THE CONTRIBUTION OF REGIONAL VARIABILITY TO BETA DIVERSITY: A CASE STUDY OF THE DEEP-WATER MARINE COMMUNITIES OF THE MIDDLE UPPER ORDOVICIAN OF EASTERN LAURENTIA

A Thesis in
Geosciences
by
Eriks Perkons

©2016 Eriks Perkons

Submitted in Partial Fulfillment of the Requirements for the Degree of
Master of Science

May 2016
The thesis of Eriks Perkons was reviewed and approved* by the following:

Mark E. Patzkowsky  
Associate Professor of Geosciences  
Thesis Adviser

Peter D. Wilf  
Associate Professor of Geosciences

Michael A. Arthur  
Professor of Geosciences  
Interim Associate Head for Graduate Programs and Research

*Signatures are on file in the Graduate School
ABSTRACT

The structure and recurrence of marine invertebrate communities along depth gradients have been recent and productive research subjects among paleobiologists studying evolutionary patterns and biostratigraphic correlation. However, the extent to which these communities vary across regional spatial scales (beta diversity) has received comparatively little attention despite being a potential source for the observed increase in gamma diversity through the Paleozoic. The fauna of the middle Upper Ordovician Salona and Coburn Formations of the Trenton group carbonates were investigated to quantitatively study community compositions along a deep subtidal to offshore gradient. The deep subtidal through offshore biofacies have previously been under-sampled, so detailed examination of these strata provides much needed quantitative community data. High resolution (5 cm scale) stratigraphic analysis, coupled with extensive fossil collection from several exposures in central Pennsylvania, allows for identification of biofacies through cluster analysis, and faunal depth preferences through detrended correspondence analysis (DCA). These biofacies, and the ecologic preferences of their taxa, were then compared with previously reported collections from the Trenton Falls area of New York, and central Kentucky near Frankfort. While several comparable biofacies were identified, most did not have obvious counterparts in other collections. Those that were comparable varied greatly between locales, despite a high degree of taxonomic overlap. Ecological parameters of individual taxa were similarly not highly conserved, and all three locales contained numerous endemic taxa. Taxonomic dissimilarity between locations increases with greater geographic distance. Variations occurred over regional geographic scales, but not all correlate directly with distance, suggesting that regional and local variation may be a potential underappreciated source of diversity within provinces.
# TABLE OF CONTENTS

LIST OF FIGURES ..................................................................................................................................... v
LIST OF TABLES ...................................................................................................................................... vi
ACKNOWLEDGEMENTS .................................................................................................................... viii

Chapter 1: Introduction .......................................................................................................................... 1
  1.1 Significance and Objectives ........................................................................................................ 1
  1.2 Geologic History ...................................................................................................................... 2
  1.3 Trenton Group in Central Pennsylvania ............................................................................. 5
  1.4 Area of Investigation .............................................................................................................. 7
  1.5 Correlation and Age Constraints ....................................................................................... 10

Chapter 2: Data and Methods ............................................................................................................. 16
  2.1 Collection and Counting Methodologies ........................................................................ 16
  2.2 Analytical Methods .............................................................................................................. 21

Chapter 3: Results ................................................................................................................................. 27
  3.1 Lithofacies Descriptions ....................................................................................................... 27
  3.2 Cluster Analysis Results ....................................................................................................... 36
  3.3 Detrended Cluster Analysis Results ..................................................................................... 42

Chapter 4: Discussion ............................................................................................................................ 49
  4.1 Environmental Gradient ...................................................................................................... 49
  4.2 Ecological Gradient ............................................................................................................. 54
  4.3 Additional Taxa ................................................................................................................... 59
  4.4 Site Comparison .................................................................................................................. 65
  4.5 Comparison Summary and Implications ........................................................................... 85

Chapter 5: Conclusions ........................................................................................................................ 89

References .............................................................................................................................................. 91

Appendix A: Faunal Counts ................................................................................................................. 102
Appendix B: Stratigraphic Columns ................................................................................................. 104
Appendix C: Biofacies ....................................................................................................................... 111
Appendix D: Rarefaction and Species Accumulation Curves .......................................................... 113
Appendix E: Faunal Lists ................................................................................................................... 115
Appendix F: Additional Photographs ............................................................................................... 117
LIST OF FIGURES

Figure 1: Generalized stratigraphic section of Upper Ordovician strata of central Pennsylvania .................................................................................................................................................................................. 4

Figure 2: Paleogeographic map of the study region ........................................................................................................................................................................................................................................ 7

Figure 3: Locations of Pennsylvania outcrops ....................................................................................................................................................................................................................................... 9

Figure 4: Locations of Kentucky, New York, and Pennsylvania collections ........................................................................................................................................................................................................................................ 9

Figure 5: Correlation chart of Kentucky, Pennsylvania, and New York strata ........................................................................................................................................................................................................................................ 12

Figure 6: Reedsville outcrop panorama ........................................................................................................................................................................................................................................................................................................ 17

Figure 7: Bedding of the upper New Enterprise Member at Reedsville ........................................................................................................................................................................................................................................ 29

Figure 8: Idealized bedding pattern of the Laminated Mudstone and Packstone & Mudstone Facies ........................................................................................................................................................................................................................................................................................................ 30

Figure 9: Bedding in the lower Roaring Spring Member at Reedsville ........................................................................................................................................................................................................................................................................................................ 32

Figure 10: Stacked tempestite beds in Reedsville ........................................................................................................................................................................................................................................................................................................ 33

Figure 11: General bedding of the Roaring Spring Member at Reedsville ........................................................................................................................................................................................................................................................................................................ 33

Figure 12: Bedding of the Coleville Member at Reedsville ........................................................................................................................................................................................................................................................................................................ 35

Figure 13: Amalgamated storm deposits at Reedsville ........................................................................................................................................................................................................................................................................................................ 36

Figure 14: 2-way cluster analysis of faunal counts ........................................................................................................................................................................................................................................................................................................ 38

Figure 15: Faunal log and DCA axis-1 scores of the Reedsville section ........................................................................................................................................................................................................................................................................................................ 46

Figure 16: DCA axis-1 and axis-2 sample scores by geologic member ........................................................................................................................................................................................................................................................................................................ 47

Figure 17: DCA axis-1 and axis-2 sample scores by biofacies ........................................................................................................................................................................................................................................................................................................ 47

Figure 18: Ecological parameters of Pennsylvania taxa ........................................................................................................................................................................................................................................................................................................ 48

Figure 19: Microphotographs of Hexactinellid spicules ........................................................................................................................................................................................................................................................................................................ 62

Figure 20: Microphotograph of macrotubular borings ........................................................................................................................................................................................................................................................................................................ 64

Figure 21: Flow aligned fossils at Reedsville ........................................................................................................................................................................................................................................................................................................ 65

Figure 22: Jaccard dissimilarity for New York, Pennsylvania, and Kentucky collections ........................................................................................................................................................................................................................................................................................................ 77

Figure 23: DCA of Pennsylvania, Kentucky, and New York samples ........................................................................................................................................................................................................................................................................................................ 78
Figure 24: Correlation of ecological parameters for taxa shared between collections ................................................................. 83

Figure 25: Spearman’s ρ for ecological parameters as a distance between collections .................................................................................. 85

Figure 26: Chert nodules at the base of the Salona Formation, Reedsville ...............117

Figure 27: Pyritized Cryptolithus cephalon, from the lower New Enterprise member, Reedsville.............................................................117

Figure 28: Deicke K-bentonite couplet at meter 5.5 Reedsville .........................118

Figure 29: Brongniartella fragments from meter 18 at Reedsville.........................118

Figure 30: Parastrophina cast from approximated meter 53 at Reedsville.............119

Figure 31: Dinorthis cast, collected at meter 56 in Reedsville...............................119

Figure 32: Amalgamated storm beds from meter 117 at Reedsville .....................120

Figure 33: Atrypid brachiopods in a Chondrites rich block at meter 119 of the Reedsville section .................................................................120

Figure 34: Gyroconic nautiloid mold (c.f. Trocholites) collected at Spring Mills .................................................................................................121

Figure 35: Corynotrypa, a cyclostomate bryozoan (Stenolaemata), here encrusting an Isotelus trilobite fragment .........................................121

Figure 36: Panorama of Lemont collection area ....................................................122

Figure 37: Panorama of Reedsville collection area ................................................122
LIST OF TABLES

Table 1: Distribution of samples between marine facies .................................................... 68
Table 2: Comparison of taxa identified in Kentucky, New York, and Pennsylvania ................................................................. 73
Table 3: ANOSIM test results for all collections by state ............................................................ 79
Table 4: Faunal counts for Pennsylvania samples used in data analysis .................................. 102
Table 5: Biofacies diversity metrics .......................................................................................... 111
Table 6: Biofacies composition data ......................................................................................... 112
Table 7: Faunal lists for Pennsylvania, Kentucky, and New York ............................................ 116
ACKNOWLEDGEMENTS

Thanks to Mark Patzkowsky, Peter Wilf, and Michael Arthur for their ongoing support and infinite patience in this project. Roger Cuffey provided valuable feedback and assistance based on his firsthand observations and extensive study of the locations and subjects under investigation. Travis Deptola and Barbara Perkons were invaluable field assistants during the long process of data collection. Without the access to the extensive fossil collections provided by Susan Butts at the Yale Peabody Museum of Natural History, and Steven Jasinski at the State Museum of Natural History, fossil collection and identification would have been vastly more difficult.
Chapter 1: Introduction

1.1 Significance and Objectives

The relative stability of communities, as identified by the recurrence of similar faunal associations under similar paleoenvironmental conditions, or biofacies, has fallen under heightened scrutiny in recent years as investigators have sought to determine the patterns and causative factors of Paleozoic community turnover and stability (e.g., Bonelli et al., 2006; Bonelli & Patzkowsky, 2008; Brett & Baird 1995; Dominici & Kowalke, 2007; Ivany et al., 2009; Patzkowsky & Holland, 1997, 1999; DiMichele et al., 2004; Holland & Patzkowsky, 2004). While biofacies recurrence has been used to determine the temporal and spatial persistence of faunal associations at relatively small ranges (typically much less than 300 km; e.g. Brett et al., 2007a), researchers have yet to fully examine these associations over larger spatial scales.

The use of gradient analysis to correlate locations along an environmental gradient has demonstrated that faunal associations can be robust, at least on local scales (Cisne and Rabe, 1978). Sepkoski (1988) studied beta diversity (a metric for comparing diversity between communities or along environmental gradients; see Whittaker, 1972) along the depth gradient, but was restricted to using large time blocks that included periods of major ecological transition and evolutionary change (Boucot, 1983; Sheehan, 1996). The study also relied on pooled collection data from the Laurentian craton of North America, obscuring regional scale beta diversity. Sepkoski found global increases in beta diversity along depth gradients over time, accounting for a portion, but not all, of the rise in global (gamma) diversity observed through the Paleozoic. Reevaluating Sepkoski’s 1988 study in light of additive diversity
partitioning, Holland (2010) supports the position of Valentine and others (1978) that increasing provinciality is the likely driver of increasing gamma diversity.

The purpose of this study is to assess this potential source of global diversity by comparing biofacies from environmentally similar but widely spaced sites from the same time interval. How these faunal associations vary in taxonomic composition can indicate the rate at which beta diversity increases over regional scales. This study centers on three outcrops of Late Ordovician carbonates of central Pennsylvania (Fig. 1), with a focus on both stratigraphy and fossil assemblages. The sites were selected due to their extensive exposures, well preserved fossil material, and the stratigraphic constraint afforded by the presence of multiple K-bentonites. Detailed lithostratigraphic records for each of the outcrops provided information on the processes of deposition and preservation. Fossil abundance data were, allowing for study of the structure of the ecological gradients, biofacies recurrence, and their response to changing environments. This study focuses specifically on the relatively narrow range of facies representing the deep subtidal environment. Ecological gradients along this local depth gradient were then compared with previously studied correlative assemblages in similar but geographically distant environments of New York and Kentucky.

1.2 Geologic History

1.2.1 Paleogeography:

During the Cambrian and Ordovician periods, vast shallow seas covered most of the Laurentian craton, leading to extensive carbonate deposition. The Laurentian landmass straddled the equator, with Central Pennsylvania located at approximately 25° south (Scotese & McKerrow, 1991). The Trenton Group carbonates formed during the Taconic Orogeny, a
period of mountain building associated with a collision between the Laurentian craton and volcanic island arcs approaching from the southwest (Hay & Cisne, 1988). Deposits from this time formed on a low latitude carbonate ramp (Witzke, 1990), distally steepened by the flexural loading from the Taconic highlands. This ramp marks the transition from a carbonate platform to an extensive foreland basin filling with siliciclastic sediments.

The basin today trends approximately northeast-southwest (Witzke 1990), extending roughly from Tennessee to Ontario, and passing through both Kentucky and New York (Hay & Cisne 1988). While the basin orientation does not position the Pennsylvania, New York, and Kentucky deposition sites on exactly the same latitude, all locations are confined to the same general climatic conditions (Witzke 1990), reducing the impact of latitudinal gradients on the biota (Krug et al. 2009). The apparent lack of barriers to dispersal along the basin axis and the relatively consistent climate reduces concerns of local effects and endemism on the comparison of ecologic gradients from widely spaced localities.

1.2.2 Tectonics:

The Ordovician was a period of global orogenesis, with accretionary events involving the collision of arc terranes and microcontinents occurring worldwide (Van Staal & Hatcher, 2010). The carbonates of the Trenton Group record the end of a long period of relatively quiet carbonate deposition on the broad, flat, epicontinental Great American Carbonate Bank, with a homoclinal ramp on the margin (Read, 1980). The approach of the Taconic volcanic arc from the south loaded the passive continental margin, downwarping and activating it. The oblique collision of the Taconic arc and the distribution of inherited Precambrian faults resulted in the uneven subsidence and deformation of the continental margin and interior (Dix & Al-Dulami, 2011). The Pennsylvania Embayment formed early and rapidly, with Pennsylvania strata
showing signs of deposition in deeper waters than coeval units in New York and West Virginia (Keith, 1989). Subduction of the approaching terrane led to increased volcanism, spreading volcanic ash over much of the Laurentian craton.

Figure 1: Generalized stratigraphic section of Upper Ordovician strata of central Pennsylvania (modified from Cullen-Lollis and Huff, 1986). The interval of study in Pennsylvania is highlighted in blue, while two key metabentonites useful for correlation, the Deike and Millbrig, are highlighted in red. Stage and series names and boundaries updated from Mitchell et al. 2004; Bergström et al. 2009; Sadler et al. 2009; and Bergström et al., 2010.
1.2.3 Environmental History

Significant environmental changes also occurred during the Upper Ordovician, primarily driven by the tectonic forces reshaping the globe. Trenton group deposition is approximately 8 million years prior to the Hirnantian glaciation of the Late Ordovician (Berry & Boucot, 1973; Smith et al., 2011) which resulted from the weathering of silicate bedrock exposed during the Taconic orogeny (Kump et al., 1999; Young et al., 2009). An earlier regional cooling is associated with the formation of the Sebree Trough (Fig. 2), which altered ocean currents and introduced cool waters from the temperate south (Ettensohn et al., 2004; Herrmann et al., 2010; Kolata et al., 2001; Herrmann & Haupt, 2010). This Mohawkian cooling has been shown to predate the catastrophic volcanism of this time period (Herrmann & Haupt, 2010; Herrmann et al., 2010). Regionally, the latitudinally comparable strata of the Cincinnati Arch, central Appalachians, and Nashville Dome show a lithologic transition from tropical-type carbonates to temperate-type carbonates during the mid to late Mohawkian (Holland & Patzkowsky, 1996; Holland & Patzkowsky, 1998) with attendant faunal changes (Patzkowsky & Holland, 1996).

1.3 Trenton Group in Central Pennsylvania

The identification and naming of strata in the Trenton group by Rogers (1858) sparked a period of heightened interest in the lithostratigraphy and fauna of these units. Early work by Collie (1903) described both the stratigraphy and paleontology of the Ordovician outcrops at Bellefonte. Subsequent studies by Whitcomb (1932), Kay (1944), Schneider (1951), and Thompson (1963) further refined both the stratigraphic descriptions and the fauna, aiding in bio- and lithostratigraphic correlation of the Ordovician outcrops of central Pennsylvania.
These paleontological studies of the Trenton fauna recorded either presence/absence data (Collie, 1903; Thompson, 1963) or relative abundance data (Kay, 1944; Schneider, 1951). While useful for correlation and general environmental interpretation, the lack of true abundance data and the lumping of collections makes quantitative comparisons of communities difficult. Gardiner-Kuserk (1988), Arens and Cuffey (1989), Slupik (1999), and Laughrey and others (2004) contributed studies on the interpreted environments of deposition for these strata, but these interpretations were not always in concurrence. Although the Trenton Group and other contemporaneous deposits have been the subject of extensive paleoecological study, research has primarily focused on the well exposed outcrops to the west, such the Cincinnati Arch in Kentucky and the Nashville Dome in Tennessee (e.g. Holland and Patzkowsky, 2004; Layou, 2009) or near the type section in New York (e.g. Brower, 2011), instead of the more limited exposures of central Pennsylvania.

Stratigraphically, the Trenton Group deposits are the uppermost strata in a thick sequence of carbonates, which record the transition from a broad carbonate bank to a distally steepened ramp. The underlying Cambrian to Middle Ordovician carbonate deposits of the Beekmantown Group and the Loysburg Formation record deposition in a rimmed carbonate shelf environment (Hobson, 1963; Faill, 1999). Above these, the Black River carbonates show signs of deposition on a deepening carbonate ramp, reaching a maximum depth in the Salona Formation of the Trenton Group (Laughrey et al., 2004). The Coburn Formation then appears to represent a slight shallowing, as the distal tempestite deposits in the Salona are replaced by more proximal storm deposits (Gardiner-Kuserk, 1988). Siliciclastic tempestites also appear through the lower Antes/Reedsville (Lehman & Pope, 1989), showing that the transition to the predominantly siliciclastic system in the upper Ordovician was not due exclusively to deepening but was also driven by an increased flux of fine grained siliciclastics from the
approaching Taconic volcanic belt and the concurrent drowning of the carbonate platform, removing the major source of carbonate sediments.

Figure 2: Paleogeographic map of the study region during the middle to late Shermanian. This postdates the central Pennsylvania strata, but is roughly contemporary with those of New York and Kentucky. Map shows the location of the Taconic foreland basin, as well as the Sebree Trough which opened during the study interval, altering ocean circulation patterns. Figure modified from Brett et al., 2004.

1.4 Area of Investigation

The Trenton Group of the middle Upper Ordovician is a fossiliferous series of marine deposits ranging across much of eastern North America (Keith, 1989). In central Pennsylvania it is divided in ascending order into the Nealmont, Salona, Coburn, and Antes formations, and is
exposed in the floors of the Valley and Ridge Province of the Appalachian Mountains (Field, 1919; Kay, 1944). These strata were deposited during the initiation of the Taconic Orogeny in an actively subsiding foreland (Bradley, 1989; Faill, 1997), with the sediments transitioning from a predominantly carbonate depositional system to one dominated by fine-grained siliciclastics in the Antes Shale (Fig. 1) (Thompson, 1963).

Middle and Upper Ordovician carbonates are well exposed in the Valley and Ridge province of central Pennsylvania. While outcrop extent is limited by the relatively rapid weathering of carbonates, numerous road cuts and quarries allow access to continuous exposures. The Trenton Group is particularly well exposed in the area, with the three localities used in this study shown in Figure 3. The Reedsville Section, located in Mifflin County, is a continuous exposure from the upper Rodman Member of the Nealmont Formation through the lowermost section of the Antes Shale. This was the most complete and extensive of the sections measured, and is situated along the westbound exit ramp of PA Route 322 at Reedsville (40° 40' 2.70" N, 77° 36' 9.26" W). The Lemont Section (40° 47' 54.96" N, 77° 49' 24.29" W) is located along the northeast side of the westbound lane of the PA Route 322 Bypass, approximately 1.8 kilometers southeast of the PA Route 26 overpass. This outcrop provides exposure from the Nealmont Formation through the Roaring Spring Member of the Salona Formation. The third measured section is located in the village of Spring Mills, and is exposed in a road cut on both sides of PA Route 45 (40° 51' 23.25" N, 77° 34' 22.95" W). The shortest section, this is almost exclusively restricted to the Roaring Spring Member of the Salona Formation, but presents exceptional bedding plane exposures on the north side of the road.

The communities to which the central Pennsylvanian samples are compared were collected in northern Kentucky and upstate New York, as shown in Figure 4. Details of these
initial studies, including collection and analysis methodologies and locations can be found in Holland and Patzkowsky (2004) and Titus (1982), respectively.

Figure 3: Locations of Pennsylvania outcrops. Centre County, in which two of the sites are located, is shown, along with the approximate location of where 20° South latitude would have been during time of deposition.

Figure 4: Locations of Kentucky, New York, and Pennsylvania collections. A represents the site of samples collected by Titus (1976, 1982, 1986), B represents the current study (Perkons), and C is located where Holland & Patzkowsky (2004) collected their samples.
1.5 Correlation and Age Constraints

1.5.1 Correlation

Initial efforts to correlate the carbonates of central Pennsylvania with each other, and with other regional units, were primarily guided by lithologic and faunal similarities. G. Marshall Kay, in his early treatise on central Pennsylvanian carbonates (Kay, 1944), used this combination of associations to correlate these strata across the state, and to extend this correlation into New York, Kentucky, and Virginia. While lithostratigraphic correlations are extremely useful for broadly tying together regional strata, they can be less useful in identifying time correlative units. Fortunately, the massive increase in explosive volcanism during the Mohawkian resulted in the deposition of numerous and widespread ash layers (now altered to metabentonites, or K-bentonites). Despite heavy diagenetic alteration of these beds, geochemical analysis can still discriminate between ash falls from different eruptive events, allowing for the identification and correlation of widely distributed ash beds. The Deicke and Millbrig K-bentonites in particular offer the means to correlate the Mohawkian strata of central Pennsylvania across the state (Cullen-Lollis and Huff 1986) as well as with other localities in eastern North America (Samson et al., 1989; Leslie & Bergström, 1997; Min et al. 2001; Mitchell et al. 2004; and Adhya, 2009). Recognizing their large areal extent, Whitcomb (1932) and Rosenkrans (1934) were among the earliest researchers to use these K-bentonites for regional correlation of the Trenton. While the correlations primarily used lithostratigraphy and biostratigraphy to distinguish the K-bentonite beds from each other, this approach was sound enough to allow generally accurate correlation between outcrops. These early attempts at tracing the K-bentonites across larger distances were hampered by a number of factors that
makes the use of K-bentonites problematic, such as difficulties in distinguishing individual beds, and the potential for any bed to be locally absent.

After the success in correlating outcrops through the Deicke and Millbrig K-bentonites, the researchers assumed that all K-bentonites would serve this purpose equally well (Rosenkrans, 1934). However, whereas the Deicke and Millbrig K-bentonites are extremely widespread and have been identified in many outcrops of the same age, not all of the K-bentonites are as ubiquitous and are often discontinuous (Whitcomb, 1932). Despite the fact that the specific correlation Whitcomb was warning about (that of the Hounsfield metabentonite across much of eastern North America by Kay in 1931) has proven to be well supported by apatite chemical analysis and melt inclusion chemistry (Mitchell et al., 2004, Adhya, 2009), the concerns are valid. A subsequent attempt to correlate the Millbrig K-bentonite of North America with the similarly widespread Kinnekulle K-bentonite of Europe (Huff et al., 1992) has since proven erroneous (Huff, 2008; Sell & Samson, 2011), highlighting the issues in correlating K-bentonites over larger geographic scales. The studies of these K-bentonites have also shown additional variability within and between the beds. Unlike the Deicke K-bentonite, which was deposited by a single event (Huff, 2008), the Millbrig is an amalgamation of ash falls from multiple eruptions, giving it a complex chemical signature (Mitchell et al., 2004; Huff, 2008; Adhya, 2009; and Sell & Samson, 2011). Despite the issues raised by these studies, the use of K-bentonites as a viable means of correlating outcrops of Mohawkian aged strata continues to be implemented to good effect.

The establishment of a regional depositional sequence framework by Holland and Patzkowsky (1996) also aids in correlation between outcrops in the Cincinnati Arch, the Nashville Dome, and the southern Appalachian mountains. This has been extended to the type section of the Trenton in New York State by Brett and Baird (2002), which they correlate with
the M4, M5, and M6 sequences of Holland and Patzkowsky (1996). Mitchell and others (2004) further supported this correlation, and also extended the sequence nomenclature to the Trenton of central Pennsylvania. They place the lower Salona Formation in the M4 sequence, and tentatively place the division between the M4 and M5 sequences at the Millbrig metabentonite, with the Roaring Spring Member and the Coburn Formation in the M5 sequence. The sequence divisions, as well as correlation between the Trenton of Kentucky, New York, and Pennsylvania are shown in Figure 5.

Figure 5: Correlation chart of Kentucky, Pennsylvania, and New York strata. Gray areas represent strata from which faunal samples were collected. Entire time span shown is within the Trenton. Figure adapted from Mitchell et al. (2004), with additional data from Brett & Baird, 2002. Vertical lined pattern indicate interpreted depositional hiatuses or periods of non-deposition, and the dashed red lines represent correlated K-bentonite beds.
1.5.2 Biostratigraphy:

Early biostratigraphic correlations relied on distinctive fauna that appeared in highly localized beds. Whitcomb (1930) used the trilobite *Brongniartella* to correlate the Trenton of Central Pennsylvania with other regional sections as well as with England, and later used *Parastrophina hemiplicata* to correlate the Coburn with the Trenton in New York (Whitcomb, 1932). While these correlations are generally useful, taxonomic ranges are dependent upon local environmental and depositional conditions, and are therefore not entirely reliable. Conodonts and graptolites provide a means of biostratigraphic correlation that is less influenced by local bottom conditions by relying on widely dispersed nektic and planktic organisms.

In a regional study based on conodonts obtained from cores and previous studies, Richardson and Bergström (2003) attempted to correlate Trenton deposits across eastern North America. In central Pennsylvania, they found that the fossils observed by Valek (1982) place both the Salona and the Coburn in the upper *A. tvaerensis* Zone, with the overlying Antes Shale likely in the *A. superbus* Zone. Working in the Coburn Formation at Reedsville, Bellomy (1999) identified the conodont *Polyplacognathus ramosus*, further supporting its placement in the *A. tvaerensis* Zone (Fig. 5). For Kentucky, Richardson and Bergström cite the conodont work of Bergström and Sweet (1966) and the graphical correlation of Sweet (1984) to establish the Lexington Limestone primarily in the *P. tenuis* and *B. confluens* graptolite Zones, with the upper Lexington Limestone and the lower Clays Ferry Formation in the *A. superbus* Zone. In northern New York, Sweet (1984) placed the transition from the *A. tvaerensis* Zone to the *A. superbus* Zone in the lower Denley Limestone.
1.5.3 Age Constraints:

Age determination of Trenton Group deposits is aided significantly by the presence of the numerous altered volcanic ash beds found throughout the strata. Two of these K-bentonites, the Deicke and the Millbrig, are important in correlating the local section with others across North America, and have been the subject of extensive chronostratigraphic and geochemical analysis (Huff et al., 1996; Leslie & Bergström, 1997; Kolata et al., 2001; Mitchel et al., 2004; Huff 2008; Adhya, 2009; Renne et al., 2010; Sell & Samson, 2011; Smith et al., 2011). The Millbrig K-bentonite has been identified as the result of multiple eruptions (Mitchel et al., 2004; Huff, 2008; Adhya, 2009; Sell & Sampson, 2011), giving the ash bed a complex geochemical signature. However, the eruptive events that deposited this ash bed were effectively simultaneous, meaning that it is still appropriate for use in geochronological studies (Smith et al., 2011).

K-bentonite layers allow for chronostratigraphic placement of widely spaced outcrops through $^{40}\text{Ar}/^{39}\text{Ar}$, $^{206}\text{Pb}/^{238}\text{U}$, and $^{207}\text{Pb}/^{235}\text{U}$ dating techniques (Samson et al. 1989; Min et al. 2001). The Salona and Coburn formations of central Pennsylvania have been correlated with the M4-M6 depositional sequences identified by Holland and Patzkowsky (1996) based on the presence of the Deicke and Millbrig K-bentonite beds (Mitchell et al. 2004). The Deicke K-bentonite has been dated to 454.6±1.1 Ma through $^{238}\text{U}$–$^{206}\text{Pb}$ single-grain analysis of zircon (Renne et al. 2010). The overlying Millbrig K-bentonite, which corresponds to the Turinian–Chatfieldian Stage boundary (Leslie & Bergström, 2005), has been dated to 455.1 ±1.4 Ma through $^{40}\text{Ar}/^{39}\text{Ar}$ single-grain analysis of sanidine by Smith and others (2011). Samples for these analyses were taken from the Lexington Quarry, Kentucky, and Decorah, Iowa, respectively. Recently reported (Mitchell et al., 2015) work on a K-bentonite from 6.3 meters above the base of the Antes Shale in Reedsville, tentatively correlated with the Calmar K-
bentonite in the upper Mississippi Valley and the Manheim K-bentonite in the Dolgeville Formation in New York (Sell et al., 2015), uses U-Pb isotopic dating of zircon phenocrysts to place this bed at 451.20 ±0.12 Ma. While this bed is well above the uppermost sampling location in Pennsylvania, these studies suggest a time span of approximately 4 million years for the study interval, much shorter than the 7.5 million year average interval length in Sepkoski’s 1988 diversity study.
Chapter 2: Data and Methods

2.1 Field and Collection Methodologies

Rocks were described using Dunham’s (1962) classification, and measurements were taken at 5 cm increments, producing 87 meter and 150 meter columns for Lemont and Reedsville, respectively. Bedding thickness terminology is based on Ingram (1954). The Spring Mills stratigraphic column was not included due to the shorter measurable exposure (25 meters on the south side of the road cut) and its oblique dissection by a highway. However, both lithologic and faunal data suggest placement of this section in the upper Roaring Spring Member of the Salona Formation, and several fossil samples were included from Spring Mills.

Fossil collections were made in all locations using exposed bedding planes as well as constrained float. Bedding planes provide a definite location within the stratigraphic context of the outcrop, but the limited number of available fossiliferous bedding planes, particularly at the Reedsville and Lemont sections, necessitated that the majority of collections were made from float. While the use of float sometimes limited precise stratigraphic determination, it was usually possible to place float samples in their stratigraphic context based on lithological traits (e.g. calcite veins, recrystallization, and grain size), preservational details of the fossils, differential weathering patterns on the outcrop (such as is apparent in Figure 6 around meters 94-100 at Reedsville), or the patterns of cyclic sedimentation, such as around meters 35-45 (also at Reedsville). An additional, broad constraint on the source of float material is the height of the outcrop. With the beds dipping at approximately 46° SE, rock fall from any particular point in the outcrop will fall down section by a maximum of around 15 meters. However, the
movement of float should be far less than this, for a greater falling distance will also result in the sample moving further from the base of the outcrop and down the talus slope. While it is possible that float could be subsequently moved through further human or natural disturbances, all float samples were collected as close to the base of the outcrop as possible in order to minimize the above described confounding factors. The location where the float is found, combined with the lithological characteristics, provides a reasonable level of confidence in constraining samples to a narrow interval.

![Figure 6](image)

*Figure 6:* Reedsville outcrop panorama, showing variable weathering patterns. The buff colored, heavily eroded section (Milesburg Member, meter 94-100) yielded multiple samples from float, which were easily constrained to the weathered interval. Salona/Coburn contact and the approximate contact of the Milesburg and Coleville Members are shown in red.

Fossil were identified to the genus level to simplify comparisons with collections by other researchers (e.g. Holland and Patzkowsky, 2004). Identifications were made with a combination of comparison with museum collections (The State Museum of Pennsylvania and the Yale Peabody Museum of Natural History) and published resources (Cooper, 1956). Brachiopods, bivalves, and ostracods were counted by totaling the number of articulated specimens, or by half the number of single valves. Valves were only counted if more than fifty percent of the valve is visible. Trilobites were tallied by counting the number of pygidia or cranidia and determining the minimum number of individuals that these specimens
represented. Crinoid columnals are abundant but difficult to identify and count. Crinoids were instead assigned to morphotypes (e.g. simple round, pentagonal, spined), which were qualitatively recorded as rare, present, common, and abundant. They were subsequently converted to abundances in order to be included in quantitative analysis by the conversion rare=1%, present=5%, common=10%, and abundant=30% of the sample total. For comparison with other studies, crinoids were simply lumped together into one group. Bryozoans were identified to the class level when possible, and were also classified by morphotype (e.g. fine ramose, robust ramose, bifoliate). Each 1 cm segment of bryozoan colony was counted as an individual to maintain consistency with previous studies (e.g. Holland and Patzkowsky 2004). While crinoids and bryozoans have frequently been excluded from collections in quantitative analysis, the counting method for disaggregated fossil material has been shown to be of minimal import, provided the taxa in question are not dominant in the assemblages (Forcino et al., 2010; Forcino 2010). Although bryozoans were dominant in some of the samples, these samples grouped strongly in the multivariate analysis, and appear to represent a true ecological signal. Counts were otherwise performed using absolute abundance data. Counts were only performed for fossil material ≥2mm in order to exclude larvae and newly settled juveniles that may not be persistent members of the community (Kidwell, 2002). Attempts were made to increase specimen counts in collected blocks by dissolving the carbonate matrix with H₂SO₄ using the method described by Vodrazka (2009), but this approach resulted in minimal additional material and was abandoned.

Multiple samples were collected within each facies in order to minimize the influence of faunal patchiness (Lafferty et al. 1994; Bennington, 2003; Redman et al. 2007; and Zambito et al. 2008). Forcino (2011) demonstrated that the effectiveness of samples to provide meaningful ecological data decreases when the number of individuals is less than 25, so
attempts were made to only use samples of this size or larger. However, due to the limited size of some of the samples collected, it was necessary to include 14 samples of less than 25 individuals in order to sample as completely as possible through the stratigraphic sections. The smallest included sample had 16 individuals, and only five other samples contained less than 20 individuals, which should minimize the influence on ecological data.

The complete data set contained 66 taxa or morphotypes with a total of 5213 individuals (excluding highly disarticulated echinoderms) in 129 samples (Appendix A), with a mean sample of 41 individuals and a median number of 25 individuals per sample. Taxa that occurred in less than 3% of samples (1 or 2 samples) were removed from the analyses, in order to reduce noise in data analysis (McCune & Grace, 2002). Taxa removed from analysis include Strophomena, Corynotrypa, Streptelasma, and Trocholites, of which only Strophomena and Corynotrypa appeared in more than one sample. Specimens of Brongniartella and Leptaena were also identified, but were not included in analysis because they were generally found as isolated specimens.

During analysis all gastropods were grouped together, due to the high frequency in which they were identified in cross section. While the vast majority of the individuals found were in the genus Hormotoma, other genera also contributed to this group, including Liospira, Lophospira, and many unidentified specimens. Atrypid brachiopods, including Zygospira and another atrypid brachiopod (c.f. Anazyga) were also grouped together due in part of identification difficulties but also to enable comparisons with other studies. The fine ramose and robust ramose bryozoans were combined into a single group for analysis, due to inconsistencies in differentiating the morphotypes. Trials run with the fine ramose and robust ramose bryozoans divided yielded similar results to the combined group. After taxonomic
grouping, and the removal of rare taxa and small samples, the final data set contained 84 samples and 33 taxa or morphotypes.

As weathering and exposure of the carbonates restricted most collecting to bedding surfaces, taxa exposed on vertical faces perpendicular to bedding were separately recorded and combined with fossil counts to determine stratigraphic ranges. This data was compiled into a meter scale faunal log for the Reedsville section, with the relative abundances of the fauna recorded as either present or abundant.

Field collection data was then compared with two other regional studies of similar age, tectonic, and depositional histories; Trenton Group in New York (Titus, 2007) and Kentucky (Patzkowsky & Holland, 2004). The Holland and Patzkowsky (2004) data are from the Lexington Limestone of the Cincinnati Arch, which is a generally contemporaneous or younger set of strata (M5-C1 sequences), while the Titus (2007) data are from Lewis County in New York State, and were all from the somewhat younger (M6) Denley Limestone (Fig. 5). The spacing of these locations allows for the comparison of communities over a range of approximately 1000 km, which is far greater than that of any comparable studies.

Differences in taxonomic treatment between the three studies used required some simplification of the faunal lists from Titus (2007) and Holland and Patzkowsky (2004) to make them comparable before analysis. These alterations are largely in line with those reported by Holland and Patzkowsky in 2004 (e.g. grouping bryozoans other than Prasopora by class or morphology, combining atrypids, and lumping gastropods), but includes some additional steps, including grouping the crinoids, and the combination of inarticulate brachiopods into a single group. Additionally, taxa occurring in less than 2% of samples were removed (Escharopora, Eridorthis, and Orthorhynchula), as were the bivalves, which were almost completely absent from the Pennsylvanian samples. Samples taken from the sand shoal facies (four samples from
Holland & Patzkowsky, 2004) were discarded as well, as these were found only in the Kentucky collection, and would represent an environment not found in Pennsylvania.

### 2.2 Analytical Methods

Analysis of the fossil collection data was all performed using R version 2.11.1 (The R Foundation for Statistical Computing, 2010). Two-way cluster analysis was performed using the R hheatmap package (version 0.6.1) to identify groups of samples with similar faunal compositions (Q-mode analysis), as well as groups of taxa which tended to occur together (R-mode analysis). Prior to Q-mode analysis, the data was relativized by row totals in order to make samples of different sizes comparable. Before R-mode analysis, the data was also relativized by row totals, and then by column maximum in order to reduce the differences between rare and very abundant taxa.

The Sørenson, or Bray-Curtis, distance metric was used for cluster analysis. Quinn and Keough (2002) recommend this metric for ecological data sets in order to avoid showing similarities between samples with no shared species. The Sørenson distance, signified by $D_{i,h}$, is a measure of the dissimilarity between the samples $i$ and $h$, as a factor of the taxa included in those samples. A dissimilarity measure is a means of quantifying how far apart two samples are when plotted in multidimensional space. Sørenson distance is a city-block metric that determines the total distance between samples as a combination of the distances in each dimension. This city-block distance is then expressed as a proportion of the total distance possible, as shown below in (2.1).
The linkage strategy used here was Ward’s method, due to its usefulness in creating space savings clusters with minimal chaining (McCune & Grace, 2002). Ward’s method is a combinatorial linking strategy, in which groups are formed by fusing objects in such a way so as to minimize increases in the error sum of squares (McCune and Grace, 2002). Creating clusters takes place by first determining the error sum of squares for all potential combinations. The fusion resulting in the smallest error sum of squares is joined first, and the process is then repeated for all objects. R-mode analysis of the dataset, in which the data is transposed in order to study taxonomic associations instead of similarities of samples, is performed in the same manner as described above. Some sources (Romesburg 1984) claim that Ward’s method is not appropriate for use with the Bray-Curtis dissimilarity metric, which should only be used with Euclidean distance. However, other researchers (McArdel & Anderson, 2001; Quinn & Keough, 2002; Singh et al, 2010) have demonstrated its effectiveness, as has experimentation during this study.

Detrended correspondence analysis (DCA) is the ordination method used to extract and identify environmental gradients from collected samples. DCA simultaneously ordinates the samples (rows) and columns (taxa) of a data matrix. The underlying algorithm is based on reciprocal averaging, which begins by randomly assigning scores to the sample units. Species scores are then determined as follows (2.2), where x is the randomly assigned scores, a_j is the total for species j, and y_j is the weighted average for species j. This equation, and the others following, come from McCune and Grace, 2002.

\[
D_{bh} = 1 - \frac{2 \sum_{j=1}^{p} \text{MIN} (a_j, a_{nj})}{\sum_{j=1}^{p} a_j + \sum_{j=1}^{p} a_{nj}}
\]
The new site scores are then calculated using the weighted average of the species score, as shown below in (2.3). In this step, \(a_i\) is the total for sample unit \(i\), and the rest of the variables are as stated above in equation 2.1.

\[
y_j = \frac{\sum_{i=1}^{n} a_{ij} x_i}{a_{ij}}
\]

(2.2)

The site score is then centered (2.4) and standardized (2.5) so that mean is equal to zero, while the variance is set to equal 1.

\[
\sum_{i=1}^{n} a_{ij} x_i = 0 \quad \text{(2.5)}
\]

\[
\sum_{i=1}^{n} a_{ij} x_i^2 = 0 \quad \text{(2.4)}
\]

This process is then repeated until the results stabilize and converge. This method of reciprocal averaging to find the sample and species scores implicitly relies upon a chi-square distance measure to determine the dissimilarity between samples, as described in (2.6).

\[
X_{ij}^2 = \sqrt{\sum_{j=1}^{p} \frac{1}{a_{++}} \left[ \frac{a_{ij}}{a_{ij} - a_{ij}} \right]^2}
\]

(2.6)

The steps above lead to the completion of Correspondence Analysis (CA) by means of Reciprocal Averaging. DCA is a further refinement of CA, in which some of the more serious problems with CA are corrected. CA often produces an arched plot, where the arch is largely a product of distortion of the first axis along the second axis. DCA removes this arch by detrending, where the axis is divided into segments and the mean score of each segment is
equal to zero. Another problem with CA is the tendency for the ordination to be compressed at either end of the axis. DCA fixes this by rescaling the axis so as to make within-sample variation comparable in magnitude.

Diversity of the central Pennsylvanian biofacies was calculated as the total number of species (S) in a sample, which can be determined by either simply counting them, or by extrapolation using the number of rare taxa to estimate the number of “hidden” taxa, such as with Chao richness (Chao & Shen, 2003). Both of these methods were used, but the Chao richness was only used to calculate total diversity for the biofacies, and not for the individual samples. Additionally, this method will underrepresent the number of hidden taxa, as the data set already had some very rare taxa removed for analysis. The species richness reported in the biofacies analysis is based on the mean richness of the individual collections. Chao richness was calculated using the specpool function in the Vegan package for R.

Evenness is estimated using Pielou’s J, which is simply ratio between the Shannon diversity index (H’) and H’ max, as shown below (Buzas & Hayek, 2005) (2.7):

\[ J' = \frac{H'}{H'_{\text{max}}} \]  

(2.7)

\( H' \) is the number derived from the Shannon Diversity Index (equation 2.8) where

\[ H' = - \sum_{i=1}^{R} p_i \log p_i \]  

(2.8)

and \( H'_{\text{max}} \) is the maximum value of \( H' \), which is found through equation 2.9:

\[ H_{\text{max}} = - \sum_{i=1}^{S} \frac{1}{S} \ln \frac{1}{S} = \ln S \]  

(2.9)
Compositional differences between samples collected at different locations were tested using \textit{vegdist} and ANOSIM (Analysis of Similarities) in the Vegan package (version 2.0-6) for R. Vegdist was used to produce the Jaccard distance, a measure of dissimilarity between sample sets. The Jaccard distance is the inverse of the Jaccard similarity, also known as the “Coefficient of Community” (Sepkoski, 1988), which is the ratio of the number of taxa shared between two samples to the total number of taxa. This distance measure is a city block metric, and can be derived directly from the Bray-Curtis dissimilarity (equation 2.1) as shown in equation 2.10, where $D_J$ is the Jaccard dissimilarity, and $D_{ih}$ is the Bray-Curtis dissimilarity.

\begin{equation}
D_J = \frac{2D_{ih}}{1 + D_{ih}}
\end{equation}

(2.10)

ANOSIM also uses the Bray-Curtis dissimilarity (equation 2.1) to create a rank order of dissimilarities between samples. Between-group and within-group dissimilarities are then compared to determine if samples of different groups are significantly more dissimilar to each other than they are to other samples within their group. This comparison of dissimilarities is described by the statistic $R$, which is defined by equation 2.11, where $r_b$ and $r_w$ are the rank dissimilarities between and within groups, respectively, and $N$ is the number of samples:

\begin{equation}
R = \frac{(r_b - r_w)}{(N(N - 1)/4)}
\end{equation}

(2.11)

The statistic $R$ produced by this equation is constrained between 0 and 1, with a score of 0 indicating no difference in the between and within group rankings, while a score of 1 indicates that all samples within each group are more similar to each other than to any sample found in another group. This observed $R$ value is then compared against a set of $R$ values created by repeatedly randomizing dissimilarity values, in order to determine if the results are statistically significant. In this study, the random set of $R$ values was calculated by randomizing
dissimilarities 1000 times. If the observed $R$ value is greater than 95% of all randomized $R$
values, then the result is considered statistically significant. Four rounds of ANOSIM
calculations were conducted, in order to compared the dissimilarities between each pairing of
collections (PA:NY, PA:KY, and NY:KY), as well as a comparison of all three studies against each
other. The $R$ values produced by each trial give a general indication of how dissimilar the
samples in any collection are from those of any other collection.
Chapter 3: Results

3.1 Lithofacies Descriptions and Interpretations

Field study of the Reedsville, Lemont, and Spring Mills sections was used to describe lithofacies found in the Nealmont through Coburn Formations. Detailed stratigraphic columns for the Reedsville and Lemont sections can be found in Appendix B.

3.1.1 Sub-Trenton units: Nealmont Formation

Facies 1: Nodular limestone: Thickly bedded fossiliferous nodular mudstones and wackestones. Few thin, shaly interbeds occur throughout, along with skeletal packstones near the base. Bedding is sharp to wavy, and the mudstones are highly bioturbated. Numerous fossils include brachiopods, bryozoans, and gastropods, with the large hyperstrophic Macurrites gastropods particularly abundant. No fossil collections were made in this lithofacies, but it provides a context to interpret the path of the environmental changes of the middle Mohawkian.

The nodular limestone facies is interpreted as having been deposited at or below the lower shoreface. While not studied in depth here, previous workers have interpreted the Nealmont as deposited in the middle to outer reaches of a distally steepened ramp (Laughrey et al., 2004), between fair weather wave base and storm wave base. The transition from wavy bedded carbonates to nodular carbonates is further interpreted as indicating an increase in water depth across the Nealmont Formation, ending in the outer ramp (Laughrey et al., 2004). Additionally, Wahlman (1992) has attributed the similar nodular bedding, wackestones and
packstones of the Grier Member of the Lexington Limestone (Kentucky) to burrowing in a shallow subtidal environment. While the Nealmont is here interpreted as having been deposited below fair weather wave base, this does agree with its placement at the shallower end of this environment. The high degree of bioturbation indicates normal marine conditions and low sedimentation rates.

3.1.2 Salona Formation

**Facies 2: Homogenous wackestone:** Dark gray to black, weathering to light gray, medium to thickly bedded (25-100 cm) sparsely fossiliferous wackestone with thin to medium interbeds of argillaceous limestone or calcareous shale interbeds (Fig. 7). This facies contains isolated skeletal elements comprised of trilobites, brachiopods, bryozoans, crinoids, nautiloids, and gastropods, with occasional shell beds primarily restricted to shale interbeds. Wackestone beds typically lack visible structures, but some plane-parallel laminations occur. Upper and lower contacts of wackestones are gradational with interbeds, but are sharp when shale interbeds are absent. Bioturbation is not apparent, but a general lack of obvious bedding structure implies high degree of biotic reworking.

This facies is interpreted to be deposited in the deep subtidal, below fair weather wave base and likely below typical storm wave base. The thick, heavily bioturbated beds of wackestone are interpreted to represent the recrystallized background sedimentation of carbonate muds transported to deeper water from the carbonate bank up-ramp. The argillaceous and shaly interbeds with the higher fossil content represent periods of reduced flux of carbonate mud, resulting in slower accumulation of largely argillaceous sediment. The faunal scarcity has been interpreted by some to indicate high salinity in a shallow restricted basin (Arens & Cuffey, 1989) but the occasional thick fossil bed of *Prasopora*, along with
abundant bioturbation, suggest at least periods of normal circulation. The preservation of numerous K-bentonites relative to the overlying strata also support the interpretation of a location below fair weather wave base, and potentially below storm wave base as well.

Figure 7: Bedding in the upper New Enterprise Member (Facies 2) at Reedsville (24 m). Carbonate beds are largely homogenous, with little apparent structure. The New Enterprise/Roaring Spring contact is visible as the dark, fissile shale bed in the top right of the image. Jacob’s staff is 1.5 m in height.

Facies 3: Laminated mudstone: Gray to dark gray, weathering to light gray or tan, medium bedded calcareous mudstone, deposited in distinctive cyclic sedimentary pattern. An idealized version of this pattern is shown in Fig. 8, however the version typically seen in Facies 3 is missing all or most of section FL (fossil lag). Cycles often begin with a thin bioskeletal lag consisting of brachiopod, bryozoan, and trilobite fragments, topped with plane-parallel and wavy laminations which may be contorted by convolute bedding, flame structures, and other soft sediment deformation features at the base. This is overlain by cross stratification (often small-scale hummocky), the upper portion of which typically contains burrows (primarily
Chondrites) filled with argillaceous material. This argillaceous mud may continue for several centimeters before being truncated by an undulatory, erosive contact with another cycle. Cycles may be missing fossil lags, convolute bedding, or capping argillaceous mudstone. Lower in the Roaring Spring Member, this facies is more likely to be missing many of these features (Fig. 8), and often appears as a bioturbated and largely featureless mudstone with argillaceous interbeds. Moving up through the member, the convolute bedding, hummocky cross bedding, Chondrites, and fossil lags become more common (Fig. 9). Overall cycles may be between 10 and 30 cm, but are typically less than 20 cm (Fig. 10).

Figure 8: Idealized bedding pattern of Facies 3 and 4. Arg: argillaceous mudstone or calcareous shale, in situ brachiopod and bryozoan fossils may be present; HCS: hummocky cross laminated mudstone, burrows (typically Chondrites) may be present; PL: planar laminations, may show convolute bedding and soft sediment deformation; FL: fossil lag, may contain micritic intraclasts not always present. In Facies 3, this pattern is most commonly found without FL, while Facies 4 more typically contains both a strongly erosive base and a fossil lag.

The laminated mudstone facies was deposited in the deep subtidal of a distal ramp. While below average storm wave base, storms of higher intensity periodically reworked the sediments, producing cyclically repetitive beds which are interpreted as distal tempestites.
Bromley & Ekdale (1984) have interpreted abundant Chondrites trace fossils such as those found here as indicating anoxic conditions, but this likely reflects the character of the sediment layers and not the overlying water, as these trace fossils have been found associated with tempestites in many environments (Vossler & Pemberton, 1988). Vossler and Pemberton (1988) suggested that these ichnofossils are a feeding trace from the mining of organic matter trapped in the oxygen-depleted sediments deposited during storm events. The fact that these trace fossils are always found in the same relative position in the repeated depositional cycles (at the interface between the cross-bedded carbonates and the overlying argillaceous mudstone/calcareous shale) supports this interpretation, but does not rule out deposition from turbidity currents. Skeletal material is typically disarticulated and shows low to moderate breakage, but little abrasion. A study by Brett and others (1997) looking at the preservation of fossil echinoderm material described several “taphofacies”, which linked preservational features of fossils with depositional environment. The preservation of the echinoderm fossil remains in the laminated mudstone facies shares some similarities with the both the “deeper, storm influenced shelf (ID)” and “distal ramp (IE)” echinoderm taphofacies, but with a higher degree of disarticulation, suggesting a longer residence time on the substrate surface and a correspondingly lower sedimentation rate. While none were found during this study, an articulated Dendrocrinus was found in the Spring Mills outcrop deposits of this facies (R. Cuffey, personal communication, May 2012).

The carbonate components of this facies represent sediments remobilized by storm events, while the argillaceous and shaly interbeds were deposited through the background sedimentation of terrigenous-derived siliciclastics. The abrupt decrease in bedding thickness and decrease in bioturbation compared to the underlying homogeneous wackestone suggest that this facies may have been deposited at greater depth, despite the more apparent influence
of storms on the sediments. These changes may be the result of the more restricted flow in the New Enterprise giving way to increased circulation as the Sebree Trough (Fig. 2) connected with the forming Pennsylvania Embayment (Keith, 1989; Kolata et al., 2001), which could have also directly influenced storm activity by altering surface water temperatures (Witzke, 1990; Brett et al., 2004).

![Bedding in the lower Roaring Spring (Facies 3) at Reedsville (54 m). Many of the sedimentary structures visible further up in the member are either lacking or greatly reduced here. Chondrites and planar laminations are present, as are the erosive bases between cycles. Jacob’s staff marked in 10cm divisions.](image)

**Figure 9:** Bedding in the lower Roaring Spring (Facies 3) at Reedsville (54 m). Many of the sedimentary structures visible further up in the member are either lacking or greatly reduced here. *Chondrites* and planar laminations are present, as are the erosive bases between cycles. Jacob’s staff marked in 10cm divisions.
Figure 10: Stacked tempestite beds at Reedsville (67 m) with abundant *Chondrites*, convolute bedding, planar laminations, and hummocky cross bedding (Facies 3). Divisions on Jacob’s staff are at 10 cm intervals.

Figure 11: General bedding of the Roaring Spring Member at Reedsville. Jacob’s staff is 1.5 m.
3.1.3 Coburn Formation

**Facies 4: Packstone and mudstone:** Generally very similar to Facies 3, but with the addition of a packstone unit: Gray to dark gray, weathering to light gray, medium bedded argillaceous mudstone, typically deposited in a repetitive cyclic pattern (Fig. 12). Cycles typically begin with a poorly sorted skeletal packstone to rudstone, which often incorporates sub-rounded to rounded rip-up clasts of medium to light gray mudstone (Fig. 13). Packstones pinch and swell laterally, and are often limited in extent to scales visible in the outcrop (<10s of meters). This is topped by planar laminated mudstone or wackestone, which may exhibit convolute bedding, flame structures, and other soft sediment deformation features. This is overlain by hummocky cross stratification, with burrows and feeding traces (primarily *Chondrites*) often abundant and filled with shaly or argillaceous material. This is then capped by dark gray calcareous shales, which are typically truncated by an erosive contact where another cycle begins. Cycles may be missing fossil lags, convolute bedding, or capping argillaceous mudstone. Overall cycles are typically between 10 and 50 cm thick.

The packstone and mudstones of the Coburn are indicative of a shift to a higher energy environment from the finer grained carbonates and thinner bioskeletal stringers found in the subjacent facies. This suggests a general shallowing, with an increasing influence of storm action on the sediments creating the rudstones and packstones as they reworked shell beds and hardgrounds. The bioskeletal material in packstones and rudstones often shows moderate abrasion and breakage, suggesting that it has been reworked multiple times (Einsele & Seilacher, 1991). The fossil beds compare favorably to the “storm dominated ramp (IC)” echinoderm taphofacies of Brett and others (1997). The increase in the number and thickness of these rudstones and packstones while moving up through the Coburn suggests continuing shallowing through this interval. The thickening of the event beds that began in the Facies 3
continues here, concurrent with a general coarsening upwards trend, suggesting the amalgamation of storm beds as the basin shallows (Einsele, 1998). Additionally, the dramatic reduction of K-bentonites suggests that the Coburn was deposited above storm wave base, allowing for the reworking of ash beds in some areas but not others, dependent on local topography and the vagaries of the storm paths (Cuffey, 1997; Ver Straeten, 2004), although a decrease in volcanism would have the same result. The cyclic depositional pattern of this facies also contains abundant *Chondrites* trace fossils occurring in the same relative position, supporting a tempestite interpretation.

![Figure 12: Bedding of the Coleville Mbr. of the Coburn Fm. at Reedsville (119 m). Jacob’s staff is 1.5 m. Note the warping of the bedding planes, which increases above this point.](image-url)
3.2 Cluster Analysis Results

3.2.1 Q-Mode results:

Q-mode cluster analysis divides the samples into seven groups, which are used to define biofacies (Fig. 14). Owing to the relatively narrow band of the environmental gradient that these collections represent, many of the dominant taxa appear in most of collections, particularly *Sowerbyella*, *Dalmanella*, crinoids, and the ramose trepostome bryozoans. Descriptions of each biofacies include the mean richness (S) when samples are rarefied at 20 individuals, along with the evenness score for the entire biofacies as measured by Pielou’s J. The diversity metrics for each biofacies are shown in Appendix C, along with mean DCA axis 1 scores of samples in each biofacies, which are discussed further below.
**Ramose Bryozoan (RB):** The samples in this cluster all contain abundant ramose trepostome bryozoan colonies, along with *Dalmanella* and crinoids. *Sowerbyella* and a diverse suite of trilobites, including *Flexicalymene, Ceraurus,* and *Isotelus,* are also common here. All ten samples from this biofacies were collected in the Coburn, and all but two of these are from the Milesburg Member. This biofacies has a high diversity (7.1) and a moderate to high evenness (0.70).

**Cryptolithus (CR):** The biofacies characterized by an abundance of *Cryptolithus* occurs in only 5 samples, and is found in both the Roaring Spring Member of the Salona Formation and the Milesburg Member of the lower Coburn Formation. Also found in all of these samples are ramose bryozoans, crinoids, and *Dalmanella,* and with *Sowerbyella* and *Rafinesquina* occurring in more than half of the samples. The three samples with *Rafinesquina* both come from the Milesburg Member, while the two without come from the Roaring Spring. All samples in this biofacies are from the Reedsville section. This biofacies has a moderate diversity (6.7), combined with the highest degree of evenness (0.79).

**Dalmanella (DA):** This cluster is defined by a high abundance of dalmanellids relative to the other taxa, but is also characterized by common *Sowerbyella,* with *Cryptolithus,* crinoids, and ramose bryozoans also found in most samples. The cluster contains seven samples, most of which are from the Roaring Spring Member, but with one each coming from the Milesburg and Coleville Members of the Coburn. All samples in this biofacies are from the Reedsville section. This biofacies has a moderate to low diversity (5.9), and moderate evenness (0.62).
Figure 14: 2-way cluster analysis of faunal counts. Faunal clusters are grouped into biofacies. RB: ramose bryozoan; CR: Cryptolithus; DA: Dalmanella; DSb: diverse Sowerbyella/Bryozoan; DSD: diverse Sowerbyella/Dalmanella; O: ostracod; SO: Sowerbyella; GA: gastropod.
Diverse Sowerbyella (DS): The diverse Sowerbyella biofacies represents the largest cluster. The presence of Sowerbyella in every sample is a unifying trait of this cluster, but this genus makes up a smaller percentage of the total number of individuals than it does in the Sowerbyella biofacies. Also abundant in the majority of these samples are Dalmanella, crinoids, ramose bryozoans, and Cryptolithus. The diverse Sowerbyella biofacies can be further subdivided into the diverse Sowerbyella/ramose bryozoan biofacies (DSb) and the diverse Sowerbyella/Dalmanella biofacies (DSd). These biofacies are rather similar, but they occur at different stratigraphic locations, with the DSb occurring primarily in the Coburn, while the DSd is found mainly in the Roaring Spring Mbr of the Salona. This is particularly interesting when compared with the results of the Holland and Patzkowsky (2004), where Sowerbyella showed a preference for deeper environments than either Dalmanella or the ramose bryozoans. The appearance of Dalmanella and Sowerbyella together in the Salona (here interpreted to be deeper than the overlying Coburn) supports this interpretation of their preferred depths. Additionally, the increase in abundance of the ramose bryozoans in the Coburn, where they become more dominant at the expense of the dalmanellids, supports the interpretation of a shallowing environment. The dalmanellid’s abundance declined as the waters shoaled out of their preferred habitat, but they did not completely disappear. Despite the break in the DS biofacies, these two subclusters are hereafter treated as a single biofacies as explained below in the discussion of DCA scores. This biofacies has a moderate diversity (6.6), and a relatively low evenness (0.61).

Ostracod (O): This cluster, comprised of eight samples, is distinguished by a high abundance of ostracods, along with Sowerbyella and ramose bryozoans. Other common taxa in these samples include Skenidioides, Tentaculites, rhombiferans fragments (c. f. Cheirocystis), Dalmanella, Conularia, and crinoid ossicles. While not included in the dataset, the hexactinellid
spicules described below (section 4.3) come primarily from samples found within this biofacies. The composition of the samples in this biofacies differs greatly from the others. These samples come primarily from the Roaring Spring Member, with five from Reedsville and two from the Lemont section. One sample was found in the Coleville Member, but aside from the abundant ostracods this sample appears to be very similar to the ramose bryozoan (RB) biofacies that is very common in the Coburn Formation. This biofacies has by far the highest diversity (9.3), as well as a high evenness (0.77).

**Sowerbyella (SO):** This cluster is defined by a high relative abundance of *Sowerbyella*. Other common taxa include ramose bryozoans, *Dinorthis, Dalmanella, Isotelus*, and crinoid ossicles. *Sowerbyella* is common through most of the samples in this study, but increases in abundance to account for over half of all specimens in this cluster. The samples were almost entirely from the Roaring Spring Member, and while most were from Reedsville, it includes samples from Lemont as well as over half of the Spring Mills samples. This biofacies has a low diversity (5.6) and the lowest evenness (0.57).

**Gastropod (GA):** This cluster is defined by the abundance of gastropods, primarily of the genus *Hormotoma*. This makes it one of only two biofacies defined by a taxon not in Cluster 2 of the R mode analysis, but *Dalmanella* is also present in all samples. Other common taxa include ramose bryozoans, crinoids, *Sowerbyella, Prasopora, Rafinesquina*, orthoconic nautiloids, and *Flexicalymene*. This is the biofacies with the second most samples, but this is largely due to a highly productive fossiliferous zone at approximately the 140-145 meter mark in Reedsville. All of the samples in this biofacies were collected from Reedsville, specifically the Coleville Member of the Coburn, which was here only studied at Reedsville. This biofacies has a low diversity (5.9) and a moderate evenness (0.63).
The biofacies were also compared through the use of rarefaction and species accumulation curves, which are included in Appendix D. The rarefaction curves were performed for each sample within the biofacies, while the species accumulation curve was performed for the entire biofacies. They both show a clear pattern of diversity similar to that described above. The ostracod biofacies has by far the greatest diversity, with the diversities of the other biofacies much more similar to each other. The lower diversity of Cryptolithus biofacies in the species accumulation curve may be the result of these samples having lower total abundances than the samples of any other biofacies.

3.2.2 R-Mode Results:

R-mode cluster analysis yielded three clusters of taxa that tend to co-occur (Fig. 14). Cluster 1 is composed of rhombiferans, Conularia, Encrinurus, Tentaculites, Skenidioides, inarticulate brachiopods, spined crinoids, the unidentified fossil dubbed “Hat Thing” due to its distinctive shape (suspected to be an echinoderm fragment), and a catch-all group of the indeterminate bryozoans. While not containing any taxa that are common enough to lend their names to a biofacies, almost all of the taxa are found most commonly in the Ostracod biofacies described above. No other R-mode cluster is as closely tied to a single biofacies as is Cluster 1. These taxa almost all reach their peak abundances in the lower Roaring Spring Member.

Cluster 2 is composed of Cryptolithus, the ramose bryozoans, simple round crinoids, Dalmanella, and Sowerbyella. These taxa are by far the most ubiquitous in this collection, and it is their relative abundances, not simply presence or absence, that differentiate most of the biofacies. Cryptolithus is the only taxon from this cluster that is largely absent from some biofacies, as it is uncommon in the ramose bryozoan, Sowerbyella, and gastropod Q-mode clusters.
Cluster 3 contains all of the remaining taxa, which are distributed through all biofacies. Gastropods and ostracods are the only common taxa in this cluster with a strong environmental signal, reaching peak abundances in the biofacies that bear their respective names. As these two important taxa occur in samples from very different environmental conditions, this cluster does not appear to be ecologically significant.

3.3 DCA Results:

Detrended correspondence analysis was used to extract and identify environmental gradients. DCA axis 1 scores for individual samples are plotted against the Reedsville stratigraphic column and faunal log in Fig. 15. The samples were coded by geologic member, which broadly correspond with depositional environment: the Roaring Spring is interpreted to be deeper than the underlying New Enterprise, and is followed by an overall shallowing trend through the Milesburg and Coleville. The similarity in the depositional environments, with most, if not all of them falling within the deep subtidal zone, made distinguishing them by member name most practical. Typically in ecological studies of collections along a depth gradient, the first DCA axis reflects depth (Webber, 2002; Holland & Patzkowsky, 2004), which seems to apply here, with negative DCA axis 1 scores corresponding to deeper water lithologies, and positive scores with shallower environments (Fig. 16). The narrow depth gradient of this study does not preclude the effectiveness of this approach, as illustrated by Holland et al. (2001), and in this case it appears to show a detectable, dampened depth signal. The samples from the New Enterprise Member ended up with intermediate DCA axis 1 scores and plot in the middle of all samples, which corroborates the inferred moderate depth, despite the small number of samples (3) from the New Enterprise. Another potential issue for this
member was the grouping of all gastropods together prior to analysis, as observations not included in the analysis found *Liospira* and other unidentified gastropods in addition to the dominant *Hormotoma*. Above the New Enterprise Member, the scores reflect the interpreted shallowing upwards transition from the Roaring Spring through the Coleville. While the lack of definite divisions between the samples from different environments may be partially attributable to the limits of constraining float, other researchers have had similar results (Holland and Patzkowsky, 2004) which they suggest may reflect community patchiness. The detection of a depth gradient that agrees with lithologic interpretations despite these confounding issues implies that the depth related signal is indeed robust.

When the samples are analyzed according to biofacies membership, the DCA plot illuminates the relationship between biofacies and the depth gradient ([Fig. 17](#)). The clusters with the lowest DCA axis 1 scores, the ostracod biofacies and the *Sowerbyella* biofacies, were collected from the deepest facies, and support the interpretations of negative axis 1 scores as corresponding to greater water depths. Additionally, the gastropod biofacies samples were collected from a shallower location in the deep subtidal facies, and generally have the highest axis 1 scores. The scores of the *Cryptolithus* and the diverse *Sowerbyella* biofacies fall intermediate of the extremes, as do their lithologically interpreted depths. The *Sowerbyella* and diverse *Sowerbyella* biofacies plot immediately adjacent to each other, suggesting that as depth decreased, the dominance of *Sowerbyella* waned and other taxa increased in abundance. The diverse *Sowerbyella* cluster, when divided into the two sub-clusters discussed above, still plots in a tight grouping. While the sub-clusters occur at different stratigraphic levels, this does not translate into a difference in DCA axis 1 or 2 scores. This analysis shows the preferred depths of the taxa, yet also indicates that the biofacies do not form solely in response to changing depth. Specifically, the ramose bryozoan biofacies and the *Dalmanella* biofacies do
not appear to follow the axis 1 depth trend as strictly. The Dalmanella biofacies was found primarily in the Roaring Spring Member, and are interpreted as coming from a more distal position on the ramp than the ramose bryozoan biofacies samples, which come almost exclusively from the shallower Coleville Member. However, the positions of these biofacies are reversed along axis 1, while still close and overlapping.

The relationship between DCA axis 1 scores and depth of deposition makes it possible to estimate how the individual taxa interact with changing water depth. DCA scores both the sample and species on the same scale, allowing for direct comparison of their relative positions. Use of DCA axis 1 scores as a proxy depth data for taxa has previously been applied to ecological datasets to model the environmental preferences of organisms along a gradient (Holland et al., 2001; Holland & Patzkowsky, 2004). Three parameters identified by Holland (1995) define a probabilistic curve describing the likelihood of collection at different relative depths. Preferred environment (PE) is taken from the axis 1 score for each taxon, which is derived from the sample scores in which each taxon is found. As lower axis 1 scores are correlated with deeper conditions, a lower PE score indicates an organism that prefers to live at greater depths than an organism with a higher PE score. Environmental tolerance (ET) is found by calculating the standard deviation of all samples in which each taxon is found, and is a range around the PE where the taxon is most likely to be found. Organisms with more stenotopic life modes will have lower ET scores, while organisms that are tolerant of a broader range of depths will have higher scores. Peak abundance (PA) is determined by the percentage of samples within the ET range in which the taxon is found, and is the abundance-dependent likelihood of collecting the taxon at its preferred environment. Each taxon's values for PE and ET scores are shown in Figure 18, but the low abundances of many taxa prohibited calculation of PA scores, preventing their inclusion.
DCA axis 2 scores, although not as robust of a signal carrier as DCA axis 1 due to inherent distortions of higher axes (McCune & Grace, 2002), here appear to show some environmental information. The splitting of the *Sowerbyella* and ostracod clusters along axis 2, despite the similar depth estimates, does reflect a difference in stratigraphic position within the lower Roaring Spring Member. Similarly, the three samples from the *Cryptolithus* biofacies that cluster lower on axis 2 are stratigraphically lower than the other two samples. A regional shift from tropical to temperate style carbonates and a potentially associated regional extinction have been linked to the time near deposition of the Deicke metabentonite by several authors. Herrmann and others (2010) place it just below the Deicke, Holland and Patzkowsky (1996) place it just above the Deicke at the M4/M5 sequence boundary, while Mitchell and other (2001) place the M4/M5 sequence boundary just above the Millbrig metabentonite. Although the location of this transition from tropical to temperate conditions is not completely clear, or even whether this shift also occurred in central Pennsylvania, the consensus appears to be that it can best be correlated to somewhere within the Salona Formation. Therefore, DCA axis 2 possibly contains information on the associated changes. Other than the lower DCA axis 2 scores of the ostracod samples and most of the *Cryptolithus* samples, this axis does not appear to convey much information. The spread seen in the samples of the gastropod biofacies on the right of the plot is less likely to be a true signal, as the primary cause for outliers with the high axis 2 scores appears to be the inclusion of relatively abundant atrypid brachiopods. These brachiopods were only occasionally found in low abundance throughout the section, but show unusually high abundances in the two samples with the highest axis 2 scores.
Figure 15: Faunal log and DCA axis-1 scores of the Reedsville section. DCA axis-1 sample scores are shown on the right. Trilobites are shown in blue, brachiopods are shown in red, bryozoans are orange, echinoderms are green, and all other taxa are black. The number of samples collected at each horizon is indicated on the left.
Figure 16: DCA axis-1 and axis-2 samples scores coded according to geologic member. The member designation also corresponds with the lithofacies assignment.

Figure 17: DCA axis-1 and axis-2 samples scores coded according to biofacies, as shown in Figure 13.
Figure 18: Ecological parameters calculated for taxa found in Reedsville, Lemont, and Spring Mills collections. Preferred Environment is shown by the DCA Axis 1 scores for each taxon. Environmental Tolerance is shown by the width of each taxon’s bar. Peak Abundance is excluded due to numerous taxa occurring in too few samples for calculation.
Chapter 4: Discussion

4.1 Environmental Gradient

When a community assembles in a particular time and place, many factors may influence taxonomic composition and relative abundance. In a marine setting these factors include interactions between the organisms and their physical environment (temperature, light levels, chemical properties of the seawater, turbidity, water energy, sedimentation rates, salinity, etc., and the variability of these characteristics) as well as interactions between the organisms making up the community (predation, competition, structural roles, etc.). In addition to the physical forces at work while the organisms were alive, later alteration of the environment (e.g. storm activity, bioturbation, mass wasting) can rework, mix, and degrade the skeletal remnants of these organisms before they are preserved in the fossil record, and have the potential to overprint the original depositional signature (Lehman & Pope, 1989; Finnegan & Droser, 2008). This makes the analysis of the sedimentary record vital, in order to differentiate between the multiple forces influencing the deposition and preservation of the sediments and fossils. While previous workers have had some success in determining the depositional environments of the Trenton Group, there is still some debate regarding the trends of relative sea level through this interval (see Arens & Cuffey, 1989 and Slupik, 1999 for opposing views on the New Enterprise environment). The relationships between the facies at a single location, as well as their variation between the outcrops of central Pennsylvania, are here discussed to understand the environmental gradient upon which the organisms were arrayed.
The largely continuous and well preserved exposure of the Reedsville section offers the best chance to understand how the environment shifts over the entire study. Facies 1, the nodular mudstone facies, is the most distinct in terms of its relationship with the adjacent facies. The transition from this deep subtidal facies to the overlying homogenous wackestone of the deeper subtidal to offshore setting is marked by a shift from nodular to massively bedded carbonates, as well as a chert bed at Reedsville.

In the strata overlying the nodular mudstone, even where obvious marker beds identify lithofacies transition, the changes between the facies are generally gradual, while the facies themselves gradually shift in character over their extent. For example, the transition from homogenous wackestone (facies 2) in the New Enterprise Member to laminated mudstone (facies 3) of the Roaring Spring Member is easily identifiable by the presence of a thick shale bed followed by a significant decrease in bedding thickness. This surface likely represents a flooding surface, immediately overlain by a condensed interval of little carbonate sedimentation relative to the background clastic sedimentation. Despite this apparent condensed interval, the lower beds of the Roaring Spring Member (laminated mudstone) are much less fossiliferous than the upper beds, a trait more similar to the underlying New Enterprise (homogenous wackestone) than the upper beds of Roaring Spring Member. They also show fewer sedimentary structures such as planar laminations, hummocky cross stratification, and *Chondrites* ichnofossils, again more similar to the underlying New Enterprise Member. Above this, the transition from the laminated mudstones to the packstone and mudstone (facies 4) at the Salona/Coburn contact is defined less by a major shift in bedding character than simply by the first appearance of thin bioskeletal packstones and rudstones (Thompson, 1963) that increase in thickness and number upsection. The overall similarities
between the lithofacies described in these outcrops likely stems from the broadly similar depositional environments in which they formed.

Overall, the facies represent a general deepening from the Nealmont to the Roaring Spring, followed by a gradual shallowing up to the Coleville. Above the Coleville, renewed deepening causes an abrupt landward shift in lithofacies, drastically reducing carbonate input before the small amount of carbonate washing in from the retreating shelf is eventually completely overwhelmed by the terrigenous siliciclastic sediment in the overlying Antes Shale.

Within this environmental transition, however, some features hint at a more complex history of sea level change. In Reedsville, the preservation of numerous K-bentonites associated with changes in bedding thickness and fossil lags can be used to tentatively identify flooding surfaces that do not result in obvious facies changes. The initial deepening at the Nealmont/Salona contact is marked by a lithologic basinward shift as well as chert nodules and a K-bentonite. The chert formation was likely aided by the presence of the ash bed directly above, which along with other metabentonites in the area may represent flooding surfaces. Support for this interpretation comes from the presence of fossiliferous lags on the bedding surfaces directly beneath some of the K-bentonites. An excellent example of this is found at meter 78 in Reedsville, where abundant Cryptolithus and bryozoan fossils are preserved with a high degree of articulation and low breakage just beneath an ash bed. The carbonate beds above this K-bentonite also show an abrupt thinning, lending further support to the interpretation that this marks a flooding surface. Several other K-bentonites are also situated immediately below abrupt decreases in bedding thickness, such as the Deicke and Millbrig K-bentonites, and those at meters 8, 28 and 60 in Reedsville. The Millbrig K-bentonite has been demonstrated to be the product of multiple eruptive events (Mitchell et al., 2004; Huff, 2008; Adhya, 2009; and Sell & Samson, 2011), a possible result of prolonged exposure on the sea floor.
due to the lower sedimentation rates and reduced energy environment following a rise in sea
levels (Ver Straeten, 2004). It is noteworthy that K-bentonites at Lemont in approximately the
same stratigraphic position as Reedsville meters 8 and 28 (Lemont meters 47 and 75) mark a
similar decrease in bedding thickness, suggesting that they do in fact mark increasing water
depth. While confident correlation of these bentonites requires geochemical analysis, their
relative positions and the similar stratigraphic changes support tentative correlation.

Alternatively, the generally increased preservation of some K-bentonites in the Salona
compared to the subjacent Nealmont and superjacent Coburn may be further support for the
interpretation of an overall deepening across the same interval, as opposed to representing
individual flooding surfaces. In this view, an initial deepening at the Nealmont/Salona contact
would have removed the ash beds from the realm of regular storm influence, with only rare,
massive storms reaching deep enough to stir up the sediments and obliterate the beds, before
later shallowing eventually brought the sea floor back above storm wave base. It seems more
likely that both of these interpretations play a role, with some ash beds preserved due to
abrupt increases in water depth, while others avoid storm influence by chance before burial
(Ver Straeten, 2004), without representing a flooding surface.

Comparing outcrops reveals some variation within the facies, particularly in the
thickness of the members. The New Enterprise Member measured at 30 meters at Lemont, but
only 23 meters at the Reedsville outcrop to the southeast, with five meters of this difference
coming from the interval between the Deicke and Millbrig metabentonites (17 meters at
Lemont compared 12 meters in Reedsville). Thompson (1963) described a generally uniform
thickness of this member, with some minor variation between locations. This difference may
simply be due to the presence of several small scale faults at Lemont that are not seen at
Reedsville, however. Individual carbonate beds in the New Enterprise are slightly thicker at
Reedsville (25 cm to 1 m) than at Lemont (15 cm to 1 m), as are the shale beds. As the bedding divisions appear to be largely dependent upon storm influence, the thicker bedding across a thinner overall interval at Reedsville suggests less frequent storm activity compared to Lemont. Thicker siliciclastic beds at Reedsville also suggest a lower influx of carbonate material relative to terrigenous sediments. These observations support the interpretation of the deeper reaches of the basin being located to the southeast, with Reedsville situated slightly deeper than the coeval portions of Lemont.

In contrast, the overlying Roaring Spring Member appears to thicken to the southeast (Reedsville) in agreement with Thompson’s observations. While not completely exposed at Lemont, the visible portion is condensed compared to the Reedsville section. One line of evidence for this is the location of a hexactinellid spicule zone at the two locations. In Lemont, this bed is located at approximately 15 meters above the top of the New Enterprise Member, whereas in Reedsville these fossils are found primarily at 27 meters above the transition. The lack of a Salona/Coburn contact at Lemont makes detailed comparison of the entire member impossible. However, the change in member thickness implied by the spicule zone agrees with Thompson, who reported an approximate doubling in thickness of the Roaring Spring at Reedsville compared to a nearby outcrop in Oak Hall (less than 1.5 km northeast of the Lemont section). Additionally, the Roaring Spring at Reedsville has slightly thicker bedding in both the carbonate beds and shale interbeds compared to Lemont, as shown in Figures 13 and 14, adding to the overall greater thickness of the member.

Overall, the facies transitions support the interpretation of a rapid deepening at the Nealmont/Salona boundary, followed by a more gradual shallowing through the Coburn. At least two additional periods of deepening likely occurred here, with a flooding surface preserved at the New Enterprise/Roaring Spring contact, and another at the meter 78 K-
bentonite. Preserved ash beds, occasional fossil lags, and changes in bedding thickness suggest multiple smaller changes in water depth during this interval, but these are difficult to distinguish from the abundant storm event beds that comprise much of the strata.

4.2 Ecological Gradient

Faunal assemblage composition changes considerably across the study interval, despite the relatively narrow range of environmental conditions represented in the strata. As the Reedsville outcrop presents the most continuous exposure and was most intensively collected, the ecological changes discussed here are based upon this location unless stated otherwise.

Much of the discussion of ecological structuring stems from the taxa's DCA axis 1 scores and the relation of these scores to the depositional environment. Numerous previous studies support this interpretation of first DCA axis, with the taxa arrayed in a similar order along the lithologically interpreted depth gradient. Holland and others (2001) used DCA of faunal collections to discern relatively minor changes in water depth in the Kope Formation near Cincinnati, Ohio, by capitalizing on the sensitivity of organisms to changes in environmental conditions. Webber (2002) similarly studied the faunal response to changing depth in the Kope Formation, positioning Sowerbyella and Cryptolithus on the “deeper” end of the spectrum, with Isotelus, Dalmanella, and the calymenids (e.g. Flexicalymene) in intermediate position, and the ramose bryozoans and Rafinesquina at the “shallower” extreme. Holland and Patzkowsky (2004) took this a step farther, comparing the relative positions of fauna along DCA axis 1 between studies in order to determine the conservation of ecological preferences across geographic and temporal scales. Both relative DCA axis 1 scores and the ecological parameters derived from these scores are used here.
Focusing only on the taxa that are either generally abundant or that show a strong preference for particular biofacies, the faunal log of the Reedsville outcrop (Fig. 15) shows some of the faunal shifts across the interval. This faunal log was constructed using a survey of the relative abundance of all apparent fossils on the outcrop combined with the Reedsville samples, which were converted to relative abundance values (abundant, present, or absent).

An initial low to moderate diversity assemblage is shown in the New Enterprise Member, where communities are dominated by *Cryptolithus, Dalmanella, Sowerbyella,* and gastropods (including *Hormotoma* and *Liospira.*) These collections cluster in the gastropod and diverse *Sowerbyella* biofacies, but with diversities below the average for collections in these clusters. The taxa in these samples tend to have moderate preferred environment (PE) scores and environmental tolerance (ET) scores. The environmental preferences suggested by the axis 1 scores agree with the interpreted position as approximately in the middle of the depth gradient here, further supported by the flooding surface identified at the New Enterprise/Roaring Spring contact and the relatively thick bedding. However, the low diversity, relative lack of bedding features, and low fossil content that distinguish the Roaring Spring from the similarly located Milesburg Member must therefore instead have resulted from restricted circulation and other environmental conditions.

Immediately above this in the lower Roaring Spring Member, interpreted to represent the deeper end of the deep subtidal environment, diversity dramatically rises to its highest point in the study interval. Samples in the ostracod biofacies were almost exclusively collected from this section. These samples share a unique faunal constituency, with ostracods, rhombiferans, conularids, tentaculids, *Calpytaulax, Skenidioides,* and several other minor taxa appearing in either their highest abundances or their only occurrences. It is also in this area that the M4/M5 sequence boundary of Holland and Patzkowsky (1996) and the associated
regional extinction (Patzkowsky & Holland, 1996) are thought to occur, although these have not been confidently located or even identified in central Pennsylvania. While the significant decrease in diversity above the Ostracod biofacies cannot be definitively tied to the extinction, it does approximately mark the last occurrence in these outcrops of several taxa, including *Skenidioides*, *rhombiferans*, *Encrinurus*, and *Brongniartella*, and is immediately above the only observed occurrence of the genus *Leptaena*. Their disappearance marks a decline in diversity that does not recover for the rest of the section.

The flooding surface topping the New Enterprise Member and the increase in depth that it signals for the lower Roaring Spring Member is also apparent in the succeeding communities. The taxa of the distinctive lower Roaring Spring assemblage have among the lowest PE scores of all fauna studied, along with most of the lowest ET scores recorded, indicating a high specificity in environmental requirements. The low PE scores suggest a deeper environment than the underlying New Enterprise, in agreement with the lithologic interpretation. Additionally, some taxa found in the New Enterprise but not the Roaring Spring, including the gastropod *Hormotoma*, are otherwise found almost exclusively in the shallower environs of the Coburn Formation. *Hormotoma* is thought to have been an algal grazer (Linsley, 1977), while the green algae upon which they likely fed are typically restricted to the waters of less than 30 m (Wray, 1977). The disappearance of *Hormotoma* until the shallower and more energetic waters of the Coburn may result from habitat tracking, with the New Enterprise being deposited higher in the photic zone than the overlying Roaring Spring.

In the upper Roaring Spring Member, after the disappearance of the diverse ostracod biofacies assemblage the community shifts to one more dominated by brachiopods. This results not as much from the addition of more brachiopod taxa (other than *Dinorthis*) as from the disappearance of most echinoderms other than the crinoids, along with most trilobites
other than *Cryptolithus*. The brachiopod *Sowerbyella*, which was already present in almost all samples, here becomes the dominant component of the community, with the *Sowerbyella* then the diverse *Sowerbyella* biofacies becoming common again as depths approach those last seen in the New Enterprise Member. *Dinorthis*, which at Reedsville is common only from the middle Roaring Spring to the lower Milesburg Members, has low PE and ET values that, along with those of the here common *Cryptolithus* and sporadic inarticulate brachiopods, indicate a deep environment that is nonetheless shallower than the lower Roaring Spring.

Above the upper Roaring Spring, the shifts in community composition are relatively minor until around the Milesburg/Coleville transition (meters 110-120). Here the previously ubiquitous *Cryptolithus* declines and eventually disappears, while the gastropods increase significantly. The trilobite *Flexicalymene* also becomes a significant member of the community, while *Conularia*, and to a lesser degree the atrypids and the unidentified “spines” (discussed in section 5.3) increase in abundance. These taxa have moderate (e.g. *Conularia* and “spines”) to high (e.g. gastropods and atrypids) PE scores, supporting the interpretation of decreasing depth. The disappearance of *Cryptolithus*, often considered a deep water genus (Shaw & Lesperance, 1994) provides further support for this interpretation. A generally continuous shallowing is indicated by both lithologic and fossil evidence, and appears to begin at the lower Roaring Spring Member.

The nature of cluster analysis dictates that when analyzing any diverse set of data, multiple discrete clusters will emerge. Previous studies have supported the conclusion that biofacies are not the highly delineated communities resulting from strong interactions between the constituents, but are instead loosely knit groups of taxa that prefer overlapping ranges of environmental conditions (Olszewsky & Patzkowsky, 2001; Holland & Patzkowsky, 2004). Given a smooth and continuous environmental gradient, biofacies would be more likely to
blend gradually into each other than to be separated by obvious discontinuities. The majority of studies that have included biofacies analysis in the marine realm have focused on a relatively broad range of depositional environments, resulting in clearly defined biofacies despite the continuous nature of biotic gradients. Collections from a shallow environment, such as a sand shoal, will likely share only the most eurytopic fauna with those from deeper environments such as the deep subtidal, resulting in profound faunal differences between collections made from end member environments, while assemblages from adjacent environments will share many taxa. However, Holland and others (2001) showed that a biotic gradient can also be detectable along relatively short environmental gradients that are otherwise not apparent from lithologic analysis alone. Similarly, a biotic gradient is readily apparent in this study despite the fact that many taxa (e.g. dalmanellids, *Sowerbyella*, crinoids, ramose bryozoans) are found along the entire depth range, giving the associations a high degree of compositional similarity. It is the relative abundance of these taxa that varies between the different environments, along with the presence appearance and disappearance of rarer taxa.

Depositional and taphonomic variation throughout the study interval must to some degree be imprinted on the preserved communities. Storm activity influence, while virtually non-existent in the New Enterprise, gradually increased through the Roaring Spring and into the Coburn. Storm reworking typically increases the diversity and evenness of assemblages relative to those deposited during background sedimentation, due to the mixing of multiple beds (Finnegan & Droser, 2008). However, as these storm deposits mix the faunal remains into the sediments, the fossils will no longer be visible only along the bedding planes, but are instead exposed along fractures that are not parallel to bedding. Fossil samples from bedding planes are therefore typically deposited either during background sedimentation or are the result of low-energy winnowing, while samples collected from the sides of beds are more likely
to be the result of storm events (Finnegan & Droser, 2008). Most samples collected during this study were from bedding planes, but upsection some samples were collected from the Coburn packstones and rudstones. These often included fossils from the sides of the beds, and therefore reflect more time-averaged communities, particularly among the gastropod biofacies. While this biofacies was more time-averaged, its diversity was no higher than that of most of the other biofacies identified. This is likely due either to the destruction of more fragile faunal remains, or it truly represents a lower diversity community.

Another consideration is that the majority of the samples come from small blocks, generally between 50 and 2500 cm². Bennington (2003) showed that patchiness in marine communities is apparent at the meter scale and above. However, the tendency for samples collected in close stratigraphic proximity to cluster together despite the generally similar depositional environments of the entire outcrops supports the conclusion that the samples accurately reflect the general composition of the communities. Either the communities were relatively homogeneous over small spatial scales, or the effects of time averaging were enough to reduce the influence of patchiness (Finnegan and Droser, 2008).

4.3 Additional Taxa

In addition to those taxa included in the biofacies discussed above, other taxa were identified but were not used in cluster analysis. These include the important marker species *Brongniartella trentonensis*, a homalonotid trilobite that is restricted to the interval between the Millbrig metabentonite and the immediately subjacent metabentonite (“Metabentonite 4”). First identified by Simpson (1890) as *Homalonotus trentonensis* and later described by Collie (1903) as *Brongniartia trentonensis*, this species was subsequently reassigned to the genus
Brongniartella, a move that has been upheld in recent cladistic parsimony analysis (Congreve & Lieberman, 2008). The fossils of this species were primarily collected from highly fissile shale beds in the interval between meters 8 and 16 at Reedsville, as well as from a bed at Lemont which was not precisely located, but was constrained to a similar stratigraphic position. The combination of the fragile character of the shale where the fossils were primarily found, as well as the large size of the trilobite, meant that it was never preserved in a bedding plane with enough other individuals to compose a sample. Despite not being included in any quantitative analysis, this species has been useful at correlating locally and, at the generic level, into Britain (Whitcomb, 1930).

Hexactinellid sponge spicules (Fig. 19) were found in the middle of the Roaring Spring Member of the Salona Formation at all three outcrops, where they have not been previously described. While hexactinellid sponges produce siliceous spicules, attempts at removing them from the matrix with 10% HCl resulted in the rapid dissolution of the spicules, demonstrating that they have been replaced with calcite. All specimens were found as isolated spicules, with no intact sponge fossils discovered. The preservation of opaline silica spicules via biologically mediated replacement with calcite has been observed in modern sponges, but this tends to lead to preservation as nodules (Warnke, 1995) or largely intact individuals (Neuweiler, 2007) as opposed to isolated spicules. However, isolated opaline spicules are prone to rapid dissolution, particularly in the deeper ocean (Land, 1976). Botting and Muir (2011) suggest that rapid burial of siliceous spicules in anoxic or dysoxic offshore sediments will often lead to replacement with pyrite, and subsequent transformation into other weathered iron minerals. This does not appear to be the case in the Roaring Spring, despite the available mechanism for rapid burial (storm events), evidence of dysoxic or anoxic sediments (abundant Chondrites), and an available source of Fe (the abundant ash deposits found throughout the Salona
Formation.) This suggests that early disarticulation of the sponges was followed by rapid burial, where silica degradation would be slower and calcite replacement could take place (Land, 1976). Later reworking of the sediment remobilized the spicules, depositing them in the fossil lags atop the bedding surface. The fragile nature of the spicules suggests that they could not have traveled far (Zhang & Pratt, 2000), and so they represent a species that lived near the depth of deposition.

Calcified hexactinellid spicules are typically found associated with stromatactis rich mud-mounds from the Silurian and younger strata (Bourque & Gignac, 1983; Desrocher et al., 2007; and Lazar et al., 2011). Older siliceous specimens are known from slope-to-basin sediments from the Mid-Whiterockian of Newfoundland (Bergström, 1979; Zhang & Pratt, 2000), and from the Lower Ordovician Bellefonte dolomite of Central Pennsylvania (Butler, 1961). However, this appears to be the first record of sponges, hexactinellid or otherwise, from the Salona Formation. The fact that these spicules were all found in the middle to upper Roaring Spring Member from all three locations surveyed suggests that either the conditions for their preservation were highly restricted, or that they only colonized the region briefly before they disappeared locally. As modern hexactinellids express a preference for cooler water conditions (Leys et al., 2004), it is possible that their appearance coincides with the shift from a warm-water to a cool-water system brought about by the opening of the Sebree Trough (Holland & Patzkowsky, 1996, 1998; Patzkowsky & Holland 1999; Kolata et al. 2001). Their disappearance shortly afterwards could also indicate that these favorable conditions existed only briefly before being eliminated by the local shoaling and increased energy that followed in the Coburn.
Figure 19: Microphotographs of Hexactinellid spicules from the Roaring Spring Member. Scale with 1 mm divisions. Clockwise from top left, samples from: Lemont, Spring Mills, Lemont, Reedsville.

A single specimen of the brachiopod genus *Leptaena* was also found in the Reedsville section at a stratigraphic position of 44 meters, placing it in the lower to middle Roaring Springs Member. While the single occurrence prevented this taxon from being included in the quantitative analysis, this is the position from which the majority of the ostracod biofacies samples were found, which also marks the period of highest overall diversity in the collection.
According to Patzkowsky and Holland (1996), this genus disappeared from eastern North America during the Mohawkian regional extinction, with the last known occurrence situated well below the Deicke metabentonite. The discovery of this genus 28 meters above this ash bed may help to extend its temporal range, and pinpoint the timing, tempo, and geographic variability of the Mohawkian regional extinction.

Another find that does not appear to have been previously reported in the Trenton of central Pennsylvania is a brachial valve of a *Sowerbyella* with numerous macrotubular borings (Fig. 20). Found in the Coleville Member of the Coburn Formation at Reedsville (101 m), this specimen has at least seven distinct tubular bore holes, which are aligned roughly parallel to the costae and originate at the anterior edge. Similar ichnofossils have been found by Vogel and Brett (2009) in strata from the Lexington through the Liberty Formation of the Cincinnati Arch, a coeval to younger suite of deposits. These authors note the strong similarity between the borings they observed and those left by polychaete and phoronid worms in the Recent, and suggest a similar origin. The macrotubular borings found here represent an early step in a progressive increase in the diversity of microendolithic borings that appear to begin in the Mohawkian. The presence of these trace fossils extends their geographic range at this early stage in habitat exploitation.
A large number of spines of unknown affiliation (Fig. 21) have also been found in samples from the lower Roaring Spring Member (one sample) through the Milesburg, where they become more plentiful (Fig. 15). These spines appear anywhere from singly to extremely high densities, as shown here, and range from 1-5 mm in length. The spines are all straight and unbranched, show only a minor taper, and are generally unornamented. Unlike the spicules discussed above, these do not appear to be replaced by calcite, but are likely still the original calcite material as evidenced by the retention of a more complex structure that would otherwise have been lost during replacement. While these spines compare somewhat favorably to those of some echinoid species (e.g. the Upper Devonian to Lower Carboniferous genus *Deneechinus*; Smith, 2005), no echinoids with such long, slender spines are known from the Ordovician. Additionally, no spines were observed with the “socketed” end that is typical for echinoids. Some brachiopods, such as the lingulid *Acanthambonia*, are known to have been covered with spines that may have aided in attaching to a substrate (Wright & Nolvak, 1997),

Figure 20: *Sowerbyella* brachial valve with macrotubular borings. Sample is from the Coleville Member of the Coburn Formation at Reedsville (101 m). Scale bar with 1 mm divisions.
but this genus is not known from the rocks of Central Pennsylvania’s Trenton either, and this
brachiopod is far too small to have supplied the spines. At present, the spines are assumed to
be either monaxon sponge spicules (see Zhang & Pratt, 2000) or possibly echinoderm spines,
but this is currently conjectural. Regardless of origin, they serve to indicate the presence of
currents some samples, as seen in Fig. 21, although their presence only in float makes it
impossible to determine flow direction.

Figure 21: Flow aligned spines at Reedsville (141 m). While the affinity of these spines is
uncertain, they appear to be consistent with those from echinoderms, or possibly sponges. Sample
is from the Milesburg Member of the Coburn Formation.

4.4 Site Comparison

Comparisons of the biofacies described above (section 3.3.1) with assemblages
identified in New York and Kentucky are the ultimate goal of this research. The differing
locations, collectors, and collecting methodologies of these samples must first be addressed.
The samples collected in New York by Robert Titus present particular difficulties, as the information for this collection had to be gathered from multiple sources. The Paleobiology Database (PBDB: Titus, 2007) provided detailed quantitative records with good taxonomic resolution, but the methodologies, locations, and stratigraphy had to be drawn from a series of papers published by Titus on the paleontology of New York's Trenton group (Titus 1976, 1982, and 1986). The combination of data from multiple sources made it necessary to create two different data sets for the New York data: an analysis list, consisting solely of the abundance data from the PBDB and used for quantitative analysis; and a faunal list (Appendix E), which is a presence/absence list created by supplementing the analysis list with the taxonomic list provided by Titus (1982). As Titus (1982) lacked detailed environmental and stratigraphic information, it was necessary to identify sedimentary facies by the biofacies in order to remove samples collected from the shoal environment. Shoal was represented in Titus (1982), but does not appear in Titus (2007). Shoal environment was determined for Titus (1982) by using the *Liospira* community, which was shown as essentially synonymous with shoal, as a proxy. The faunal list is used below, except in section 4.4.4 where quantitative analysis was performed on the analysis list.

Several additional steps were necessary to make both taxa lists comparable. For the faunal list, synonymous names were combined when applicable (*Encrinurus* with *Encrinuroides* (Ludvigsen, 1979; Titus, 1982), and *Calliops* with *Calyptaulax* (Shaw, 1968)), while closely related taxa that may be easily confused were combined (e.g. *Dalmanella* and *Paucicrura* combined to dalmanellids). Crinoids were lumped into a single group as they were only consistently identified below class level in New York. All inarticulate brachiopods were reclassified as inarticulates, and bryozoans were placed into groups defined by class or morphology. Bivalves were removed due to poor preservation in Pennsylvania which...
prohibited identification. For the analysis list, these steps and a few additional ones were taken. When closely related and easily confusable taxa were identified to a greater precision in one collection than another, the higher taxonomic grouping was used. This included combining *Anazyga*, *Protozyga*, and *Zygospira* as atrypids, and lumping all gastropods (a result of the poor preservation of this group in Pennsylvania making identification unreliable). Lastly, all taxa occurring in less than 2% of samples were removed, which excluded only three genera (*Eridorthis*, *Escharopora*, and *Orthorhynchula*).

### 4.4.1 Temporal and Paleoenvironmental Site Comparison

All three study sites come from strata deposited in the Trenton Group, a set of beds deposited over a period of 4 to 5 million years. None of these studies spanned the entire duration of the Trenton however, instead showing varying degrees of temporal overlap (Fig. 5), as demonstrated by conodont and graptolite biostratigraphy. Holland & Patzkowsky (2004) cover the largest span of the Trenton, from near the *P. undatus/P. tenuis* boundary up into the *A. superbus* Zone. Titus collected from the shortest time span, with samples interpreted to come from the very upper *A. tvaerensis* Zone into the *A. superbus* Zone. The Pennsylvania samples represent an intermediate length of time, beginning slightly before the Holland & Patzkowsky samples in the *P. undatus* Zone, and continuing until just before the end of the *A. tvaerensis* Zone. This means that while the Titus collection is entirely within the range of Holland & Patzkowsky and while there is considerable overlap between the collections of Holland & Patzkowsky and this study, Titus and this study overlap little, if at all (Fig. 5). This is an unavoidable result of restricting collections to similar depositional environments, and which stems from the diachronous nature of the deep water facies of the Trenton group, and the asynchronous and discontinuous nature of the deepening associated with the Taconic collision.
Despite this diachronous evolution of the sedimentary basins in Pennsylvania, Kentucky, and New York, their stratigraphy suggests similar depositional environments in each location (Shanmugam & Lash, 1982; Mitchell et al., 2004, Brett et al., 2004). While comparing non-contemporaneous communities introduces the risk of capturing major evolutionary turnover or within-taxon shifts in environmental response instead of regional variability, these possibilities are minimal, and are addressed in sections 4.4.2 through 4.4.4.

Environmental differences must be considered in addition to the differences in the time periods. While the central Pennsylvania samples were all collected from strata representing the deep subtidal environment, those from New York and Kentucky were collected from sand shoal facies through the deep offshore (Table 1). The small number of deep subtidal samples from Kentucky and New York made it unfeasible to rely on this environment exclusively, so the entire faunal lists from both collections were used. As this added many samples from neighboring environments, it is useful to look at how many unique taxa this introduced.

Samples from the shoal facies were not included in this study, but are discussed here to highlight the influence of environment on diversity and community composition. Additionally, as the shallow subtidal and offshore environments were not represented in the Pennsylvania samples, it is worth considering how inclusion of these samples impacts richness.

<table>
<thead>
<tr>
<th></th>
<th>Shoal</th>
<th>Shallow Subtidal</th>
<th>Deep Subtidal</th>
<th>Offshore</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pennsylvania</td>
<td>0</td>
<td>0</td>
<td>84</td>
<td>0</td>
</tr>
<tr>
<td>Kentucky</td>
<td>4</td>
<td>35</td>
<td>19</td>
<td>36</td>
</tr>
<tr>
<td>New York</td>
<td>0</td>
<td>39</td>
<td>13</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 1: Distribution of samples between marine facies in the analysis list. Environmental interpretations for New York and Kentucky were taken from the Paleobiology Database, from which the faunal counts were drawn.
Four taxa included in the Kentucky analysis were restricted to the shoal and/or shallow subtidal environments. Only one, the calcareous algae *Solenopora*, was found exclusively in the shoal environment, while the specimens identified as “gastropod” and a crinoid were restricted to the shallow subtidal, and the brachiopod *Orthorhyncula* was found in both. With bryozoans lumped into class-level or morphologic groupings for analysis, and with the exclusion of crinoids and bryozoans from the shared/unique taxa list, this should have minimal influence on overall taxa lists and community comparisons.

The New York collection had a much higher percentage of taxa found exclusively in the shallow subtidal or shoal environments, possibly resulting from the much heavier sampling focus on shallow subtidal facies. However, many of these taxa were also found in the much more heavily sampled deep subtidal facies of Pennsylvania. Of the taxa found exclusively in the shoal environment, all three were brachiopods (*Rhynchotrema*, *Hesperorthis* and *Plectorthis*). Numerous other taxa were restricted to the shoal and shallow subtidal facies of New York, but many of these were also found in the deep subtidal of Pennsylvania (*Strophomena*, *Streptelasma, Conularia, Encrinurus (Encrinuroides), Calliops (Calyptaulax), Hormotoma, and Liospira*), while *Cyclonema* was shared with the deeper facies of Kentucky.

Of the taxa unique to New York, many were bryozoans (33.3% of all New York bryozoans were restricted to shoal and shallow subtidal) or crinoids (50% of those identified), which were excluded from analysis, along with bivalves (60% identified were from only shoal & shallow subtidal). Identified gastropods were mostly found only in shallower facies (71.4%), but only two of these were not identified in deeper facies of Pennsylvania or Kentucky. Of the trilobites, only one (*Hypodicranotus*) that was exclusively shallow was not found in deeper facies in Pennsylvania or Kentucky, but this is an extremely rare taxon that is typically found in deeper facies (according to occurrences reported in the PDBD as of 2/1/14).
Essentially, the inclusion of large numbers of samples from adjacent facies does not appear to significantly impact the richness of the collections through addition of exclusively shallow water taxa. While onshore-offshore and out of habitat transport of faunal remains has the potential of alter fossil assemblage composition, this type of transport is generally considered to be minimal (Miller et al., 1992; Kidwell, 2008). Major drivers of out of habitat transport in the deep marine setting are generally limited to varieties of mass movements such as turbidity currents (Kidwell & Flessa, 2008), which were not recognized in any included section. Storm induced bottom currents typically move parallel to the coast as geostrophic flows (Duke, 1990), and are unlikely to result in out of habitat transport (Zuschin & Stanton, 2002). The sharing of taxa between adjacent communities along the depth gradient is therefore likely due to the overlapping environmental ranges of the organisms, instead of resulting from transport.

4.4.2 Qualitative Comparison of Assemblages

As previously discussed, cluster analysis of fossil assemblages produces groups of samples with similar taxonomic compositions and abundances, called biofacies. In the case of the collections examined here however, this approach highlights the issue of scale in biofacies identification. The length of the gradient being studied, in this case defined primarily by depth, does not control how many biofacies can be identified in a collection. The Pennsylvania collection of 84 samples was interpreted to yield seven biofacies from essentially a single environment (deep subtidal, but possibly including some offshore samples), while the New York strata which included many more environments (sand shoal through offshore) in 56 samples was divided by unspecified means into only four biofacies in the original study (Titus, 1982). The Kentucky collection spanned a similar range of environments to the New York
collection, and produced eight biofacies from 87 samples (Holland & Patzkowsky, 2004). While
the methods used by Titus to recognize biofacies were not explained, the number of samples
included appears to have a greater impact on the number of communities described in a
collection.

This study did not attempt to reproduce the biofacies described in Kentucky and New
York, and in fact it appears that the original entire data set used to produce the New York
biofacies was not made available on the Paleobiology Database. Holland and Patzkowsky
reported their biofacies of Kentucky with the percent contributions of taxa, while Titus only
reported relative abundances. However, the biofacies of Pennsylvania and Kentucky can still
be compared (Pennsylvania biofacies data are listed in Appendix C, and Kentucky biofacies
data are shown in Appendix 2 of Holland & Patzkowsky, 2004), and can be broadly compared
with the communities described by Titus (1982).

Of the seven biofacies identified in Pennsylvania and the eight identified in Kentucky,
three are defined by shared taxa: Dalmanella, Sowerbyella, and ramose trepostomes. Despite
the dominance of these eponymous taxa, the relative abundances and the secondary taxa
differed. The dalmanellid biofacies in Kentucky count atrypids and modiomorphid trilobites as
the second and third most abundant taxa, both of which were absent in the Pennsylvanian
biofacies of the same name. Ramose bryozoans were common in both, but contribute 12.6% of
the individuals in Pennsylvania, compared with 3.2% in Kentucky. The Sowerbyella biofacies
also show major differences, with atrypids being major components in Kentucky but absent in
Pennsylvania. The diverse Sowerbyella biofacies of Pennsylvania appears to be more similar
however, sharing dalmanellids, Cryptolithus, and calymenid trilobites, despite Sowerbyella
contributing a smaller percentage of individuals in Pennsylvania. The ramose trepostome
biofacies in Kentucky is dominated by these bryozoans, while in the similar ramose bryozoan
biofacies of Pennsylvania they are abundant, but less so than *Dalmanella*, and comprise less than a quarter of the individuals counted. *Sowerbyella*, the third most abundant taxon in Pennsylvania, is completely absent from the Kentucky biofacies. A fourth pair of biofacies (*Cryptolithus* in Pennsylvania and *Rafinesquina* in Kentucky) does not share a similar name, but *Rafinesquina* is the second most abundant taxon in the *Cryptolithus* biofacies, its highest contribution in the collection. *Cryptolithus*, while accounting for almost 29% of the individuals in its eponymous biofacies, is the second rarest in the *Rafinesquina* biofacies. Some taxa, such as ramose trepostomes, dalmanellids, and *Isotelus*, are relatively abundant in both biofacies, and several other taxa are shared, but at very different abundances.

Difficulties in comparing the structure of these faunal assemblages are at least partially related to differences in methodologies, but also seem to reflect true ecological differences. The eponymous taxa in the biofacies of each collection are not always identified or present in other collections. For example, *Encrinurus* is not identified by Holland & Patzkowsky (2004), *Trematis* is not identified by Holland & Patzkowsky (2004) or in Pennsylvania, and *Rhynchotrema* was not identified in Pennsylvania. Additionally, the *Constellaria/Cyclonema, Rhynchotrema*, and *Solenopora/Herbertella* biofacies of Kentucky are all largely defined by taxa not found in Pennsylvania. Atrypids and *Herbertella* were important constituents of many biofacies of Kentucky, while minor or missing in Pennsylvania. Alternatively, taxa may be present in low quantities, but not found in enough samples to define a biofacies. Gastropods are rare in Kentucky, but define biofacies in Pennsylvania (*Hormotoma*) and New York (*Liospira*). *Cryptolithus*, while abundant in Pennsylvania, was never more than a minor taxon in Kentucky, and is completely absent in the New York collection. The biofacies of New York cannot be compared as easily, as they lack abundance data, and none of them share similar
names to those of Pennsylvania and Kentucky. Overall, these differences strongly suggest different ecological structuring at the three locations.

The absence of a rarer taxon from a site may be due to omission by the collector, but robust or highly distinctive organisms such as *Parastrophina* and *Cryptolithus* are more likely to be missing due to a true absence from the strata. Both Holland & Patzkowsky (2004) and Titus (1982) identified some groups to greater precision than the current study (particularly bryozoans, crinoids, bivalves, and gastropods), but trilobites and articulate brachiopods were identified to comparable levels. The presence or absence of these organisms likely serves as a reliable indicator of ecological differences.

**Table 2**: Number of observed, shared and unique taxa identified in the Pennsylvania, Kentucky, and New York collections. Bivalves, bryozoans, crinoids, and nautiloids are excluded due to uneven taxonomic resolution between collections. The included taxa are listed in Appendix E.

<table>
<thead>
<tr>
<th>No. of Taxa</th>
<th>PA</th>
<th>NY</th>
<th>KY</th>
<th>No. Shared</th>
<th>PA : KY</th>
<th>PA : NY</th>
<th>KY : NY</th>
<th>All</th>
<th>No. Unique</th>
<th>PA</th>
<th>KY</th>
<th>NY</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachiopod</td>
<td>12</td>
<td>12</td>
<td>10</td>
<td>Brachiopod</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>Brachiopod</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Gastropod</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>Gastropod</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>Gastropod</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Inarticulate</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>Inarticulate</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>Inarticulate</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Trilobite</td>
<td>9</td>
<td>6</td>
<td>6</td>
<td>Trilobite</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>Trilobite</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Other</td>
<td>7</td>
<td>5</td>
<td>6</td>
<td>Other</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>Other</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>TOTAL</td>
<td>32</td>
<td>31</td>
<td>32</td>
<td>TOTAL</td>
<td>14</td>
<td>18</td>
<td>15</td>
<td>9</td>
<td>TOTAL</td>
<td>8</td>
<td>10</td>
<td>8</td>
<td>26</td>
</tr>
</tbody>
</table>

The relative contribution of major groups to each of the three collections can be seen in **Table 2**. Among the taxa considered, articulate brachiopods are the most diverse group described at all three locations. While all locations shared many brachiopods, Pennsylvania and Kentucky each had a significantly higher proportion of unique brachiopods (taxa found at neither of the other locations) than New York, which only had one unique taxon (*Plectorthis*, which was only tentatively identified in Pennsylvania). Similarly, while trilobite diversity was very high in all three collections, Pennsylvania and Kentucky had a relatively high number of unique taxa, but New York had only one (*Hypodiceranotus*). Furthermore, almost all trilobites found in New York were also found in Pennsylvania, while neither shared many with Kentucky.
The high diversity of trilobites and brachiopods found in the relatively short depth gradient of Pennsylvania, along with the high proportion that are shared with Kentucky and New York, suggests that these taxa are either particularly eurytopic or that they are particularly diverse in the deep subtidal environment that dominated the Pennsylvania samples. Gastropods, inarticulate brachiopods, and other rarer taxa show different patterns, but the uneven identification for these groups between collections makes them less reliable indicators. It is worth noting that while bivalves were excluded from this comparison, they were found in Pennsylvania only as very rare (limited to four samples) and extremely poorly preserved fossils, with most occurrences limited to unidentifiable internal molds. This raises the possibility that taphonomic biases may have significant impact on the relative contribution of different taxonomic groups to communities. Additionally, bryozoans were the most diverse taxa in New York with 24 genera, which is the only site from which they were extensively identified. They were however plentiful in both Kentucky and Pennsylvania, so their contribution to overall diversity is likely significant, but cannot be considered here.

When viewed through the lens of Sepkoski's “Evolutionary Faunas” (Sepkoski, 1981), the described communities in all three states are populated primarily by members of the Paleozoic Fauna, including the dominant articulate brachiopods, stenolaemate bryozoans, and gastropods. Trilobites are the only member of the Cambrian Fauna to have a strong presence. The distribution of these taxonomic groups generally fits the pattern observed by Jablonski and others (1983), with more modern clades originating nearshore and spreading into the deeper waters, where they replace the members of the more archaic fauna. By the time of the Trenton Group deposits in the mid-Caradocian, the Paleozoic Fauna had expanded to the distal reaches of the outer shelf, with the Cambrian Fauna still abundant at greater depths. This matches the observations in central Pennsylvania and Kentucky, where Paleozoic fauna are generally
dominant, except in the deeper reaches of the basin, where trilobite diversity reaches its peak. This pattern does not hold true in New York, however. Here the trilobites had intermediate PE scores, and were collected from the entire depth gradient. However, aside from the abundant *Isotelus* and calyeminds, most trilobites were relatively rare, and would be more likely to be missed from the undersampled deeper facies.

4.4.3 Quantitative Comparison of Assemblages

The biofacies of Pennsylvania and Kentucky can be compared using diversity metrics, including mean richness (S), Shannon’s H, and evenness via Buzas and Gibson’s E (Table 5 in Appendix C). Richness is simply the total number of taxa, while Buzas and Gibson’s E describes how evenly distributed individuals are between taxa. Shannon’s H is a diversity measure that incorporates both taxonomic abundance and evenness, with rare taxa having a reduced impact relative to simple richness (Holland, 2010). Biofacies that share the same or similar names (*Dalmanella/dalmanellid, Sowerbyella/diverse Sowerbyella, ramose trepostome/ramose bryozoan*) do not necessarily have similar diversity metrics. The dalmanellid biofacies of Kentucky included many more samples than the *Dalmanella* biofacies of Pennsylvania, but had a much lower richness (5:7.3) and much higher evenness (0.85:0.32). Both the *Sowerbyella* and diverse *Sowerbyella* biofacies of Pennsylvania were identified in more samples than the *Sowerbyella* biofacies of Kentucky, and had a higher richness (8.4/7.9:7.1), but much lower evenness (0.25/0.25:0.65). The comparably sampled ramose bryozoan biofacies shows higher diversity (9.2:7.6) but lower evenness (0.4:0.7) in Pennsylvania than Kentucky. Lastly, the *Cryptolithus and Rafinesquina* biofacies, compared here due to the shared high abundance of *Rafinesquina*, both had a relatively high richness (7.4:8.4). Both had the highest evenness of their collections, but the Kentucky biofacies was far more even (0.49:0.91).
While these metrics were directly compared for these biofacies, all biofacies showed similar trend of higher diversity but lower evenness in Pennsylvania than Kentucky, again pointing to different structuring of the communities. Note, however, that Finnegan & Droser (2008) have shown that storm beds exhibit higher evenness and richness, so biofacies collected from locations experiencing different degrees of storm influence may not be completely analogous.

Direct comparison of the taxonomic differences of the three collections with the Jaccard dissimilarity index ($d_J$) provides a means of measuring the degree to which diversity increases as geographically separated collections are combined. Higher values of $d_J$ indicate a higher proportion of taxa that are not shared between collections, meaning that $d_J$ is a measure of beta diversity. The values of $d_J$ have been converted to actual distances in Figure 22. These scores demonstrate a major increase in diversity when sites along the basin axis are compared, ranging from 44% between New York and Pennsylvania, and 55% between New York and Kentucky. Differences in gradient length do not necessarily lead to higher dissimilarity values, as the shortest gradient (Pennsylvania) shares a higher proportion of taxa with both New York and Kentucky than these longer gradients share with each other. The complete lack of temporal overlap between New York and Pennsylvania likewise did not lead to increased dissimilarity. If major evolutionary turnover had occurred during the study interval, these two collections would have shared the fewest taxa, with interval-spanning Kentucky in an intermediate position. These results show that taxonomic differences between similar locations within a single basin can rival those between adjacent environmental zones (Sepkoski, 1988). While this regional variation would have been subsumed within the continental-scale analysis of Sepkoski (1988), the high degree of within-environment variability found here suggests that high sampling intensity on regional spatial scales is necessary to capture the true diversity of any time period.
Figure 22: Jaccard dissimilarity between paired collections. The distance shown between states is directly proportional to their dissimilarity: greater distances indicate greater gains in beta diversity when combining collections. Kentucky and New York have the highest proportion of unshared taxa, while Pennsylvania and New York have the lowest.

DCA of the combined dataset of all three collections produces a compact arrangement of samples, as seen in Fig. 23. While simplifying the faunal lists may have obscured some local variation among some taxa, particularly bivalves, gastropods, and bryozoans, the collections exhibit a high degree of similarity despite their geographic and temporal distances. Additionally, the depth signal appears to be preserved on DCA Axis 1, with shallower samples earning higher scores and deeper samples earning lower scores. This signal is particularly strong among the Kentucky samples, but is still visible, if compressed, in the New York samples.

The DCA plot also can be used to infer the degree of similarity between collections. The Kentucky collection appears to have a high degree of variability between samples, as they span the entire range of the plot. They tend to cluster mostly on the right, with only the deeper offshore samples plotting much to the left of 0 on DCA axis 1. Both the New York and Pennsylvania collections plot entirely to the left of about 1 on DCA axis 1, and with most plotting to the left of 0. This produces a high degree of overlap between New York and Pennsylvania, while both share little space with any Kentucky samples not from the offshore
environment. This suggests a much greater similarity between the New York and Pennsylvania collections than between either and the Kentucky collection.

**Figure 23**: DCA of Pennsylvania (triangles: current study), Kentucky (circles: Holland & Patzkowsky, 2004), and New York (stars: Titus, 1982) samples. Samples are coded by location and interpreted depositional environment.

While the M4/M5 regional extinction observed elsewhere in eastern Laurentia (Patzkowsky & Holland, 1997; Layou, 2009) seems to correlate with the Pennsylvania section (possibly just above the high diversity ostracod biofacies), all other samples, including the entirety of the New York and Kentucky collections, postdate this event. Therefore, all samples aside from the lowermost Pennsylvania samples were deposited after the formation of the Sebree Trough brought cooler water into the area (Kolata, 2001). Surprisingly, despite the inclusion of a several (potentially) pre-extinction samples, these samples do not cluster separately when all three collections are plotted together (located near [-0.2, 0.5] in Fig. 23). This suggests that the environmental factors that precipitated the biotic changes occurred
earlier in Pennsylvania than elsewhere in the region, or that too few samples were collected from the lower New Enterprise Member to provide an adequate picture of the pre-extinction faunal assemblage.

Table 3: ANOSIM test results for all collections, as grouped by state. All R-values determined by separate ANOSIM tests, each run with 5000 permutations. All null-hypotheses (that there is no significant difference between community compositions for any of the locations) were rejected.

<table>
<thead>
<tr>
<th>Groups (collection pairings)</th>
<th>R-value</th>
<th>Significance level % (p)</th>
</tr>
</thead>
<tbody>
<tr>
<td>PA : KY</td>
<td>0.3105</td>
<td>0.001</td>
</tr>
<tr>
<td>PA : NY</td>
<td>0.1994</td>
<td>0.001</td>
</tr>
<tr>
<td>NY : KY</td>
<td>0.1225</td>
<td>0.001</td>
</tr>
<tr>
<td>All</td>
<td>0.2215</td>
<td>0.001</td>
</tr>
</tbody>
</table>

ANOSIM test results for the three collections (Table 3) show a surprisingly high degree of similarity. The null-hypothesis, that collections would display random variation, is strongly rejected, but the low R-values indicate that between-collection differences are not vastly greater than within-collection differences. Similar use of ANOSIM testing to study between- and within-bed variation has returned much higher R-values than those shown here (Bonelli et al., 2006). While R-values describe relative similarity and are not directly comparable between studies, the extreme difference in scores requires explanation. One likely cause is the simplification of the faunal data required to make the data sets comparable. This removed much of the dissimilarity that may have been observable if all collections taxa were identified to genera level. However, another important factor is the environmental and temporal span of the samples included in the current study. Bonelli and others (2006) restricted their collection to a single environment, and compared samples that were either contemporaneous or represented two narrow intervals of time. The collections compared here consist of much longer time ranges and include multiple depositional environments, leading to greater within-collection variability. When these collections are compared to each other, samples from similar
ages and depositional environments could be expected to be more similar to each other than to other samples from the same collection but different ages or environments, resulting in R-values closer to 0. The greater similarity between the Kentucky and New York collections may be partly a result of the similar environmental gradient they represent, while the lower similarity between Kentucky and Pennsylvania likely relates the shorter gradient and time interval sampled in the latter.

4.4.4 Comparison of Ecological Parameters among Localities

Comparing ecological parameters of three geographically distant ecologic gradients with varying degrees of temporal overlap allows investigation of the contributions of time and space to community structure. Geographically, the Pennsylvania samples were collected from approximately halfway between the New York and Kentucky sites, but slightly closer to New York (Fig. 4). Temporally, Pennsylvania and New York are completely non-contemporaneous, yet both overlap with Kentucky; Pennsylvania with the older strata, and New York with the younger (Fig. 5).

DCA scores were determined for each collection independently, using the taxonomic combination and synonymization steps discussed above. Pairwise correlation of shared taxas’ ecological parameters from the compared collections was performed, with the results for preferred environment and environmental tolerance shown in Fig. 24. Peak abundance (PA) is not considered here, as small sample sizes yielded invalid results for some taxa. Strength of correlation is shown using Spearman’s correlation coefficient rho (ρ), with a result of 1 indicating perfect positive correlation. A rho of 0.5 or greater is considered to be a strong correlation, while a smaller value is considered to indicate a weak correlation, following the arbitrary distinction used by Holland and Zaffos (2011). Spearman correlation was chosen
over Pearson’s $r$ due to its lower sensitivity to outliers. Significance tests (p-values) are included as well, but as discussed by Holland and Zaffos (2011) p-values are influenced strongly by sample size.

Preferred environment (PE) scores were the most highly correlated, particularly between Kentucky and New York (Fig. 24e). The large geographic distance between sites has little impact on the environmental preferences of most taxa. The brachiopods *Platystrophia* and *Strophomena* are the main outliers in this pairing, with *Platystrophia* found in deeper water facies in New York than in Kentucky, and the reverse true for *Strophomena*. The relationship is weaker between Pennsylvania and New York (Fig. 24c) but still significant. Here, several taxa appear to prefer shallower environments in New York than in Pennsylvania, including several trilobites (*Ceraurus, Isotelus*, and the encrinurids), as well as the brachiopod *Dinorthis*, and the dalmanellids are the only group to strongly show the reverse. As dalmanellids are highly abundant in all three locations, a true shift in environmental preference of just this one taxon would impact observed faunal associations. Correlation between Pennsylvania and Kentucky (Fig. 24a), while the only non-significant correlation, is still relatively high, with a Spearman’s $\rho$ of 0.41. This suggests that preferred environment is highly conserved despite geographically and temporally separation. The dalmanellids again show a preference for shallower water in Pennsylvania, but the generally weaker correlation lowers confidence in these results.

The weaker PE relationship between Pennsylvania and either of the other two collections is perhaps expected, considering the different depositional environments they represent, but the statistical significance despite this difference is surprising. The complete lack of temporal overlap between the Pennsylvania and New York collections, even when combined with environmental differences, does not result in a mismatch between PE scores. Similarly, the exceptionally strong correlation between the New York and Kentucky collections
compared to either with Pennsylvania may result from their similar range of environments represented in the former two. However, their greater distance also suggests that environmental preferences do not necessarily vary with increased geographic separation.

Correlations between collections' environmental tolerance (ET) scores are weaker and more variable than for PE. The Kentucky and New York correlation is again the strongest (Fig. 24f), with both the highest Spearman’s ρ and significance values. Several outliers are apparent, notably *Strophomena* again, which is more eurytopic in Kentucky, and the grouped gastropods, which are more stenotopic in Kentucky. *Sowerbyella* also shows a lower ET in Kentucky, which potentially has a great impact on faunal assemblage composition due to its high abundance in all collections. New York and Pennsylvania also showed a strong and significant correlation between the ET scores of their shared taxa. Pennsylvania and Kentucky again show the weakest correlation, with both a very low Spearman’s ρ (0.1393) value and weak significance (0.6194) value (Fig. 24b). Interestingly, most taxa in all three collections show relatively similar ET scores, with the lower end populated by the inarticulate brachiopods and a few less common taxa. This raises the possibility that ET scores of taxa are inordinately impacted by the number of samples in which they are found. While this may in fact reflect more highly restricted environmental tolerances, it may also be an artifact of their relative rarity. A eurytopic but rare taxon would be more likely to return a low ET score, as the odds of collection from the entirety of its range decrease with fewer samples. As an extreme case, a taxon found in only one sample will have an ET score of 0, regardless of its true environmental tolerance. In the Pennsylvania collection, and possibly all collections, taxa found in more sparsely populated environments will be counted less often, due to the necessary bias towards densely fossiliferous slabs to ensure large enough samples. This may introduce something similar to the edge effect, as their deepest occurrences are less likely to be included.
Figure 24: Correlations of ecological parameters for taxa. Preferred environment and environmental tolerance values for each taxon reported in collection pairs are plotted, with a best-fit linear regression line added.
An alternate view is shown in Fig. 25, where inverse Spearman’s ρ values (1-ρ) are used to illustrate ecological distances between collections. Here, the strength of correlation (Spearman’s ρ) is inversely proportional to the spacing of the collections. Kentucky and New York are the closest in terms of both PE and ET, while Kentucky and Pennsylvania are by far the furthest, indicating weak correlation of ecological parameters between locations. In general, PE scores appear to correlate better than ET scores across the geographic and temporal ranges considered here. These findings largely agree with those of Holland & Zaffos (2011), who found that PE is highly conserved across time spans of millions of years, while ET is less so. Kentucky and New York, the collections with the greatest geographic separation, show stronger correlation between PE scores than those for ET. The closer, but more temporally separated collections of New York and Pennsylvania show lower correlation overall, but both ET and PE scores show comparable variation. These results imply that in addition to higher conservation of PE scores across long time spans, they are also more highly conserved across geographic distances than ET. However, these results also suggest that the stronger correlation of PE is better conserved with distance than with time. While this effect may here be related to the differing lengths of ecological gradients sampled, if it is replicated in further study it would imply that while environmental tolerance can shift more quickly than preferred environment, its potential range of drift is more constrained. It would therefore be easier for an organism to shift to a new environment than to adapt to a wider range of habitats.

Comparison of ecological parameters between locations is complicated by the non-contemporaneity of the collections. If the environmental preferences and tolerances of taxa shift over time, then any observed differences may simply be the accumulation of this drift over millions of years. However, many taxa have elsewhere been shown to conserve their ecological parameters over time periods much longer than considered here (9-10 Myr; Holland and
Zaffos, 2011), and environmental preferences are generally well conserved on geologic timescales (Hopkins et al., 2014). Any observed shifts would therefore likely be capturing evolutionary changes within the groups, while the lack of changes would suggest that any ecological differences are the result of the emigration or extirpation of taxa (Stigall, 2012) and not within-clade evolutionary turnover.

Figure 25: Representation of Spearman’s $\rho$, comparing biotic response to environmental changes in Central Pennsylvania, New York, and Kentucky. Distances between the locations shown above are directly proportional to $1-\rho$, with greater distance indicating lower correlation. Collections from New York and Kentucky show the greatest similarity in PE and ET, while Kentucky and Pennsylvania show the lowest degree of correlation between values.

4.5 Comparison Summary and Implications

The multiple methods of comparing faunal assemblages used here produced broadly similar results, but also some disagreement.
Dissimilarity between locations appears to correlate with geographic distance, as demonstrated by use of the Jaccard dissimilarity index. The relatively close Pennsylvania and New York locations were the most similar, while New York and Kentucky, the locations separated by the greatest distance, were the least similar. The inclusion of more locations with stricter controls on the collection methodologies could better quantify the degree to which distance influences taxonomic turnover.

Comparison of the ANOSIM results (Table 3) with the DCA plot (Fig. 23) reveals some differences. The DCA plot shows the New York and Pennsylvania collections plotting much closer to each other than to the Kentucky collection, while ANOSIM indicates greater similarity between New York and Kentucky. While simplifying multidimensional data to fewer dimensions can result in distortion (McCune & Grace, 2002), this discrepancy, along with the issues discussed above, suggest that ANOSIM may be better suited to comparing datasets that are limited to the same environment instead of the entire gradient compared here. This would require more extensive data of the deep subtidal environment from New York and Kentucky than is currently available.

The comparison of ecological parameters shows the greatest similarity between the New York and Kentucky collections, with the least similarity between those of Pennsylvania and Kentucky. This agrees with the ANOSIM results, but contrasts with the DCA results. While ecological parameters do not measure the same aspects of the assemblages as ANOSIM or DCA, they do provide insight into the factors that determine the arrangement of fauna along an ecological gradient. As mentioned above, some discrepancy between ANOSIM and DCA results is expected, but the general concordance between the ecological parameters and the ANOSIM suggest that they are in fact measuring similar aspects of assemblages.
The faunal differences between locations are here interpreted to show regional variability, but could conceivably result from evolutionary turnover across the study interval due to the use of non-contemporaneous collections. However, the Ordovician Radiation was essentially over by the middle to late Ordovician (Sepkoski, 1988; Servais et al., 2009), with the Paleozoic Fauna having reached a temporary maximum diversity (Sepkoski, 1995). Similarly, the rate of offshore expansion of the Paleozoic Fauna decreased greatly by the late Ordovician, with partitioning of the depth gradient stabilizing as the Paleozoic Fauna reached the edge of the shelf (Jablonski et al., 1983). While this expansion would have greatly restructured the shelf communities as it progressed, the deceleration by the late Ordovician suggests that this major evolutionary event would not be a primary cause of regional community variation on the time scales of the current study. With communities of all collections dominated by members of the Paleozoic Fauna, this major faunal transition likely occurred prior to the study interval, at least in this region of Laurentia. The M4-M5 sequence transition has also been identified as a period of increased turnover. While placement of this transition in the Pennsylvania section is currently tentative, it is considered to be at or below the Millbrig K-bentonite in the lower Salona, below which only three samples were collected. In Kentucky, the transition occurs at the base of the section, and it is well below the base of the New York section. Fallout from this transition may have continued to alter community compositions in all three sections, but the fact that the section including this event (PA) and the section farthest from it (NY) shared the most taxa suggests its impacts on this study were minimal. The long interval could also capture individual taxa shifting their environmental preferences over time, as they expand, contract, or shift their location along the depth gradient, conceivably causing taxa to appear or disappear if their new range moves them in or out of the observed depth gradient. However,
environmental preferences have been shown to be generally conserved over geologic time scales, as well as for the specific taxa shared between locations in this study.

The length of the gradient was also not a primary driver in diversity, as evidenced by the relatively high richness observed in Pennsylvania, and the relatively small decrease in richness that resulted from removal of the shallower end of the gradient in New York and Kentucky. Instead, much of the observed differences in the assemblages typically involved the addition or subtraction of taxa, as well as faunal associations not observed elsewhere.

Other potential and untested causes of variability do exist, however. These include easily observable differences between locations, such as substrate composition, which was more strongly siliciclastic in Kentucky than New York or Pennsylvania. Subtler differences, such as climate, oceanic circulation, slope orientation, volcanic activity, or other unknown sources could also possibly account for some of the observed variations. The difficulty in ascribing these faunal differences to any particular cause or combination of causes is precisely why this type of regional variation may be so important yet underappreciated: they can potentially occur between any two locations.

This all strongly suggests that taxonomic turnover in the deep-water assemblages between study locations is a significant source of beta diversity regionally. While Sepkoski (1988) found that continent-scale increases in beta diversity could not account for the observed Paleozoic increase in gamma diversity, the current findings suggest that regional beta diversity, even within a single depositional basin, may provide an additional contribution. As the data sets used were not directly comparable, additional intensive sampling would be welcome, particularly in the deep subtidal, and particularly in New York. Despite the complications described, more uniform collection and description would be helpful, and is required to more firmly test these findings.
Chapter 5: Conclusions

1) The Salona and Coburn Formations in the Trenton Group of central Pennsylvania record a period of rapidly increasing depth, followed by a more gradual shallowing, but remain almost entirely within the deep subtidal facies. This interpretation is supported by both lithologic and faunal data.

2) The fauna of the Trenton Group of central Pennsylvania comprise a moderately high-diversity deep water assemblage. Cluster analysis and detrended correspondence analysis can divide this assemblage into seven biofacies arrayed along the depth gradient within the deep subtidal facies. These biofacies are primarily controlled by changes in water depth, as opposed to the temperature driven changes reported elsewhere in the basin.

3) The biofacies recognized in central Pennsylvania compare poorly with those recognized in comparable strata from the middle Upper Ordovician of New York and Kentucky, despite a high degree of taxonomic overlap. Assemblages differ in both the presence and abundance of taxa, indicating significant differences in community structure along the depth gradient.

4) Despite the differing faunal associations observed at the three locations, the addition of taxa in each collection appears to be driven largely spatial distance, and not solely by increased depth gradient length, with beta diversity measured at up to 55% over regional scales. This suggests that within the study interval a hidden source of beta diversity may
be assemblage variation at scales smaller than those typically considered for provinciality. Beta diversity along the depth gradient increases with geographic separation as well as with changing depth, likely accounting for some of the increasing gamma diversity observed during the Paleozoic Era.

5) The geographic and temporal ranges of several taxa have been extended by collection within the study area. These include the first observation of hexactinellid sponges in the Salona Formation; a single specimen of the brachiopod *Letpaena* in the lower to middle Roaring Springs Member of the Salona Formation, marking its first regional observation above the Deicke metabentonite; and the discovery of macrotubular borings in a *Sowerbyella* valve, extending the geographic range that this trace fossil has been found during the early stages of its appearance.

6) More extensive sampling is required of all locations. The deep subtidal is largely undersampled at other locations, making comparison with the Trenton of central Pennsylvania difficult. The strata studied here appear to be excellent candidates for exploring regional scale variation of assemblages, due to the abundant coeval exposures in the eastern portion of North America.
REFERENCES


Chao, A, and T. J. Shen. 2003. ‘Nonparametric estimation of Shannon's index of diversity when there are unseen species in sample.’ Environmental and Ecological Statistics 10:429-443


Ettenson, F. R., J. M. Kasl, and A. K. Stewart. ‘Structural inversion and origin of a Late Ordovician (Trenton) carbonate buildup: evidence from the Tanglewood and Devils Hollow members, Lexington Limestone, central Kentucky (USA).’ Palaeogeography, Palaeoclimatology, Palaeoecology 210:249-266.


Herrmann, A. D., K. G. MacLeod, and S. A. Leslie. 2010. ‘Did a volcanic mega-eruption cause global cooling during the Late Ordovician?’ *PALAIOS* 25:831-836.


Layou, K. M., 2009. 'Ecological restructuring after extinction: the Late Ordovician (Mohawkian) of the Eastern United States.' PALAIOS 24:118-130.


Leys, S. P., K. Wilson, C. Holeton, H. M. Reiswig, W. C. Austin, and V. Tunnicliffe. 2004. 'Patterns of glass sponge (Porifera, Hexactinellida) distribution in coastal waters of British Columbia, Canada.' Marine Ecology Progress Series 283: 133–149.


McCune, B., and J. B. Grace. 2002. 'Analysis of Ecological Communities.' MjM Software Design, Glenedden Beach, OR.


Pope, M., and J. F. Read. 1997. 'High-resolution stratigraphy of the Lexington Limestone (Late Middle Ordovician), Kentucky, U.S.A.: A cool-water carbonate-clastic ramp in a tectonically active foreland basin.' in N.P. James and J. A. D. Clarke, eds., Cool-water Carbonates, SEMP Special Publication 56: 411-429


Renne, P. R., R. Mundil, G. Balco, K. Min, and K. R. Ludwig. 2010. ‘Joint determination of \(^{40}\text{K}\) decay constants and \(^{40}\text{Ar}^* / ^{40}\text{K}\) for the Fish Canyon sanidine standard, and improved accuracy for \(^{40}\text{Ar} / ^{39}\text{Ar}\) geochronology.’ *Geochimica et Cosmochimica Acta* 74:5349-5367.


Sepkoski, J. J. Jr. 1988. 'Alpha, Beta, Gamma- Where does all the diversity go?' *Paleobiology* 14:221-234.


Shaw, F. C. 1968. 'Early Middle Ordovician (Chazy) trilobites of New York.' *New York State Museum and Science Service Memoir* 17:1-163.


Webber, A. J. 2002. ‘High-resolution faunal gradient analysis and an assessment of the causes of meter-scale cyclicity in the type Cincinnatian Series (Upper Ordovician).’ *PALAIOS* 17:545-555.


## APPENDIX A: Faunal Counts

<table>
<thead>
<tr>
<th>Geologic Unit</th>
<th>Cebadella &amp; Asperella</th>
<th>Ortholithus &amp; Trilobites</th>
<th>Ortholithus &amp; Echinoderms</th>
<th>Ortholithus &amp; Brachiopods</th>
<th>Ortholithus &amp; Ostracods</th>
<th>Ortholithus &amp; Gastropods</th>
<th>Ortholithus &amp; Bivalves</th>
<th>Ortholithus &amp; Bryozoans</th>
<th>Ortholithus &amp; Bryo. Tablets</th>
</tr>
</thead>
<tbody>
<tr>
<td>R/R002/15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R004/16</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R003/19</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R002/32</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R007/34</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R002/39</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R006/40</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R005/50</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>R/R006/53</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R008/53</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R007/53</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>R/R003/57</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R004/58</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>12</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R006/60</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R006/69</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R016/74</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R019/79</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R008/84</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R022/88</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R021/88</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R021/90</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R023/93</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R/R027/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>R/R028/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R030/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R032/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R034/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>R/R036/101</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>6</td>
<td>16</td>
<td>0</td>
</tr>
</tbody>
</table>

### Table 4: Faunal counts of samples collected from Lemont, Reedsville, and Spring Mills localities.

This table includes only samples used in data analysis.
<table>
<thead>
<tr>
<th>Sample ID</th>
<th>Faunal Counts</th>
</tr>
</thead>
<tbody>
<tr>
<td>R/R3-01/139</td>
<td>0 0 0 0 0 0 3 0 0 0 3 0 0 1 3 0 0 27 0 0 6 1 0 0 0 0 0 0 0 2 0 0 0 2 0 0 0 10 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-01/139</td>
<td>0 0 0 0 0 0 0 9 2 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-01/141</td>
<td>0 0 0 0 0 0 3 0 0 0 0 0 0 5 0 3 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 3 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-015/141</td>
<td>0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 4 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-017/142</td>
<td>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-018/141</td>
<td>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-019/141</td>
<td>0 0 0 0 0 0 3 0 0 0 0 0 0 1 0 0 1 11 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 1 0 3 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-016/142</td>
<td>0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 4 0 0 0 3 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-017/142</td>
<td>0 0 0 0 0 0 3 0 0 0 0 2 0 0 0 14 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 3 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-020/142</td>
<td>0 0 0 0 0 0 11 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R2-002/101</td>
<td>0 0 0 0 0 0 1 0 0 4 2 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 3 0 0 0 0 8 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R2-003/154</td>
<td>0 0 0 0 0 0 0 8 0 0 0 0 0 0 0 2 0 0 0 6 0 0 0 0 0 1 0 0 3 0 0 0 0 0 0 0 0 0 15 0 5 0 1 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-021/160</td>
<td>0 0 0 0 0 0 14 0 0 0 0 16 0 0 0 0 0 0 0 0 3 0 0 4 0 0 0 0 0 0 9 0 0 0 0 3 0 5 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R4-021/15</td>
<td>0 0 0 0 0 0 1 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-021/15</td>
<td>0 0 0 0 0 0 11 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-020/158</td>
<td>0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 0 16 1 0 0 1 0 0 0 0 1 0 0 0 0 0 7 2 0 0 0 0 0 1 0 0 0 15 4 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-020/158</td>
<td>0 0 0 0 0 0 0 3 0 0 0 0 0 0 0 0 25 3 0 0 0 0 0 0 0 0 0 0 0 0 0 8 0 0 0 0 0 0 1 1 0 0 4 9 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-020/158</td>
<td>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
<tr>
<td>R/R3-020/158</td>
<td>0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0</td>
</tr>
</tbody>
</table>

Faunal counts, cont.
APPENDIX B: Stratigraphic Columns

<table>
<thead>
<tr>
<th>Object</th>
<th>Symbol</th>
<th>Legend</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spicules</td>
<td><img src="image" alt="Spicules" /></td>
<td>Soft sediment deformation</td>
</tr>
<tr>
<td>Crinoids</td>
<td><img src="image" alt="Crinoids" /></td>
<td>Cross bedding</td>
</tr>
<tr>
<td>Trilobites</td>
<td><img src="image" alt="Trilobites" /></td>
<td>Planar laminations</td>
</tr>
<tr>
<td>Bryozoans</td>
<td><img src="image" alt="Bryozoans" /></td>
<td>Nodular bedding</td>
</tr>
<tr>
<td>Brachiopods</td>
<td><img src="image" alt="Brachiopods" /></td>
<td>Hardground</td>
</tr>
<tr>
<td>Gastropods</td>
<td><img src="image" alt="Gastropods" /></td>
<td>Erosive contact</td>
</tr>
<tr>
<td>Nautiloids</td>
<td><img src="image" alt="Nautiloids" /></td>
<td>Wavy bedding</td>
</tr>
<tr>
<td>Ostracods</td>
<td><img src="image" alt="Ostracods" /></td>
<td>Faulting</td>
</tr>
<tr>
<td>Bioturbation</td>
<td><img src="image" alt="Bioturbation" /></td>
<td>Chert</td>
</tr>
<tr>
<td>Chondrites</td>
<td><img src="image" alt="Chondrites" /></td>
<td>Bioskeletal lag</td>
</tr>
<tr>
<td>Pyrite</td>
<td><img src="image" alt="Pyrite" /></td>
<td>Packstone</td>
</tr>
<tr>
<td></td>
<td><img src="image" alt="Pyrite" /></td>
<td>Recrystallized sparry bed</td>
</tr>
<tr>
<td></td>
<td><img src="image" alt="Pyrite" /></td>
<td>Shale</td>
</tr>
</tbody>
</table>

Facies 1: Nodular limestone

Facies 2: Homogenous Wackestone

Facies 3: Laminated Mudstone

Facies 4: Packstone and Mudstone

Legend for stratigraphic charts objects.
Lemont Section stratigraphic column (part 1).
Lemont Section Stratigraphic column (part 2).
Reedsville Section stratigraphic column (part 1).
Reedsville Section stratigraphic column (part 2).
Reedsville Section stratigraphic column (part 3).
Reedsville Section stratigraphic column (part 4).
Table 5: Community metrics for Pennsylvania and Kentucky samples discussed in section 3.2. S refers to mean taxonomic richness, Shannon Index H describes both abundance and evenness of constituent taxa, while Buzas and Gibson’s E describes taxonomic evenness. The four leftmost biofacies are shared or similar (in the case of the Cryptolithus and Rafinesquina biofacies) between Pennsylvania and Kentucky.
Table 6: Percent abundance of taxa in each biofacies, determined from the combined total of all samples in each biofacies. Biofacies are arranged with increasing DCA axis-1 scores from left to right, interpreted here as deeper assemblages on the left, and shallower assemblages on the right.
APPENDIX D: Rarefaction and Species Accumulation Curves

Taxa accumulation and rarefaction curves by biofacies, Part 1
Taxa accumulation and rarefaction curves by biofacies, Part 2
## APPENDIX E: Faunal Lists

<table>
<thead>
<tr>
<th></th>
<th>Pennsylvania</th>
<th>Kentucky</th>
<th>New York</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bivalve</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bivalve</td>
<td></td>
<td>Actinopterella</td>
</tr>
<tr>
<td></td>
<td>Ambonychia</td>
<td></td>
<td>Colpomya</td>
</tr>
<tr>
<td></td>
<td>Deceptrix</td>
<td></td>
<td>Ctenodonta</td>
</tr>
<tr>
<td></td>
<td>Whiteavesia</td>
<td></td>
<td>Endodesma</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Whiteilla</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td><strong>Brachiopod</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dalmanella</td>
<td>dalmanellid</td>
<td>Paucicrura</td>
</tr>
<tr>
<td></td>
<td>Platystrophia</td>
<td>Platystrophia</td>
<td>Platystrophia</td>
</tr>
<tr>
<td></td>
<td>Rafinesquina</td>
<td>Rafinesquina</td>
<td>Rafinesquina</td>
</tr>
<tr>
<td></td>
<td>Strophomena</td>
<td>Strophomena</td>
<td>Strophomena</td>
</tr>
<tr>
<td></td>
<td>Sowerbyella</td>
<td>Sowerbyella</td>
<td>Sowerbyella</td>
</tr>
<tr>
<td></td>
<td>Dinorthis</td>
<td></td>
<td>Anazyga</td>
</tr>
<tr>
<td></td>
<td>Hesperorthis</td>
<td>Rhynochotrema</td>
<td>Hesperorthis</td>
</tr>
<tr>
<td></td>
<td>Leptaena</td>
<td>Zygospira</td>
<td>Plectorthis</td>
</tr>
<tr>
<td></td>
<td>Parastrophina</td>
<td>Hebertella</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protozyga</td>
<td>Heterorthina</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Skenidioides</td>
<td>Orthorhynchula</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>12</td>
<td>12</td>
<td>10</td>
</tr>
<tr>
<td><strong>Bryozoan</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prasopora</td>
<td>Prasopora</td>
<td>Prasopora</td>
</tr>
<tr>
<td></td>
<td>Stictopora</td>
<td>Stictopora</td>
<td>Stictopora</td>
</tr>
<tr>
<td></td>
<td>Corynotrypa</td>
<td>Corynotrypa</td>
<td>Corynotrypa</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Escharopora</td>
<td>Escharopora</td>
</tr>
<tr>
<td></td>
<td>bifolate</td>
<td>Constellaria</td>
<td>Amplexopora</td>
</tr>
<tr>
<td></td>
<td>f.r. Bryozoan</td>
<td>bifiolate trep.</td>
<td>Arthoclema</td>
</tr>
<tr>
<td></td>
<td>fenestrate</td>
<td>cryptostome</td>
<td>Bythopora</td>
</tr>
<tr>
<td></td>
<td>r. r. Bryozoan</td>
<td>encrusting trep.</td>
<td>Coeloclema</td>
</tr>
<tr>
<td></td>
<td></td>
<td>ramosite trep.</td>
<td>Crownopora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Dekayia</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Diplolecma</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Eridotrypa</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Graptodictya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hallopora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Nematopora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Newportopora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pachydictya</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Phylloporina</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Protocrisina</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pseudostictoporella</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Spatipora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Stictoporella</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Stomatopora</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ulrichostylus</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>3</td>
<td>4</td>
<td>24</td>
</tr>
<tr>
<td>Category</td>
<td>Example 1</td>
<td>Example 2</td>
<td>Example 3</td>
</tr>
<tr>
<td>-----------------</td>
<td>---------------------------</td>
<td>---------------------------</td>
<td>---------------------------</td>
</tr>
<tr>
<td>Crinoid</td>
<td>Rhaphanocrinus</td>
<td>Anomalocrinus</td>
<td>Cincinnaticrinus</td>
</tr>
<tr>
<td></td>
<td>Crinoid</td>
<td></td>
<td>Cleiocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Cyclomonile</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Dendrocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ectenocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Iocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lichenocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Merocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Reteocrinus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Schizocrinus</td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Gastropod</td>
<td>Liosira</td>
<td>Liosira</td>
<td>Liosira</td>
</tr>
<tr>
<td></td>
<td>Hormotoma</td>
<td></td>
<td>Hormotoma</td>
</tr>
<tr>
<td></td>
<td>Cyclonema</td>
<td>Sinuites</td>
<td>Lexaplexus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>gastropod</td>
<td>Sinuites</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Fusipira</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Trochonema</td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Inarticulate</td>
<td>Lingula</td>
<td>Trematis</td>
<td>Lingula</td>
</tr>
<tr>
<td></td>
<td>Inarticulate</td>
<td>Lingulella</td>
<td>Trematis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Petrocraenia</td>
<td>Schizocrania</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pseudolingula</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>2</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Nautiloid</td>
<td>Geisonoceras</td>
<td></td>
<td>Geisonoceras</td>
</tr>
<tr>
<td></td>
<td>Trocholites</td>
<td></td>
<td>Trocholites</td>
</tr>
<tr>
<td></td>
<td>orthoconic</td>
<td></td>
<td>Cameroceras</td>
</tr>
<tr>
<td></td>
<td>Leurocycloceras</td>
<td>orthoconic</td>
<td>Cyrtorizoceras</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Endocrus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Oconeas</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Orthocras</td>
</tr>
<tr>
<td>Total</td>
<td>3</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Trilobite</td>
<td>Flexicalymene</td>
<td>Flexicalymene</td>
<td>Flexicalymene</td>
</tr>
<tr>
<td></td>
<td>Isotelus</td>
<td>Isotelus</td>
<td>Isotelus</td>
</tr>
<tr>
<td></td>
<td>Calyptaulax</td>
<td></td>
<td>Calliops</td>
</tr>
<tr>
<td></td>
<td>Ceraurus</td>
<td></td>
<td>Ceraurus</td>
</tr>
<tr>
<td></td>
<td>Cryptolithus</td>
<td>Cryptolithus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Encrinurus</td>
<td></td>
<td>Encrinuoides</td>
</tr>
<tr>
<td></td>
<td>Brongniartella</td>
<td>Acidaspis</td>
<td>Hypodicanorotus</td>
</tr>
<tr>
<td></td>
<td>Bumastus</td>
<td>Decoroproetus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Illaenus</td>
<td>Gravicalymene</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Other</td>
<td>Scyphozoan: Conularia</td>
<td>Scyphozoan: Conularia</td>
<td>Scyphozoan: Conularia</td>
</tr>
<tr>
<td></td>
<td>Coral: Streptelasma</td>
<td></td>
<td>Coral: Streptelasma</td>
</tr>
<tr>
<td></td>
<td>Ostracod: indet.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rhombiferia: Rhombiferia</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cornulites: Cornulites</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Graptolite: indet</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tentaculid: tentaculid</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>5</td>
<td>6</td>
</tr>
</tbody>
</table>

**Table 7:** Faunal lists for Pennsylvania, Kentucky, and New York. Bolded taxa are shared between two collections, while taxa shared between all three collections are bolded and underlined.
APPENDIX F: Additional Photographs

Figure 26: Chert nodules at the base of the Salona Formation, Reedsville. Phone for scale.

Figure 27: Pyritized Cryptolithus cephalon, from the lower New Enterprise member, Reedsville. Specimen is approximately 1 cm across.
Figure 28: K-bentonite couplet at meter 5.5 Reedsville. The Deicke K-bentonite is the thicker (approximately 20 cm thick), whitish, crumbling bed above (to the right) of the red stained bed.

Figure 29: Two cephalons (left) and three pygidia (right) of the generally rare but locally abundant trilobite *Brongniartella*, from meter 18 at Reedsville. Pencil for scale.
Figure 30: *Parastrophina* cast from approximately meter 53 at Reedsville; fossil width is 1.3 cm.

Figure 31: *Dinorthis* cast, collected at meter 56 in Reedsville. Specimen measures approximately 2 cm across.
Figure 32: Amalgamated storm beds from meter 117 at Reedsville. Each visible bed is approximately 1 cm thick.

Figure 33: Atrypid brachiopods in a Chondrites rich block at meter 119 of the Reedsville section. Individuals measure approximately 5 mm across.
Figure 34: Gyroconic nautiloid mold (c.f. *Trocholites*) collected at Spring Mills. Sutures faintly visible in cross section. A second specimen was also found in the same sample.

Figure 35: *Corynotrypa*, a cyclostomate bryozoan (Stenolaemata), here encrusting an *Isotelus* trilobite fragment. Specimen collected from the Roaring Spring member at Lemont. Scale visible to the left shows 1 mm markings.
Figure 36: Panoramic view of Lemont collection area

Figure 37: Panoramic view of Reedsville collection area