcrops in the region.

1. Introduction

During the Carboniferous Period of Earth history (approx. 359-299 million years ago), repeated growth/decline of continental glacial masses in the southern hemisphere produced cycles of sediment globally that track these changes around the supercontinent Pangea (Embry et al., 1994). In the midcontinent region of present-day North America, the sedimentary expression of the cycles crops out as repeated patterns of clastic and carbonate sediments referred to as cyclothems (Strotz & Lieberman, 2020). The so-called gray "core" shales are representative of offshore marine paleo-environments (Olszewski & Patzkowsky, 2001) and typically contain a diverse, well-preserved fauna useful for paleoecological interpretations (Malinky & Heckel, 1998). As a whole, cyclothems have astrobiological relevance because they track changing oxygen levels that existed in the marine environments from gray color (oxic to slightly dysoxic water) to black color, representing anoxic conditions of Oceanic Anoxic Events (OAE, Johnson & Hanger, 2015) associated with local to mass extinctions (Reershemius & Planavsky, 2021).

The Foraker Formation occurs in outcrop from Oklahoma to Iowa, and is dated as the youngest Carboniferous (303-299 million years ago), or Gzehlian Age (Baars,1990; Sawin et al., 2006). The gray "core" shale of the Foraker Fm. is the Hughes Creeks Shale Member (HCS) which is exposed in southeastern Nebraska in Richardson County as road cuts (Figure 1) which have limited existence due to sedimentation and vegetation overgrowth from "highway beautification" projects (R. Pabian, pers. comm, 2004). When available, exposures of the HCS in Richardson County are extremely fossiliferous, and large collections can be built up for further analyses, especially for the most abundant taxa of the Phylum Brachiopoda.

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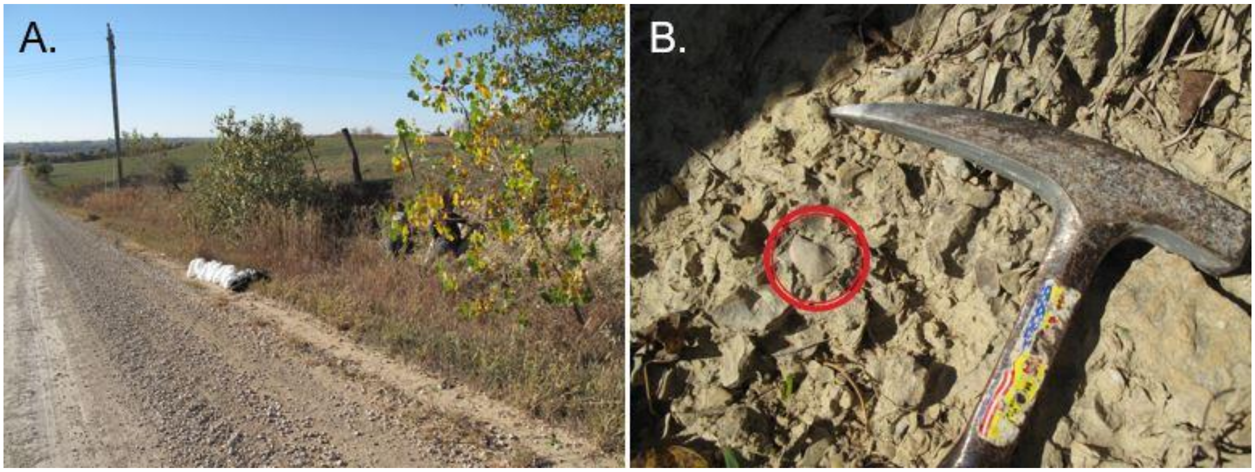

Figure 1: Typical field road cut of Hughes Creek Shale (HCS). A: Locality 10 in October, 2015. The locality is now fully covered by sediment and vegetation. B: Close up view of same outcrop showing fossiliferous nature of HCS at this locality. Red circle encloses a whole articulated specimen of the target species, *Neochonetes granulifer*.

The brachiopod *Neochonetes granulifer* is among the most common fossil recovered in the HCS and in several other Carboniferous gray shales, and whole specimens of all sizes can be studied as ancient populations of a spectrum of ages from juveniles to adults (Jacobs, 1976). Samples of abundant, target species such as *N. granulifer,* are useful in numerous ways in paleoecological studies (e.g. Cadee, 1982; Cate & Evans, 1992; Dodd et al., 1985).

2. Methods

Three locations (Figure 2) from Padian and Diffendal (2003) were chosen for extensive collecting in the time period of 2005-2013 because the road cuts were fresh and all contained abundant, well-preserved HCS fauna. Surface collections and bulk-sediment sampling efforts have built up a large collection in the UW-W Paleontology/Stratigraphy labs for study. In the sub-set collections of *N. granulifer*, all whole specimens (not fragments) were separated and counted as # of articulated individuals + # of pedicle valves + # of brachial valves, to give a total number of individuals from which the percentage of articulated specimens was calculated. The percentage of pedicle valves was calculated from the total number of disarticulated specimens (# pedicle valves + # brachial valves).

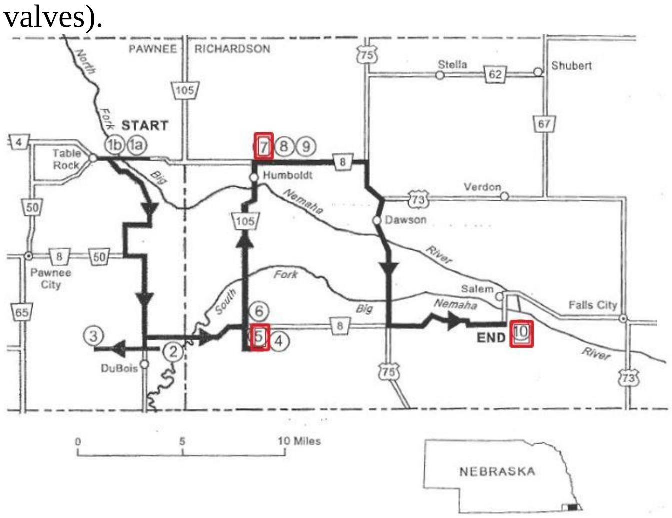

Figure 2: Locality map of Carboniferous localities in southeastern Nebraska (adapted from Pabian & Diffendal, 2003). Hughes Creek Shale (HCS) strata exposed at localities 5, 7 and 10, marked by red squares.

For *N. granulifer*, the length of the pedicle valves from all whole, articulated specimens were measured using standard Vernier calipers as shown in Figure 3. The brachial valves for the species are slightly smaller for length measurement and so were not used in this analysis as they are not directly comparable. All measurements are found in Supplemental File #1. These data were used to generate size-frequency histograms. Subsequent statistical analyses were performed with the software PAST (Hammer et al., 2001).

Figure 3: Ventral view of specimen of *N. granulifer* from locality 5. Length was measured from anterior to posterior on the shell, and shown as the red bar, with length of 12.43mm. All specimens were measured in similar manner.

3. Results

For taphonomic study, the percentage of articulated and disarticulated specimens was calculated as well as the percentage of each valve (pedicle and brachial). In a situation of "perfect" preservation, a bivalved organism like *N. granulifer*, is buried shortly after death, with both valves still connected together. If they do happen to separate, then the number of brachial and pedicle valves in a sample from a small sampling area should be equal. Deviations from this "perfect" scenario occur when unburied individuals become disarticulated and then multiple processes of current transport, biotic interactions and so forth move the different sized/shaped valves in contrasting styles. Table 1 shows the various counts of specimens. The percentage of articulated individuals is just over 50% for localities 5 and 10 and below 50% for locality 7. In contrast the percentage of pedicle valves among the disarticulated individuals is less than 50% for localities 5 and 10, but greater than 50% for locality 10. Thus, all localities deviate from the "perfect", rapid burial scenario outlined above, and so paleoecological conclusions must be made with consideration that size-frequency data may be biased by taphonomy. Locality 7 has a different taphonomic signature than 5 and 10 which could reflect differences in the paleo-environments between 7 and 5/10 pre-burial, or that they are sampled from different stratigraphic levels within the HCS, and thus different times.

Table 1: Counting metrics for taphonomic analyses.

	Locality 5	Locality 7	Locality 10
# articulated	201	207	109
# pedicle valves	44	212	28
# brachial valves	92	103	38
# all	337	522	175
% articulated	59.6	39.7	62.3
% pedicle valves	32.4	67.3	42.4

Length measurement data are reported in Supplementary File 1. Size-frequency histograms are shown in Figure 4. For Locality 5, 201 specimens were measured, with a mean length of 9.47mm. Testing for normality with the Shapiro-Wilk test, $p = 0.0026$, or non-normal. Grubbs test revealed no outliers, so all data were used for subsequent analyses. Bootstrapping the data 10,000 times produces 95% confidence intervals around the mean of 9.11 to 9.82. For locality 7, 207 specimens were measured with a mean length of 7.48mm. Testing for normality with the Shapiro-Wilk test, $p = 0.007$, or non-normal. Grubbs test revealed no outliers, so all data were used from subsequent analyses. Bootstrapping that data 10,000 times produces 95% confidence intervals around the mean of 7.20 to 7.75. For locality 10, 109 specimens were measured but a Grubbs test revealed one outlier which was removed. The remaining 108 specimens had a mean length of 9.16mm. Testing for normality with the Shapiro-Wilk tests, $p = 1.22 \times 10^{-3}$, or non-normal.

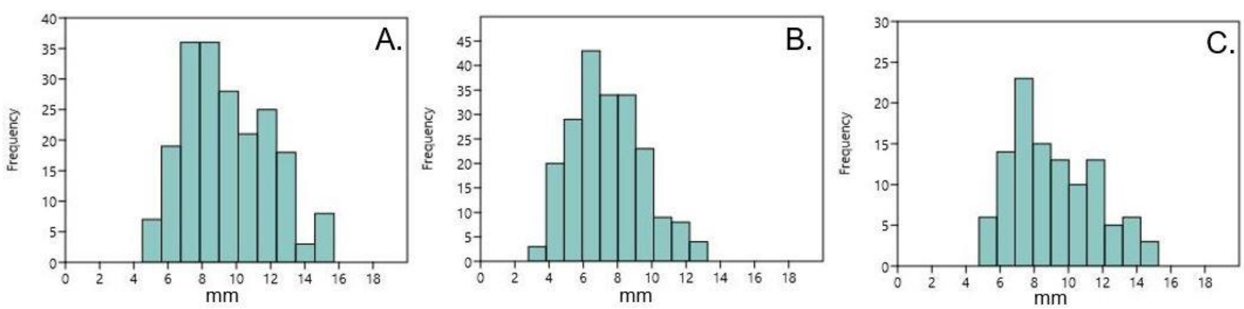

Figure 4: Size Frequency Histograms of length measurements of *N. granulifer*. A: Locality 5; B: Locality 7; C: Locality 10.

As the confidence intervals of localities 5 and 10 overlap with each other, but not with those of locality 7, a series of statistical tests using PAST software (Hammer et al., 2001) were used to test the potential significance of the pattern. All three distributions were non-normal, so the non-parametric options in PAST were used. These tests are set up to test null hypotheses of either equal medians or equal (overall) distributions between any two localities, and are shown in Table 2. In summary, one cannot falsify null hypotheses of equality of populations from locality 5 and 10. In contrast, all tests reject null hypotheses of equality between localities 5 or 10 with locality 7, confirming the confidence intervals from bootstrapping.

Table 2: Statistical comparisons of length measurements of *N. granulifer* in mm for localities 5, 7 and 10. All tests are non-parametric due to non-normality of the 3 data sets. Assumptions and algorithms for all tests are described in Hammer et al. (2001). For Mann-Whitney and Kruskal-Wallis tests, the null hypothesis is H_0: median $_{loc\ x}$ = median $_{loc\ y}$. For Kolmogorov-Smirnov and Epps-Singleton tests, the null hypothesis is H_0: distribution $_{loc\ x}$ = distribution $_{loc\ y}$

Locality Comparison	Mann-Whitney	Kolmogorov-Smirnov	Epps-Singleton	Kruskal-Wallis
5 X 7	$p = 5.49 \times 10^{-18}$ reject H_0	$p = 2.16 \times 10^{-9}$ reject H_0	$p = 4.20 \times 10^{-6}$ reject H_0	$p = 5.47 \times 10^{-15}$ reject H_0
7 X 10	$p = 3.18 \times 10^{-8}$ reject H_0	$p = 8.29 \times 10^{-5}$ reject H_0	$p = 5.23 \times 10^{-9}$ reject H_0	$p = 3.17 \times 10^{-8}$ reject H_0
5 X 10	$p = 0.23675$ cannot reject H_0	$p = 0.403$ cannot reject H_0	$p = 0.77185$ cannot reject H_0	$p = 0.2365$ cannot reject H_0

4. Discussion and Conclusions:

Significant similarity between localities 5 and 10 has been reported before (Johnson & Hanger, 2015) for a different brachiopod species, incorrectly reported as *Dyoros* sp., now identified as *Quadrochonetes geronticus* after detailed study of additional collections. The present study confirms the similarity between localities 5 and 10, but recognizes that while *N. granulifer* is also abundant at locality 7, the population paleoecology of the species shows significant difference.

Methods of field collection and laboratory processing were the same for all localities, so operator error is ruled out. Potential explanations for these differences are then constrained by the taphonomic analyses from Table 1. Articulation percentages and pedicle valve percentages indicate that while varying among all three localities, the rapid burial scenario for preservation of these populations was not likely. Paleo-environmental conditions of localities 5 and 10 suggest some coincidence of processes with different conditions at locality 7.

Two explanations for differing paleo-environmental conditions are possible. Pabian & Diffendal (2003) present evidence of deepening water condition from South to North in the southeastern Nebraska outcrops. Figure 2 shows that if this is the case, localities 5 and 10 are at similar latitudes (and presumably paleo-latitudes), while locality 7 is almost 10 miles further North into deeper marine conditions. In addition, the sporadic field conditions like those shown in Figure 1 mean that exact identification and correlation of any given localities is difficult. As an example, Holterhoff & Pabian (1990) originally described the locality 5 strata as the Permian Red Eagle Formation rather than the later determination (Pabian & Diffendal, 2003) of Carboniferous Foraker Formation. Mudge & Yochelson (1962) note that the HCS within the Foraker Fm. varies in faunal content upwards throughout its thickness. The fusulinid foraminifer, *Triticites ventricosus*, is recorded as being very abundant in the upper part of the formation and only common in the lower half. In the UW-W collections, uncounted thousands of specimens of *T. venticosus* are from Locality 7, while <10 each are recovered from localities 5 and 10. Locality 7 could be correctly identified as HCS strata, but from a different level (and thus different deposition time) of the Member.

In summary, *Neochonetes granulifer* was found to be abundant at three separate localities in southeastern Nebraska. As one of the dominant taxa found in the Carboniferous Hughes Creek Shale Member of the Foraker Formation, it served as proxy for the entire fauna. The length measure of the shells of *N. granulifer* provided the data that generated size-frequency histograms for statistical comparison. Two localities (5 and 10) were statistically indistinguishable from each other but significantly dissimilar from the third (7). Two causes are possible for these results – variable paleo-environmental conditions related to depth and/or paleo-latitude, and stratigraphic age difference, establishing hypotheses for future studies.

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