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UNIVERSITY OF CINCINNATI

MAY 19, 19 99

I, KURT ROSENKRANTZ

hereby submit this as part of the requirements for the degree of:

MASTER OF SCIENCE

in GEOLOGY

It is entitled COMPOSITIONAL VARIATION
IN CINCINNATIAN MUDSTONE COMMUNITIES
(UPPER ORDOVICIAN OF OHIO, INDIANA
AND KENTUCKY): IMPLICATIONS FOR
COORDINATED STASIS

Approved by:

David L. Meyer

Nigel CH

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COMPOSITIONAL VARIATION IN CINCINNATIAN MUDSTONE COMMUNITIES (UPPER ORDOVICIAN OF OHIO, INDIANA AND KENTUCKY): IMPLICATIONS FOR COORDINATED STASIS

A thesis submitted to the

Division of Research and Advanced Studies
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE

in the Department of Geology
of the College of Arts and Sciences

1999

by

Kurt J. Rosenkrantz

A.B., Harvard University, 1994

Committee Chair: David L. Meyer

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Abstract

The Upper Ordovician Cincinnatian Series in its type area consists of cyclically alternating limestones and mudstones deposited in a shallow, distal ramp setting. While most mudstones are barren or sparsely fossiliferous, some horizons, known popularly as "butter shales", contain a diverse and well-preserved macrofauna of mollusks, inarticulate brachiopods, and trilobites. Coordinated stasis, a theory of whole-community stability and punctuated turnover at geologic time scales, provides a framework for assessing patterns of variation and/or stability in these assemblages through the type Cincinnatian.

Faunal abundance data collected for this study were combined with previous studies to form a database spanning most of the Cincinnatian Series. Along traceable horizons, lateral heterogeneity on outcrop and regional scales was insignificant relative to variation between units. In general, younger (Richmondian) samples could be distinguished from older (Edenian/Maysvillian) samples by larger body size for most taxa, the addition of several new genera (*Corallidomus*, *Pholadomorpha*, *Ancienta*), and a shift in the most abundant taxa from *Sinuites* in the older samples to lingulids in the younger samples. Although a suite of common taxa appeared in most samples, at least five horizons contained unique associations of unusual taxa.

Analysis of persistence of taxa through the Cincinnatian, holdover of taxa from the Middle Ordovician, and carryover of taxa into the Silurian show that the Cincinnatian mudstone faunas were too variable in composition to conform to the coordinated stasis model. Multivariate analyses further demonstrate the lack of recurrent faunal associations that could indicate strong ecological relationships. Instead, it appears that most taxa responded independently to a variety of environmental parameters.

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I could not have completed this project without the generous help and tremendous support I received from many people. Foremost is my advisor Dr. David Meyer, who introduced me to the Cincinnatian, took me diving, mentored me in the basics of fieldwork and specimen preparation, and most of all supported and encouraged me when doubts crept in. Dr. Arnie Miller showed great interest in the project and in my development as a scientist as well. His timely criticism helped me to focus and sharpen my arguments at every stage. Dr. Nigel Hughes (U.C. Riverside), my third committee member, educated me in trilobite taphonomy and gave me access to important museum collections of mudstone fauna.

I gratefully acknowledge the large number of people who advised and aided me in each phase of this study. Dr. Gordon Baird (SUNY Fredonia), Sharon Diekmeyer, and Dan Cooper took me into the field to locate promising "butter shale" beds. The Kirschners, Campbells, Duane Wells and Jim Cruey gave me permission to collect fossils on their property--without the cooperation of such individuals, field paleontology would surely die. Maria Wheeler and her Uncle John collected fossils at Hannah Creek, Chad Mussell measured trilobites, and Drs. Robert Frey and John Pope (Miami U.) helped me identify specimens. Dr. Warren Huff taught me X-ray diffraction, Dr. Mary Droser (U.C. Riverside) introduced me to the world of trace fossils, and Drs. Steve Holland (U. Georgia) and Ben Dattilo gave invaluable advice and encouragement.

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Introduction

While earlier researchers focused primarily on description and classification of individual taxa, the study of recurrent assemblages in ancient faunas, or paleocommunities, began in earnest during the 1960s with landmark studies by Ziegler (1965), Ziegler et al. (1968), and Bretsky (1968, 1969). Until the 1980s, most of these paleocommunity studies either related faunal transitions to environmental gradients (Ziegler et al., 1968; Bretsky, 1968 and 1969; Watkins, 1978) or focused on life habits and guild structures (e.g. Walker, 1972); relatively few studies examined how communities changed through time.

In the meantime, the concept of punctuated equilibrium (Eldredge and Gould, 1972) reset paradigms of how evolution transpires within individual lineages. With the suggestion that lineages typically experienced episodic changes, it was logical to ask whether entire assemblages might show similar patterns. In 1983, Boucot proposed dividing the Phanerozoic into twelve "Ecological-Evolutionary Units" or EEUs. Throughout each of these broad time intervals, the basic structure of communities across all environments remained relatively stable. After major extinction events, new community types formed from surviving taxa, along with "new genera and species derived from subsequent adaptive radiations" (Boucot, 1983, p. 5). Boucot's EEUs were revised and related to Sepkoski's (1990) evolutionary faunas by Sheehan (1996).

More recently, based on extensive documentation of Silurian and Devonian faunal data from New York, Brett and Baird (1992) proposed the idea of "coordinated stasis", suggesting that stasis and punctuated change were coordinated among species within the same community. Through the Silurian and Devonian in upstate New York, Brett and Baird documented 10 "Ecological-Evolutionary Subunits", or E-E subunits, ranging in duration from 2 to 8 million years (Brett and Baird, 1995). Each subunit was characterized by a high degree of persistence of species (averaging 74%), while carryover between subunits was minimal, ranging from 9% to 55% with an average carryover of 22%. Brett

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and Baird (1995) and other workers (Morris et al., 1992) suggested that these patterns of coordinated stasis would be discovered elsewhere in the fossil record, and could provide a new paradigm in ecological and evolutionary theory, much as punctuated equilibrium had done in the 1970s.

The hypothesis of coordinated stasis has two primary components. The first is that, within an E-E subunit, morphological change within individual lineages is relatively insignificant (Brett et al., 1996). The second is that community structure--the dominant species, trophic relationships, and faunal associations--is stable within an E-E subunit and significantly changed between E-E subunits (Brett et al., 1996). To fully test the coordinated stasis hypothesis, it is therefore necessary to measure morphological change within species and to analyze community structure through time.

This study is focused on the second component of coordinated stasis: the degree of stability and persistence in recurrent mudstone faunal assemblages of the Cincinnatian Series (Upper Ordovician of Ohio, Indiana and Kentucky). The study has three primary goals:

1) To record the faunal assemblage of a recurrent biofacies spanning a period of approximately five million years (Holland and Patzkowsky, 1996), in order to assess whether patterns of stability and turnover proposed by the coordinated stasis hypothesis apply to this interval.

2) To use ecologic, taphonomic, stratigraphic, sedimentologic and ichnologic data to deduce environmental variables affecting community composition.

3) To assess the strength of ecologic bonds, as demonstrated by recurrence of particular species/genus associations within the sampled communities, in order to evaluate proposed intrinsic causes (i.e. "ecological locking") of the coordinated stasis pattern.

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Chapter 1: Geologic Setting

The strata of the Cincinnatian Series (Upper Ordovician) exposed in the region of southwest Ohio, north-central Kentucky, and southeast Indiana, consist of interbedded carbonates and terrigenous mudstones deposited on a shallow, epicontinental ramp. The controls on deposition of these rapidly alternating lithologies have been an object of study for the past 40 years (e.g. Ford, 1967; Anstey and Fowler, 1969; Harris and Martin, 1979; Tobin, 1982; Jeanette and Pryor, 1993, Holland et al., 1997).

While most mudstones in the Cincinnatian are relatively unfossiliferous, some horizons contain a diverse and well preserved fauna of inarticulate brachiopods, trilobites, and mollusks, which contrasts with the bryozoan and articulate brachiopod assemblages that characterize Cincinnatian limestones. Informally known as "butter shales" and renowned among local collectors, these fossiliferous mudstones are the subject of this study.

A brief note on stratigraphic and lithologic terminology

The Elementary Guide by Bucher et al. (1939) popularized an essentially biostratigraphic classification of Cincinnatian formations. During the 1960s, many of these "bioformations" were consolidated into large lithostratigraphic units, such as the Dillsboro Formation (Brown and Lineback, 1966), the Tanners Creek Formation (Hatfield, 1968), and the Bull Fork Formation (Peck, 1966). Recent authors (Tobin, 1980, 1986; Schumacher et al., 1991; Holland, 1993), have argued that many of the old biostratigraphic units *are* in fact distinct lithologically and better match important sequence boundaries. These units also proved useful for this study. The Formation and Member names and a simplified stratigraphic column are shown in Figure 1.

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Figure 1 - Cincinnatian lithostratigraphy used in this report, and simplified distribution of lithologies throughout the interval. Formation names from Caster et al., 1955; Schumacher, 1992; and Holland, 1993. Absolute age from Holland and Patzkowsky, 1997. Lithological distribution based on Brandt, 1980 (Figure 1).

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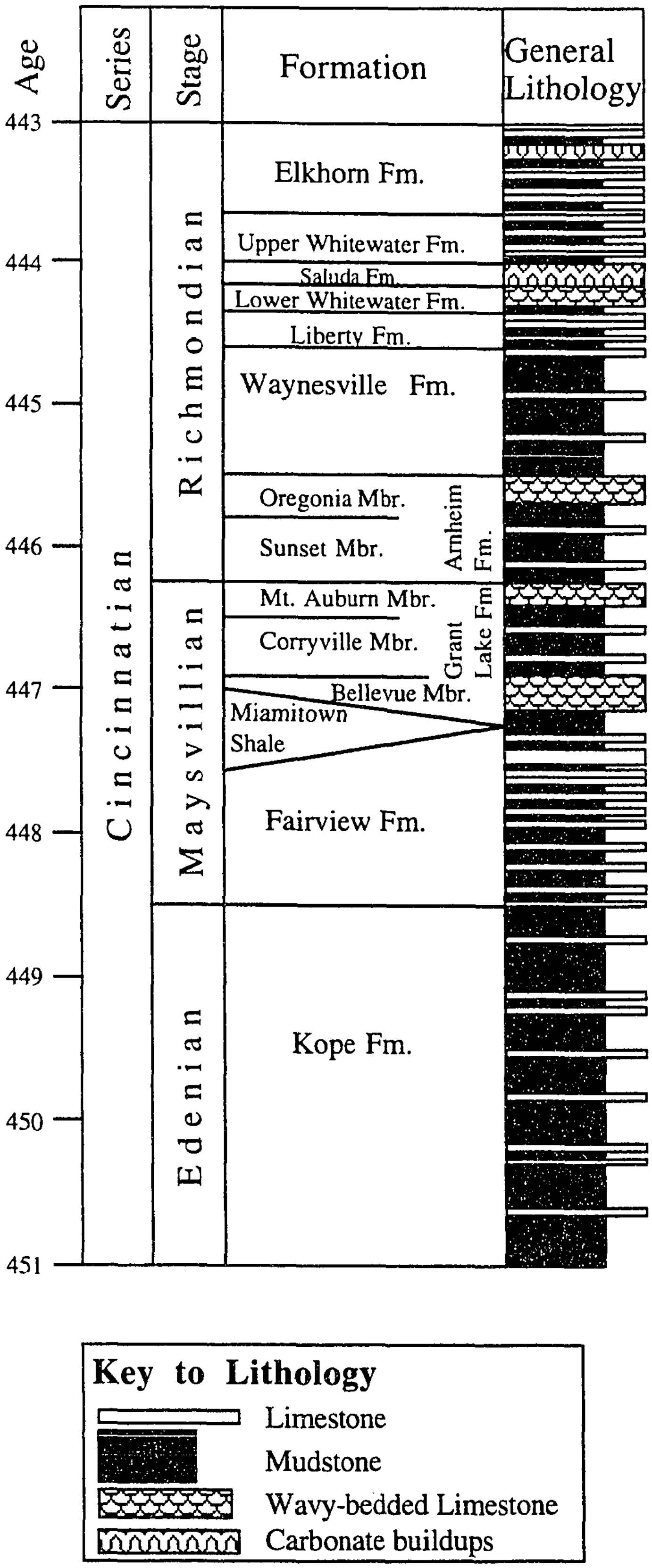

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Because most of the muddy rocks in the type Cincinnatian (especially those that contain well preserved faunas) lack distinctive bedding planes, they are classified in this study as "mudstone", rather than the more common term "shale".

Models of deposition of Cincinnatian strata

The limestones and mudstones of the type Cincinnatian Series were deposited on a shallow, gently northwest dipping carbonate ramp (Holland, 1993). The terrigenous component was derived from the rising Taconic mountains about 850 km to the east (Tobin, 1982), and the type Cincinnatian strata were deposited in a mixed zone between deltaic complexes to the east and carbonate platforms to the west (Figure 2).

An interesting element of Cincinnatian stratigraphy is the occurrence of storm beds. In the Late Ordovician, the Cincinnati area was positioned in a subtropical setting about 20° south of the equator (Figure 3). The position of eastern North America was ideal for the formation of tropical storms. The equivalent Martinsburg Formation of southwestern Virginia also contains well documented storm deposits (Kreisa, 1981). In the Cincinnatian, these deposits generally consist of cross-bedded or planar-bedded calcareous siltstones, or calcisiltites, often with a basal shell lag (Tobin, 1982; Goldman, 1993). Other evidence includes gutter casts, tool marks, and rip-up clasts (Goldman, 1993). Some workers (Brandt, 1980; Tobin, 1982; Brandt-Velbel, 1985) have taken this concept a step further by claiming that the fine grained mudstones formed as a result of storm deposition as well. This rapid deposition of storm beds most likely accounts for the often spectacular preservation of fossils within many of the mudstones (Brandt, 1980; Frey, 1983; Brandt-Velbel, 1985).

In 1969, Anstey and Fowler proposed topographic control over limestone vs. mudstone deposition in the Eden mudstone (Kope Formation). According to this view, localized "islands" of filter feeding organisms colonized slight topographic highs that provided some relief from mud deposition. A constantly shifting seafloor caused the burial

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Figure 2 - Upper Ordovician depositional environments in Eastern North America. Modified from Peterson, 1994.

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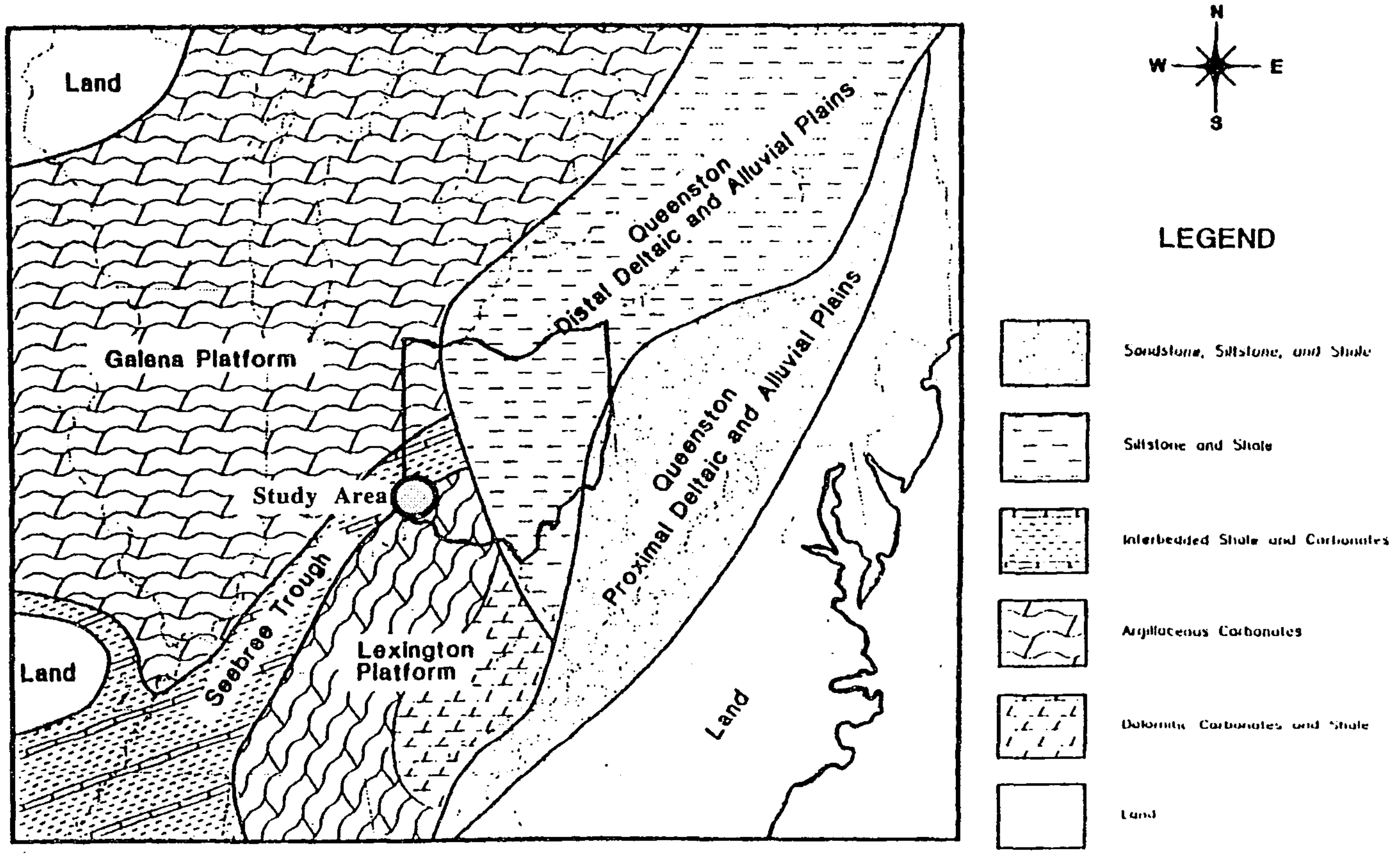

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Figure 3 - Paleogeographic reconstruction showing position of North America and proposed storm tracks in the Upper Ordovician. From Dattilo, 1994.

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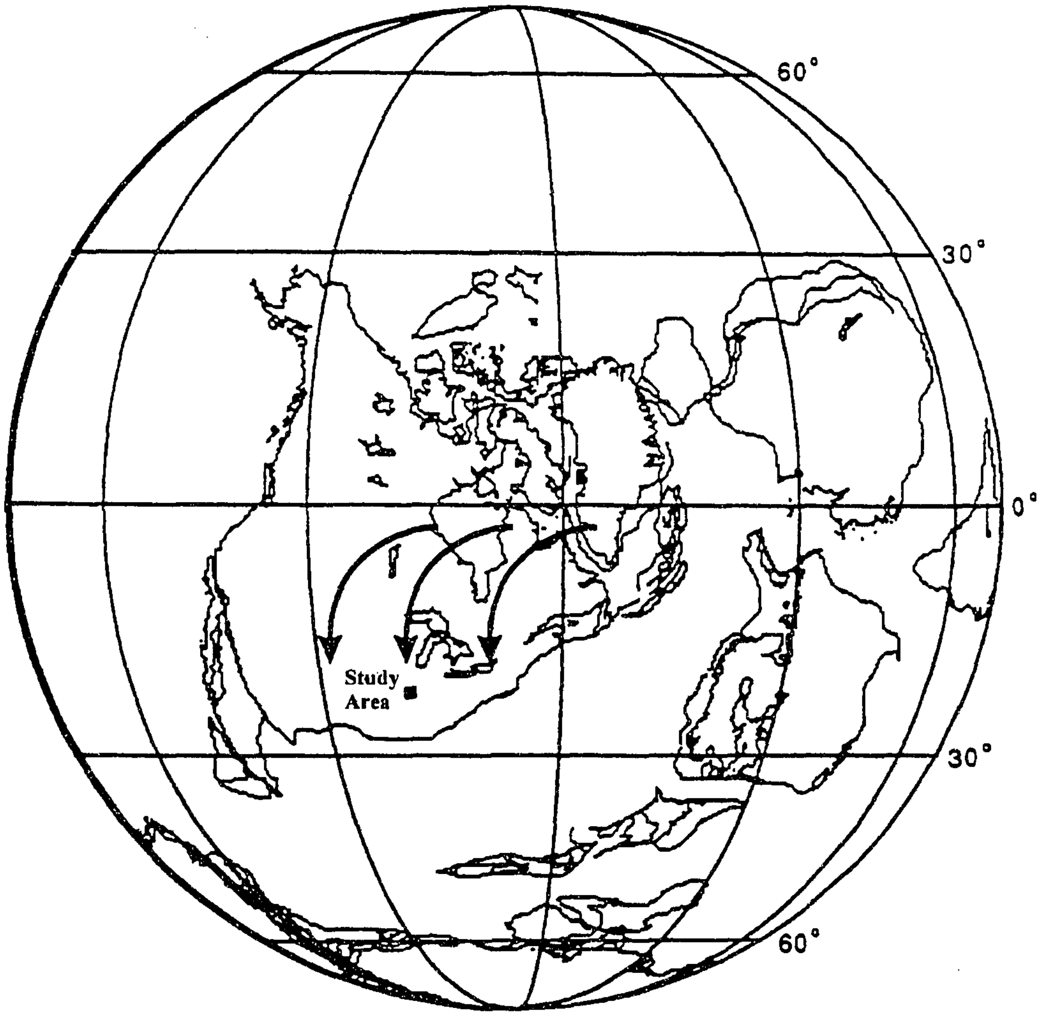

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of these carbonate patches by terrigenous mud. The fact that individual Kope limestone beds tend to pinch out after a short distance supports this hypothesis (but is also consistent with the storm deposition models described below). Based on morphological data from bryozoans and sedimentary features such as ripples, a water depth of about 65 feet (20 m) was estimated for the Kope mudstones (Anstey and Fowler, 1969). This depth estimation, below normal wave base but above storm wave base, has been accepted by most workers.

A second mechanism for limestone formation that does not directly involve cyclicity is ecological succession (Harris and Martin, 1979; Figure 4). In this model (based on data from Richmondian strata), small, thin shelled brachiopods such as *Onniella* initially colonize a muddy substrate. As skeletons accumulate, the substrate is gradually stabilized, allowing for colonization by bryozoans, crinoids, and other epifauna. In support of this model, Harris and Martin (1979) showed that the central portion of thick limestones often contained a more diverse assemblage of epizoans than the bottom, top, or lateral margins. Again, sudden or gradual deposition of muds is the agent thought to kill these communities, allowing the process to begin again. A nearly identical mechanism was proposed by Tobin (1980) to account for similar Maysvillian beds.

As mentioned above, Tobin (1982) raised the prospect that storm deposition accounted for not only the calcisiltites, but the mudstones as well:

> Conversely, terrigenous sediments were never deposited in fair weather on the Cincinnatian shelf because of the greater distance from the Taconics. Thus, if storms had not occurred during Late Ordovician time, only carbonates would have been deposited, and stratification would probably have been limited to thick, major facies changes. (Tobin, 1982, p. 114)

Therefore, in Tobin's view, the main control on carbonate deposition was the flux of terrigenous sediments transported by strong storm generated currents.

The final model mentioned here is that of Jennette and Pryor (1993). By measuring and correlating several closely-spaced outcrops representing the Kope to Fairview transition, Jennette and Pryor were able to demonstrate that, although individual limestone beds tend to pinch out laterally, individual shoaling upward packages on the order of two to

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Figure 4 - Proposed model of succession in Cincinnatian communities. From Harris and Martin, 1979.

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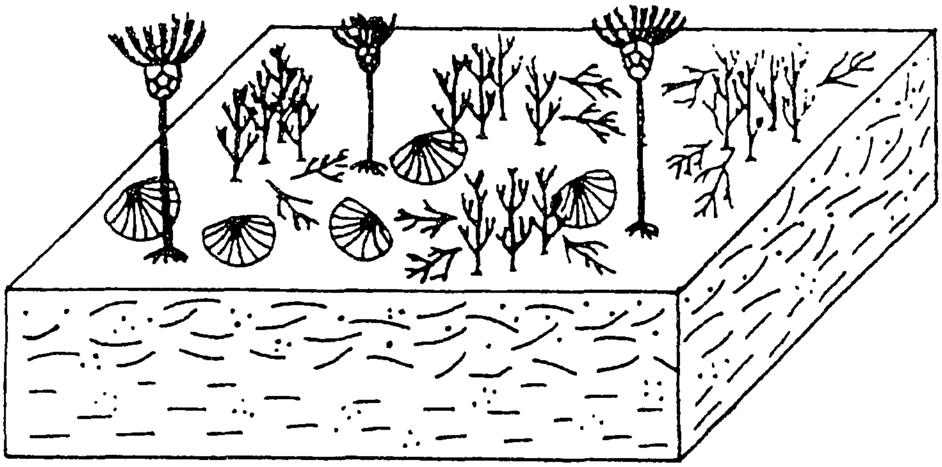
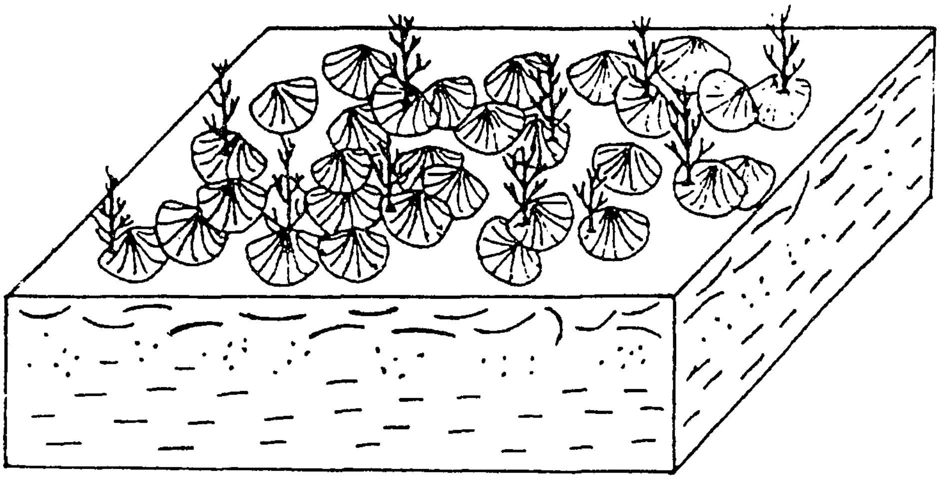
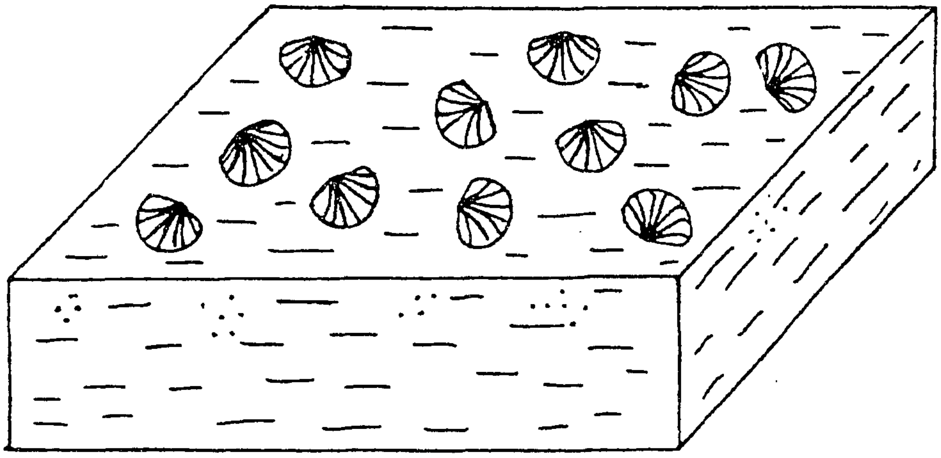


MATURE COMMUNITY



SUCCESSION



COLONIZATION

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Figure 5 - Correlation of shoaling-upward packages in Kope and Fairview formations. From Jeanette and Pryor, 1993.

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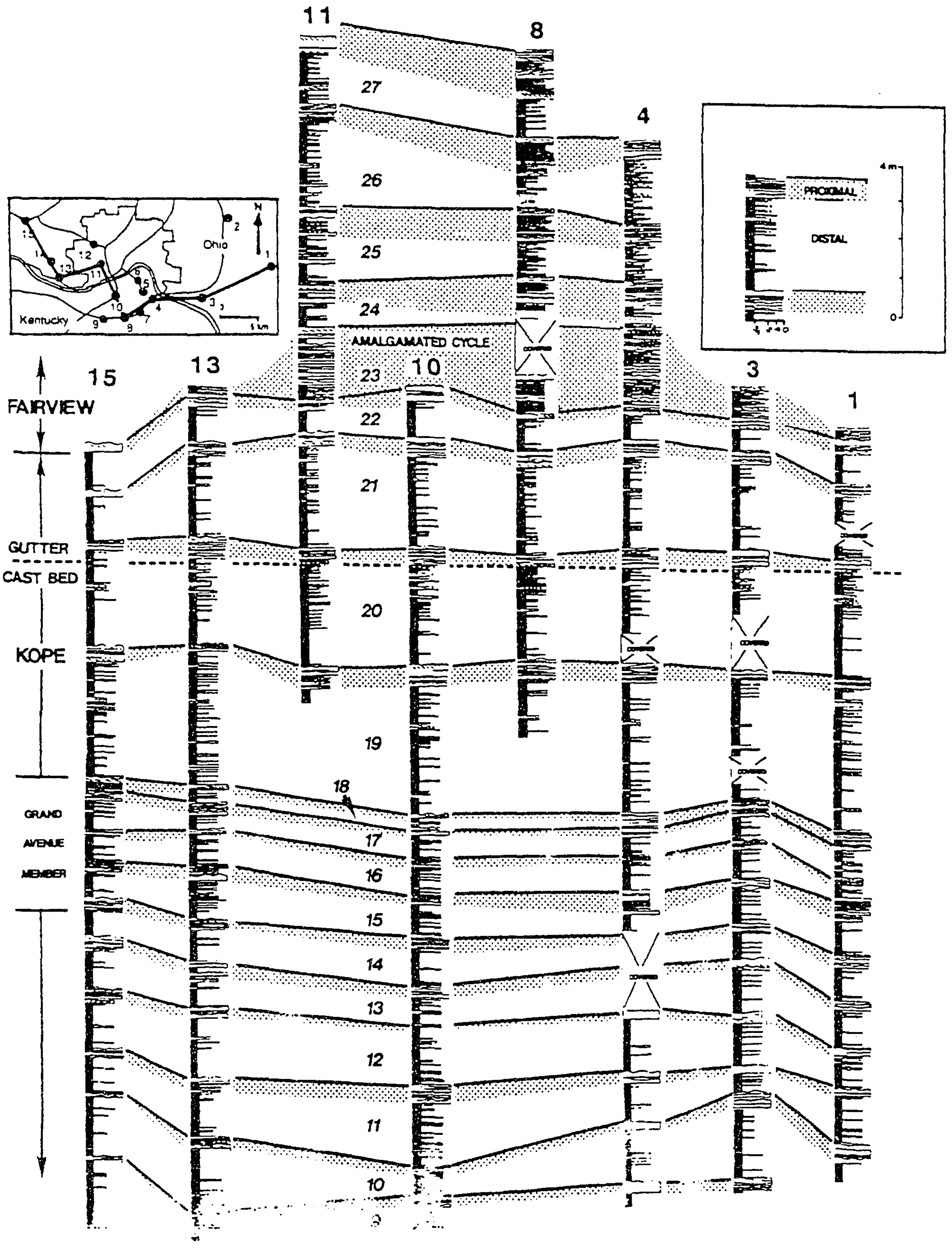

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five meters thick could be traced laterally and correlated (Figure 5). The lateral continuity of limestone rich packages provides strong evidence against the "patchy" models proposed by Anstey and Fowler (1969), and Harris and Martin (1979), at least for the Kope and Fairview formations. The consistently repeating structure of these cycles led Jennette and Pryor (1993) to invoke a periodic external control (glacial eustacy) for their deposition. Thus, whereas Tobin hypothesized that changes in flux of terrigenous sediment accounted for the alternations in mudstones and limestones at this scale, Jennette and Pryor suggested that changes in sea level were the primary control. An even more detailed study (Holland et al., 1997) also posits sea level changes as the most likely factor influencing deposition of carbonates and muds, but shows that cycles are highly variable in architecture and difficult to identify consistently. In fact, successive attempts by these workers to delineate cycles yielded differing interpretations of the same stratigraphic data (Holland et al., 1997).

According to these models, the presence of thick limestone beds is generally indicative of proximal depositional environments, and thus represents relatively shallow, onshore facies. Mudstone rich facies, on the other hand, indicate deposition in deeper water. An alternative indicator of paleobathymetry is the presence of storm beds. Kreisa (1981) stated that in shallow water facies, storm deposits are often amalgamated, are thicker, and occur more frequently than in distal facies. This pattern has been observed in the Cincinnatian as well (Jennette and Pryor, 1993).

Sequence stratigraphy

From the mudstones and thin limestones of the Kope Formation to the wavy bedded carbonates of the Bellevue formation, there is an increase in the percentage of carbonates relative to mudstone. Other indications, including a faunal change from thin shelled, delicate fossils in the Kope (such as the orthid brachiopod *Onniella*) to robust, well abraded fossils in the Bellevue (Diekmeyer, 1990), support the idea that this is a shallowing upward succession. A similar pattern can be seen in the Corryville to Mt.

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Auburn beds, the Sunset to Oregonia beds (both members of the Arnheim Formation), and the Waynesville through Saluda sequence leading to a major unconformity at the Ordovician Silurian boundary.

Recent workers (Holland, 1993; Goldman, 1993; Dattilo, 1994; Pope and Read, 1995; Holland and Patzkowsky, 1996, Holland et al., 1997) have applied the principles of sequence stratigraphy to these shallowing upward packages. In Holland's (1993) original model (Figure 6), rapid rises of sea level and much more gradual falls resulted in compressed lowstand and transgressive systems tracts followed by thick highstand systems tracts. Transgressive surfaces and maximum flooding surfaces were basically the same. More detailed studies by Dattilo (1994) and Goldman (1993) revealed that these sequences were more symmetrical, with well developed transgressive systems tracts. The most recent report by Holland and Patzkowsky (1996) shows six sequences in the Cincinnatian, labeled C1 through C6 (Figure 7). In this study, quantitative samples have been taken from sequences C1, C2, C3, and C5. One additional locality from C4 is also discussed. The studied mudstone biofacies does not occur in sequence C6.

Summary

In this study, the following depositional aspects of the fossiliferous mudstones are addressed:

1) The position of these mudstones relative to sequence boundaries and maximum flooding surfaces.

2) The presence of organisms useful as indicators of depth, rate of sedimentation, current, and stability of the substrate.

3) The extent of burrowing within the mudstones.

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4) The relative amounts of clay and silt in the mudstones relative to one another and to other, more "typical" Cincinnati mudstones.

5) The relationship of patterns of faunal change in the mudstone communities to sequence boundaries and to shallowing upward successions within these sequences.

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Figure 6 - Water depth curves for the Cincinnatian Series, based on transitions in facies. From Holland, 1993.

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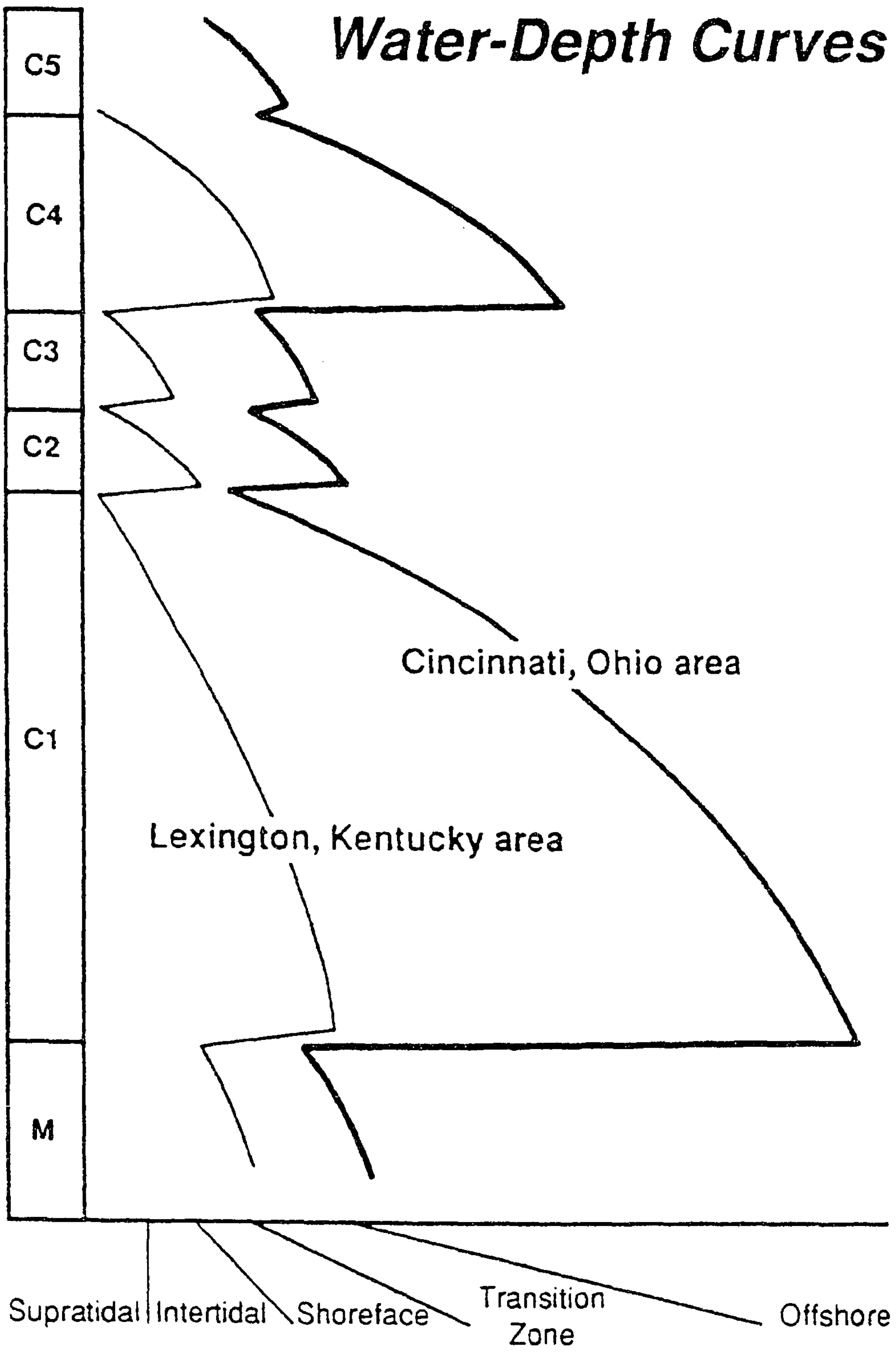

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Figure 7 - Sequence stratigraphy of Middle and Upper Ordovician in North America, with absolute ages and formation names. From Holland and Patzkowsky, 1996.

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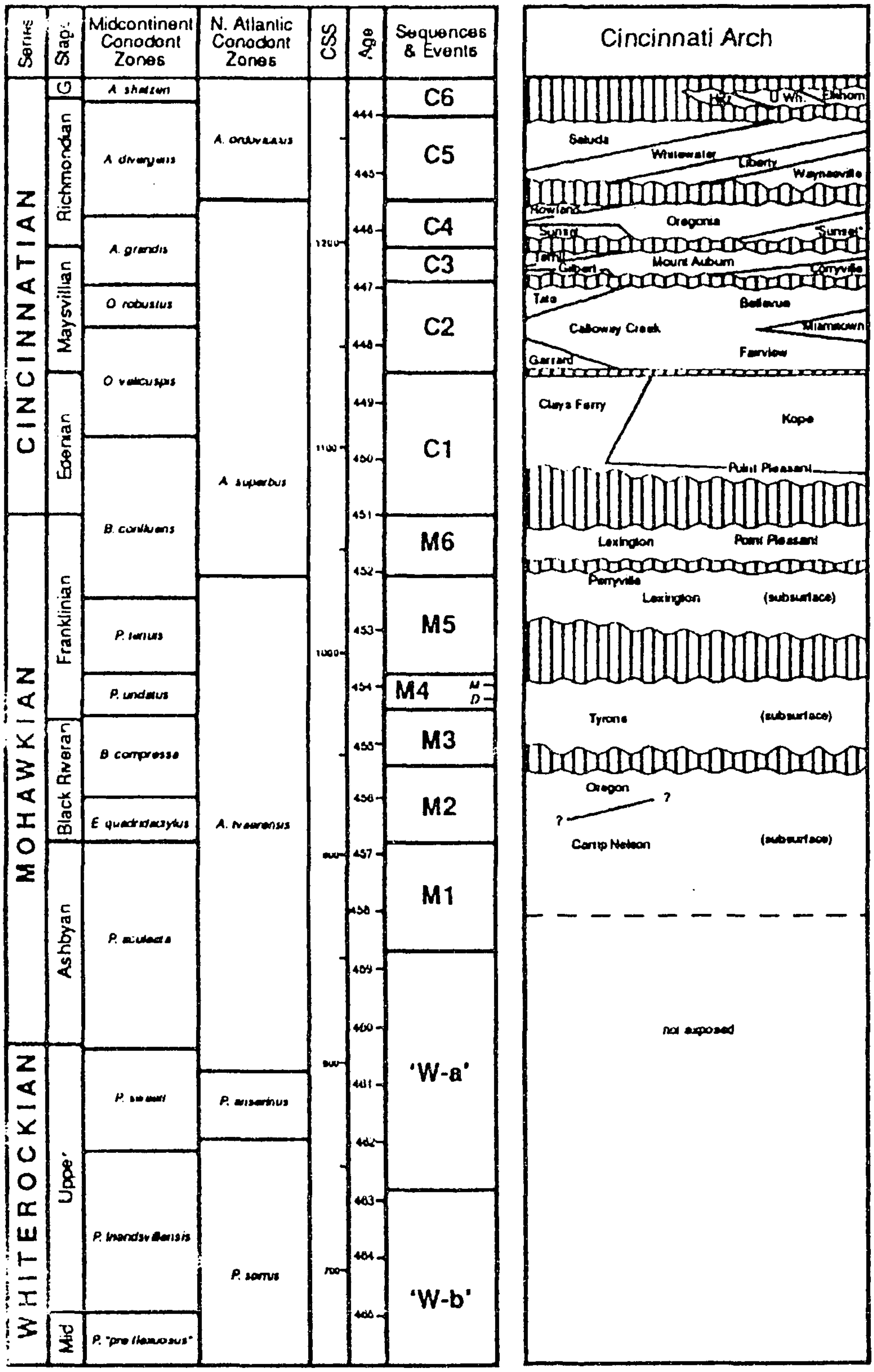

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Chapter 2: Previous Paleocommunity Studies

Although the majority of studies of Cincinnatian paleocommunities have focused on the articulate brachiopod/bryozoan dominated assemblages found in carbonates, a few researchers have explored the well-preserved but less accessible faunas of the mudstones. A brief summary of these studies is given below.

Bretsky's (1968, 1969) classification of communities in the Upper Ordovician of the Appalachian Basin were not only landmark studies in community paleoecology, but have a great deal of relevance to faunas of the Cincinnati Arch. Many of the genera mentioned by Bretsky (1969) are also major constituents in the Cincinnatian.

The main difference between Appalachian and Cincinnatian depositional environments was the amount of terrigenous influx. Sandstone and siltstone, largely absent in the Cincinnatian, are the dominant lithologies in much of the Upper Ordovician of the Appalachian Basin (Bretsky, 1969). A second major difference is the interpretation of limestone and terrigenous lithologies. In the Cincinnatian, mudstone rich zones are generally thought to represent offshore, deeper water deposition, while carbonate rich intervals represent more proximal, high energy conditions. In the Appalachian basin it is the opposite--the mudstones and siltstones are generally interpreted to be more proximal than the carbonates, representing shallower water and higher energy conditions.

Bretsky (1968, 1969) defined three communities found in these lithologies: a *Sowerbyella-Onniella* community, which inhabited mixed siltstone and mudstone lithologies of moderate depth; an *Orthorynchula-Ambonychia* community, which inhabited proximal sandstone and siltstone facies; and the *Zygospira-Hebertella* community, which inhabited distal mudstone and carbonate facies from shallow to deeper depths. As in the Cincinnatian, pelecypod mollusks were important in environments with greater amounts of terrigenous material, while brachiopods and bryozoans flourished in cleaner, carbonate rich zones. As Miller (1989) also noted, the presence of pelecypods was more dependent on

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substrate type than depth. A subsequent quantitative study of similar strata (Springer and Bambach, 1985) expanded the number of communities to five, including a *Lingula* community and a bivalve community. In this study, *Lingula* was interpreted as characteristic of shallow, nearshore environments (Springer and Bambach, 1985). This may contrast with the Cincinnatian, where lingulids appear in sediments usually associated with deeper water (Richards, 1972). As with the pelecypods, the appearance of lingulids in deeper water mudstones in the Cincinnatian was probably related to availability of a suitable substrate (Richards, 1972).

The first major quantitative studies of Cincinnatian communities were conducted by Fox (1962, 1968), who distinguished six assemblage zones (increased to eight in 1968) in the Richmond Group based on counts on limestone slabs. This analysis was further refined by Frey (1978), who distinguished no less than 18 faunal zones in the Richmondian strata. Frey (1978) was also among the first to consider the soft-bottom assemblages, noting that pelecypods, gastropods, trilobites, and crinoids all seemed to favor the muddier substrates.

The first quantitative study of Cincinnatian mudstone communities was also conducted by Frey (1983, 1987a), who investigated the *Treptoceras duseri* zone in the Waynesville Formation (Richmondian) of southern Ohio and southeast Indiana (in Indiana, the zone is denoted the "trilobite shale"). Concurrently, Guiseffi (1982) analyzed faunal abundances in three mudstone communities of the Mt. Hope Member of the Fairview formation (Maysvillian). Quantitative data from Guiseffi (1982) and Frey (1987a, 1987b) have been added to the data collected in this study to form a comprehensive database of Cincinnatian mudstone faunas.

Other relevant studies of Cincinnatian mudstones and constituent faunas include Brandt's (1980, 1985) work on the morphology and paleoecology of the trilobite *Flexicalymene meeki*, Tobin's (1980, 1982) investigation of Edenian and Maysvillian

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mudstone petrology and deposition, and Ferree's (1994) excavation of a trilobite-rich locality in the Sunset member of the Arnheim Formation.

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Chapter 3: Methods

Because extensive weathering and slumping has made location of and collection from mudstone horizons difficult on many of the region's roadcuts, most collection in this study was done from streambanks, which generally contain cleaner outcrops with fresher, relatively unweathered mudstone, more suitable for sedimentological and ichnological analysis. The disadvantages of this choice were a decrease in stratigraphic control and less opportunity to sample along a horizontal transect. The following criteria were used to select localities:

1) Relative "purity" of mudstone beds, with a minimum thickness of 15 cm and few calcareous lenses.

2) Presence of whole body fossils integrated into the mudstone, as opposed to thin "shell-hash" layers composed of disarticulated brachiopod valves and fragmented bryozoans.

Quantitative samples of fossils were compiled from nine mudstone horizons distributed throughout the Cincinnatian interval. This was combined with an additional seven samples collected by Guiseffi (1982) and Frey (1987a, 1987b), to form a database of 16 samples representing 12-13 distinct horizons, five formations, and four of Holland and Patzkowsky's (1996) six depositional sequences (Figures 8, 9).

For all samples referred to in this study, a bulk sampling method was used, as opposed to sampling horizontally along a bedding plane (these mudstones generally lack distinctive bedding planes). At each site excavated by the author, a grid of string and nails was placed over the area to be excavated, dividing the unit vertically into 10 cm intervals (Figure 10). As the rock was quarried out piece by piece, the position of each fossil was recorded with three coordinates: distance from left edge, height above base, and depth

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Figure 8 - Stratigraphic distribution of all samples in this study.

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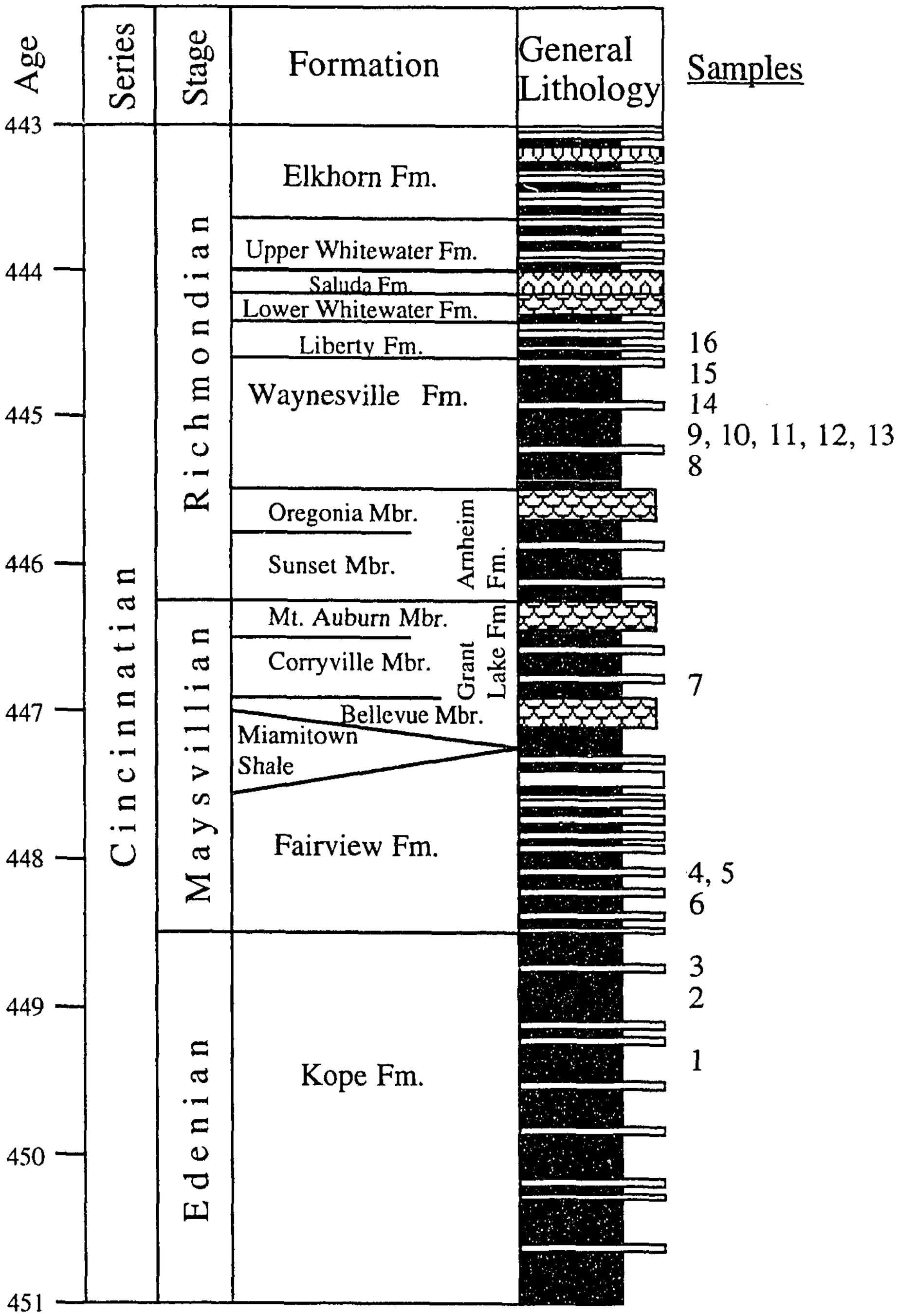

Key

1. Orphanage Road (Frey, 1987b)
2. Backbone Creek
3. Backbone Upper
4. Reading Road (Guiseffi, 1982)
5. Springdale (Guiseffi, 1982)
6. Harrison (Guiseffi, 1982)
7. Dornbusch
8. Russell Lower
9. East Fork Blue Creek
10. Russell Middle
11. Bon Well Hill (Guiseffi, 1982)
12. Harper's Run (Frey, 1987a)
13. US Rt. 42 (Frey, 1987a)
14. Russell Top
15. Hannah Creek
16. Clear Fork

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Figure 9 - Locations of sites referred to in this study relative to Ordovician deposits in the Cincinnati area.

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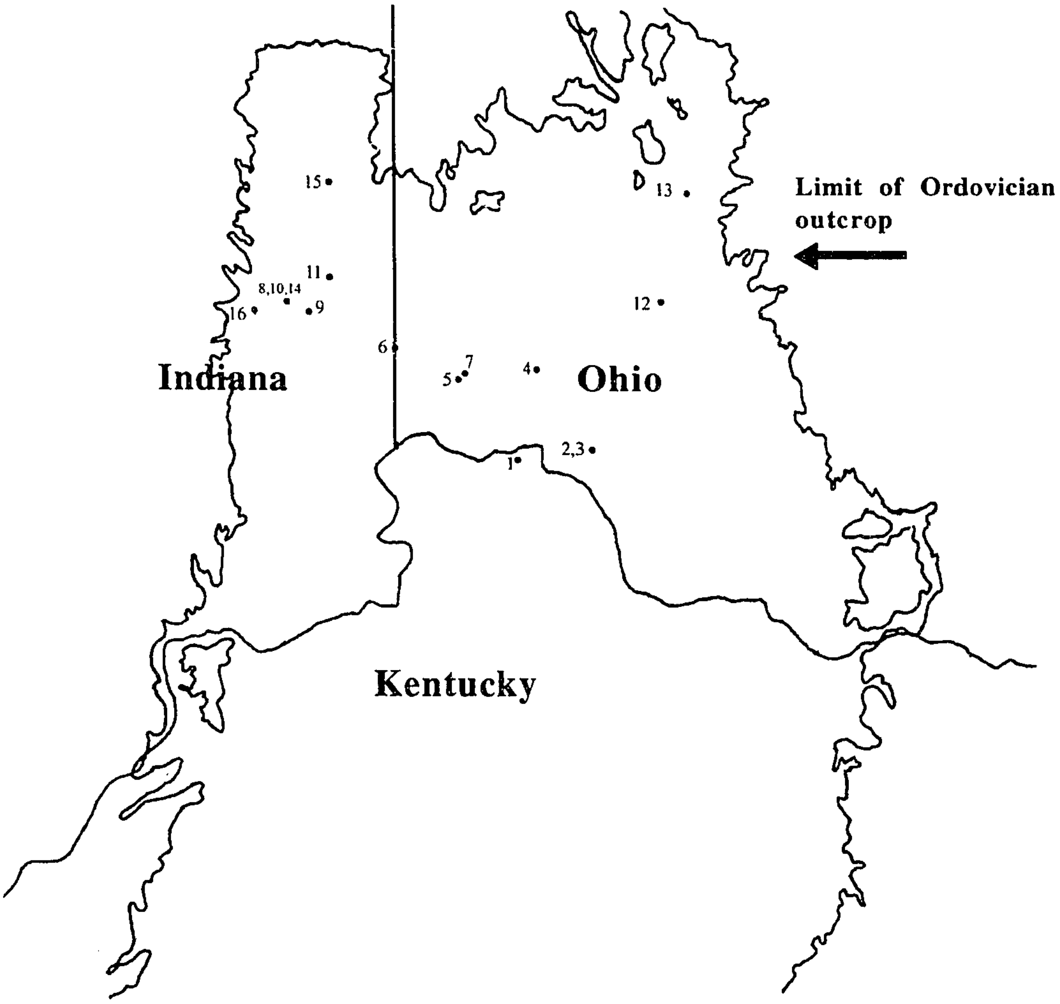

Key

1. Orphanage Road (Frey, 1987b)
2. Backbone Creek
3. Backbone Upper
4. Reading Road (Guiseffi, 1982)
5. Springdale (Guiseffi, 1982)
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12. Harper's Run (Frey, 1987a)
13. US Rt. 42 (Frey, 1987a)
14. Russell Top
15. Hannah Creek
16. Clear Fork

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Figure 10 - String and nail grids used for collections at Russell Branch Middle (top) and Hannah Creek (bottom). Rock hammer and 30 cm ruler for scale.

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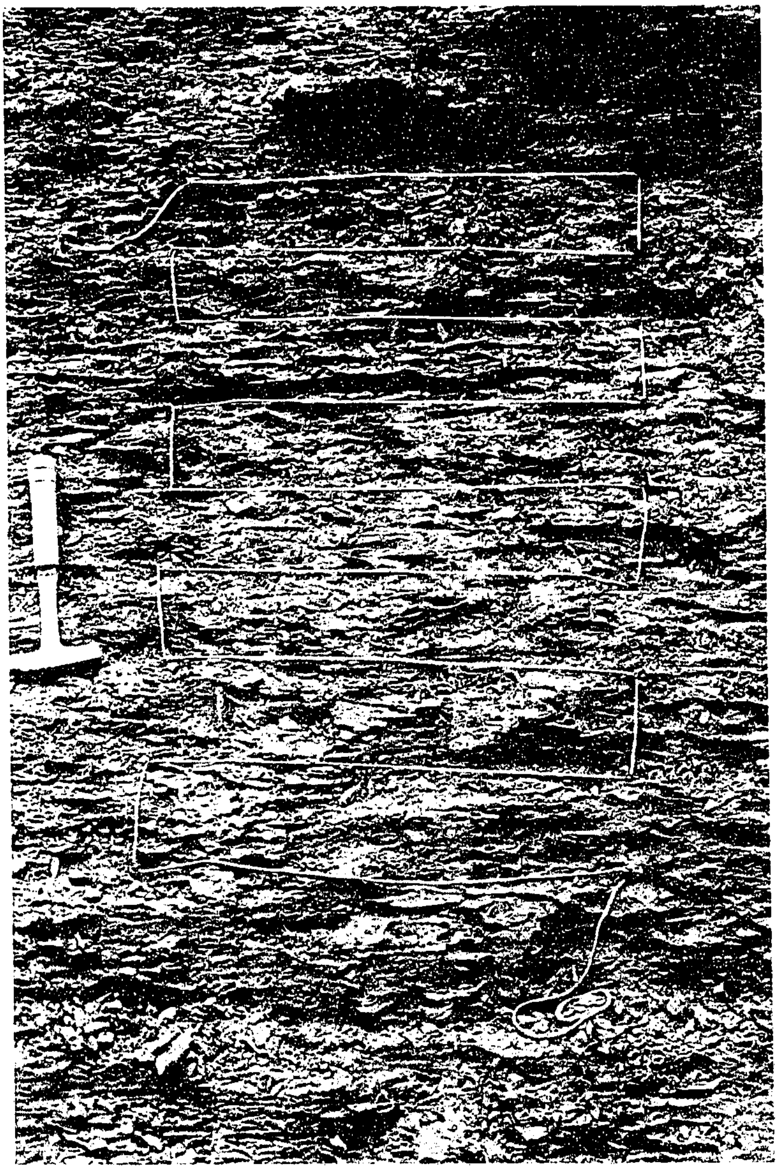

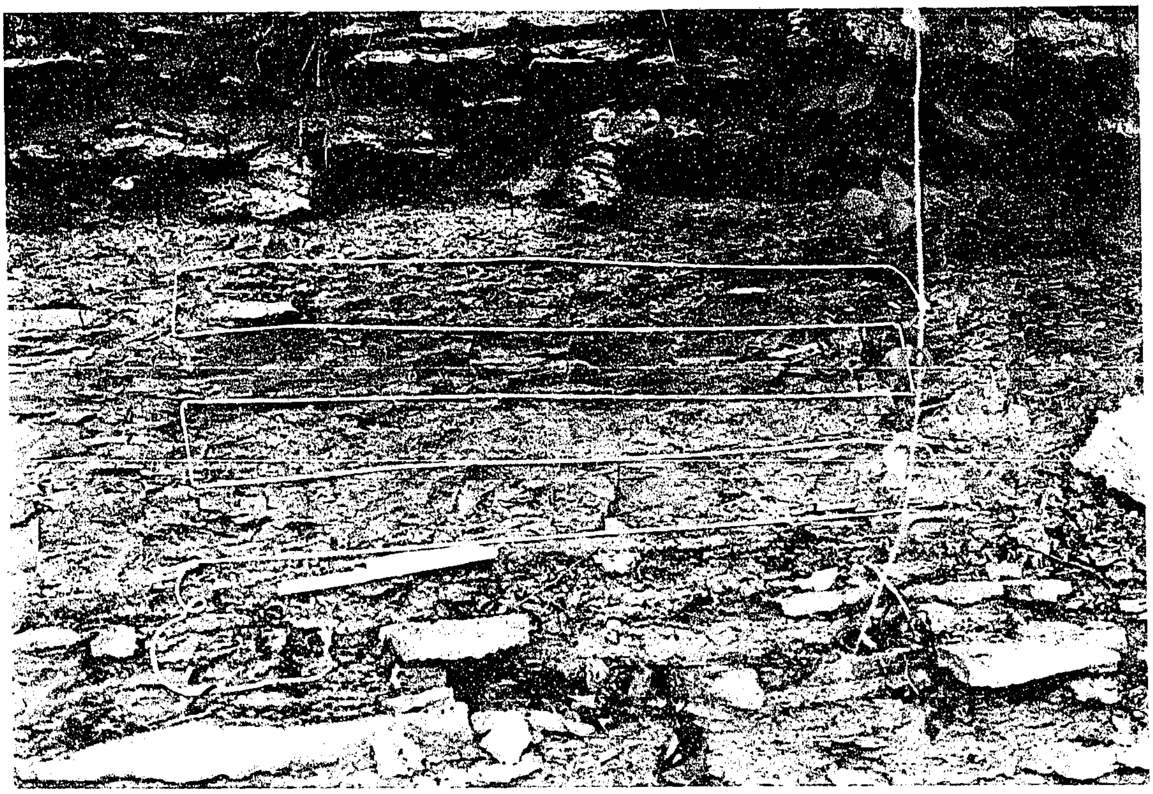

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below surface. For very common fossils, such as fragments of *Flexicalymene* trilobites or lingulid brachiopods, only the vertical 10 cm interval was noted. As each interval was quarried, the approximate volume of mudstone removed and sampled was measured, so that the number of occurrences per liter of mudstone could be calculated. An attempt was made to sample vertically through the whole mudstone horizon at each locality to detect any successional patterns through the unit. Where possible, at least two sites were excavated at each locality.

To calculate abundances of bivalved taxa (brachiopods and pelecypods), the total number of individuals was found by adding the number of the most common valve found (left or right for pelecypods, brachial or pedicle for brachiopods) to the number of whole articulated specimens. For some taxa (such as the lingulids) I was unable to distinguish the two valves due to poor preservation or fragmentation. In this case, one half of the total number of disarticulated valves was added to the number of whole individuals. Lengths of intact bivalve valves were also measured.

For trilobites, calculating the total number of individuals is problematic due to molting. While the presence of free cheeks attached to a cephalon in *Flexicalymene* indicates a carcass rather than exuvia (Brandt, 1980), it is otherwise impossible to distinguish disarticulated sclerites as originating from ecdysis or a carcass (Speyer, 1987). Because there is no foolproof solution to this problem, in the interests of consistency the method of Guiseffi (1982) was used. Number of individuals was calculated as the number of whole specimens plus one tenth the number of the most common sclerite (cranidium or pygidium), to account for ecdysis (Guiseffi, 1982). Total length of intact, prone specimens was recorded, as well as glabellar and pygidium length for all specimens.

Two brachiopods, *Rafinesquina* and *Onniella*, occurred in thin layers containing hundreds of individuals. In these cases, their presence was recorded but not included in quantitative samples. Also noted but not counted were bryozoans, which were usually fragmented and difficult to identify in the field.

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At each site, with the exception of the heavily weathered East Fork locality, several rock samples were taken for analysis of ichnofabric and mineralogy. Additional rock samples were taken from trilobite and mollusk rich beds in the Arnheim Formation (Ferree, 1994) and the upper Waynesville "Harvey Branch" locality.

Identification

In this study, identification of most fossils has been made only to the genus level for two reasons. First, in the mudstones, pelecypods were generally preserved as external molds, lacking critical details of dentition that distinguish species (Frey, pers. comm.). Second, most Cincinnatian species names have not been updated from the early part of this century, and many have a range of only one formation (Dalvé, 1948; Holland, 1996a). For example, of 70 articulate brachiopod species listed by Holland (1996a), only 27 (39%) appear in more than a single formation. This high turnover in species, which may be a byproduct of oversplitting, obscures the significance of community comparisons at this level. For example, the orthid brachiopod *Onniella* appears as *Onniella emacerata* in the Kope and as *Onniella meeki* in the Waynesville Formation, the only difference being a nearly imperceptible change in shape (Daley, 1993). It is unlikely that *Onniella meeki* had a different lifestyle or played a different role in the community than *Onniella emacerata.* Species level comparison, therefore, would not reflect the similarity of *Onniella* dominated communities in the Kope and Waynesville formations.

The taxonomic level of genus, on the other hand, is useful because genera are more easily identified and persist for longer intervals. Of the 23 genera listed by Guiseffi (1982) in the Maysvillian Mt. Hope Member, 20 (87%) persist into the Richmondian Stage. In contrast, only around 36% of the Mt. Hope species can be found in the Richmondian. In the Cincinnatian, the level of genus is most useful for comparison of communities throughout the interval.

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A second problem in identification were the lingulids. Two genera of lingulids have been recorded in Cincinnatian mudstones: *Pseudolingula* and *Lingulops* (Kramer, 1972). The only reliable method of distinguishing these two genera is a difference in musculature, which can be observed from muscle scars on valve interiors. Almost invariably, lingulids found on split mudstone slabs exposed the valve exterior only, with the interior adhered to the rock. The difficulty of accurately identifying lingulids was illustrated by Frey (1983, 1987a) and Guiseffi (1982). At the Bon Well Hill outcrop, Frey identified the lingulids as *Lingulops vanhornei* and Guiseffi identified the lingulids as *Pseudolingula convingtonense*. Lacking reliable identifications, all specimens of *Lingulops* and *Pseudolingula* in this database have been identified only as "lingulids".

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Chapter 4: Results

A list of the fauna inhabiting the Cincinnatian mudstones and their associated life habits (modified from Frey, 1987b) is shown in Table 1. Unlike the faunas of Cincinnatian limestones, which are dominated by bryozoans and articulate brachiopods, the mudstone communities contain a preponderance of mollusks. Of the 50 genera identified in this study, 29 are mollusks, including 18 pelecypods. Other important components of the mudstone faunas (Figure 11) are trilobites (especially *Flexicalymene* and *Isotelus*) and inarticulate brachiopods (represented by lingulids and *Trematis*). When articulate brachiopods, such as *Onniella* and *Rafinesquina*, do appear, they usually occur in thin (one shell thick) layers that may represent shell lag deposits from storms or living assemblages colonizing a temporarily stable substrate (Harris and Martin, 1979). Apart from these layers, the only articulate brachiopod to occur frequently within the mudstones is *Zygospira*, perhaps the most ubiquitous of Cincinnatian brachiopods.

The dichotomy between the mudstone and limestone assemblages, coupled with the beautiful preservation of fossils within these lithologies--including articulated trilobites and lingulids found in life position (Brandt, 1980; Guiseffi, 1982; Frey, 1983, 1987a and 1987b; this study)--indicate that the mudstone assemblages are bicoenoses (life assemblages), rather than transported skeletal remains from other areas. Because of the high quality of preservation and lack of discernible bedding planes, these mudstones have been interpreted by several authors as distal obrution deposits (Brandt, 1980; Frey, 1983; Brandt-Velbel, 1985; Hughes and Cooper, 1999).

The percentage abundances of genera in the sixteen sites included in this study are shown in Table 2. The following section contains a summary of the data for each site. Trends, patterns, and interpretations of these data will be presented in the following chapters. The following eight types of data will be presented:

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Table 1 - List of fauna documented in mudstone horizons and associated life habits.

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Phylum	**Class**	**Genus**	**Life Habit**
Arthropoda	Trilobita	*Amphilichas*	Mobile detritus feeder or grazer
		Flexicalymene	Mobile detritus feeder or scavenger
		Homotelus	Mobile detritus feeder or grazer
		Isotelus	Mobile scavenger/predator
		Platycorphe	Mobile detritus feeder or grazer
Brachiopoda	Articulata	*Hebertella*	Epifaunal suspension feeder
		Platystrophia	Epifaunal suspension feeder
		Plectorthis	Epifaunal suspension feeder
		Rafinesquina	Epifaunal suspension feeder
		Unidentified brachiopod	Epifaunal suspension feeder
		Zygospira	Epifaunal suspension feeder
	Inarticulata	Lingulids	Infaunal suspension feeder
		Trematis	Epifaunal suspension feeder
Echinodermata	Crinoidea	*Cincinnaticrinus*	Epifaunal suspension feeder
		Iocrinus	Epifaunal suspension feeder
Mollusca	Cephalopoda	*Treptoceras*	Nekto-benthonic predator
		Trocholites	Nekto-benthonic predator
		Unidentified cephalopod	Nekto-benthonic predator
	Gastropoda	*Cyrtolites*	Mobile detritus feeder or grazer
		Fusispira	Mobile detritus feeder or grazer
		Liospira	Mobile detritus feeder or grazer
		Lophospira	Mobile detritus feeder or grazer
		Loxoploxus	Mobile detritus feeder or grazer
		Ruedemania	Mobile detritus feeder or grazer
		Sinuites	Mobile detritus feeder or grazer
		Sphenospira	Mobile detritus feeder or grazer
		Unidentified gastropod	Mobile detritus feeder or grazer
	Pelecypoda	*Ambonychia*	Epifaunal suspension feeder
		Caritodens	Epifaunal suspension feeder
		Cleidophorus	Infaunal deposit feeder
		Corallidomus	Epifaunal suspension feeder
		Cuneamya	Infaunal suspension feeder
		Cycloconcha	Infaunal suspension feeder
		Cymatonota	Infaunal suspension feeder
		Cyrtodontula	Epifaunal suspension feeder
		Deceptrix	Infaunal deposit feeder
		Eridonychia	Epifaunal suspension feeder
		Lyrodesma	Infaunal suspension feeder
		Modiolopsis	Epifaunal suspension feeder
		Obalina	Indeterminate
		Orthodesma	Infaunal suspension feeder
		Pholadomorpha	Epifaunal suspension feeder
		Psiloconcha	Infaunal suspension feeder
		Rhytimya	Infaunal suspension feeder
		Whiteavesia	Epifaunal suspension feeder
	Rostroconcha	*Technophorus*	Epifaunal suspension feeder
Other		*Ancienta*	Nekto-benthonic predator
		Conularia	Epifaunal suspension feeder(?)
		Cornulites	Attached suspension feeder
		Hyolithes	Nekto-benthonic predator
		Spatiopora	Encrusted suspension feeder
		Stromatocerium	Epifaunal suspension feeder
		Tetradium	Epifaunal suspension feeder

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Figure 11 - Reconstruction of a Cincinnatian mudstone paleocommunity, illustrating the twenty most common taxa and their inferred life habits.

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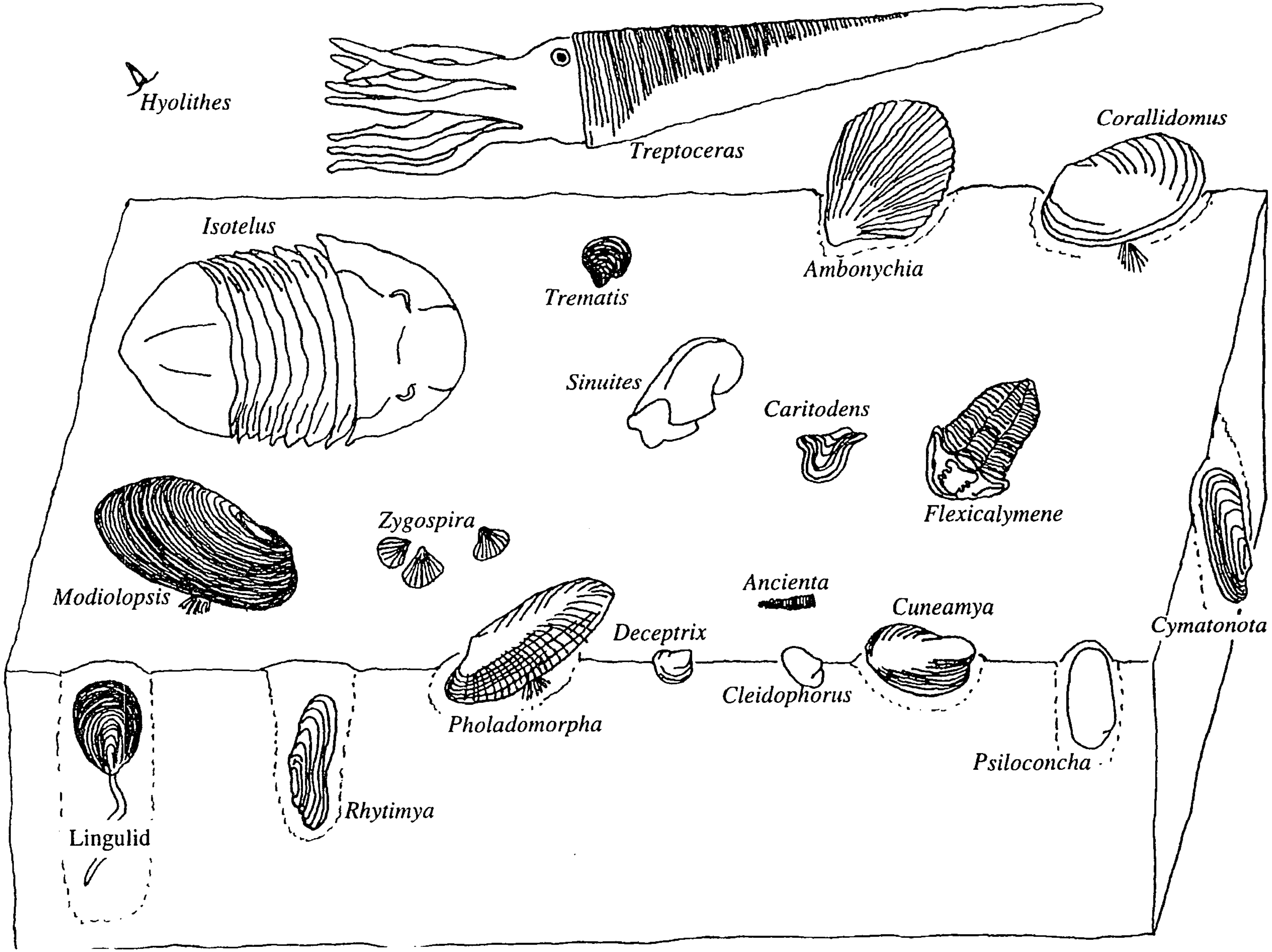

Table 2 - Percentage abundance of genera in sampled mudstone horizons.

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			Kope			**Fairview**			**Corryville**	**Waynesville**
			Orphanage	Backbone	Backbone Upp	Reading Road	Springdale	Harrison	Dornbusch	Russell Lower
Total individuals:			110.00	91.25	13.70	275.00	304.00	261.00	110.60	69.30
Phylum	**Class**	**Genus**								
Arthropoda	Trilobita	*Amphilichas*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Flexicalymene	4.55	6.25	1.46	4.36	1.64	4.21	6.42	4.04
		Homotelus	2.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Isotelus	0.00	6.58	7.30	5.82	4.28	8.43	0.00	0.00
		Platycorphe	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.33
Brachiopoda	Articulata	*Hebertella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Platystrophia	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00
		Plectorthis	0.00	0.00	0.00	1.82	0.00	0.00	0.00	0.00
		Rafinesquina	0.00	0.00	0.00	0.36	2.96	0.00	0.00	0.72
		unidentified brach.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Zygospira	20.00	21.37	7.30	*	*	*	3.62	0.72
	Inarticulata	lingulids	0.00	1.64	0.00	4.00	2.30	5.36	81.83	36.80
		Trematis	0.00	0.00	40.15	1.45	1.64	5.36	2.26	0.72
Echinodermata	Crinoidea	*Cincinnaticrinus*	0.00	0.05	0.00	0.00	0.00	0.00	0.00	1.44
		Iocrinus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Cephalopoda	*Treptoceras*	6.36	4.38	7.30	0.00	0.00	0.00	0.00	11.54
		Trocholites	2.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		unidentified ceph.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gastropoda	*Cyrtolites*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Fusispira	3.64	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Liospira	0.91	2.19	0.00	0.00	0.00	0.38	0.00	0.00
		Lophospira	5.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Loxoploxus	0.00	0.00	0.00	0.00	0.33	0.38	0.00	0.00
		Ruedemania	11.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Sinuites	22.73	21.92	0.00	38.18	25.99	19.92	0.00	0.00
		Sphenospira	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		unidentified gast.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pelecypoda	*Ambonychia*	5.45	2.74	18.25	8.36	10.86	7.28	0.00	0.00
		Caritodens	0.00	0.55	0.00	4.36	1.64	2.30	4.52	0.00
		Cleidophorus	6.36	4.93	0.00	1.45	1.97	3.07	0.00	16.59
		Corallidomus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Cuneamya	0.00	0.55	0.00	6.91	14.14	6.13	0.00	1.44
		Cycloconcha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Cymatonota	0.00	1.64	0.00	1.82	1.97	4.60	0.90	0.00
		Cyrtodontula	2.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Deceptrix	0.00	9.32	0.00	0.36	3.62	1.92	0.00	0.00
		Eridonychia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Lyrodesma	0.00	0.00	0.00	1.45	2.96	1.92	0.00	0.00
		Modiolopsis	1.82	1.64	10.95	4.00	2.63	2.68	0.45	0.00
		Obalina	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Orthodesma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Pholadomorpha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Psiloconcha	0.00	8.22	0.00	8.00	10.20	11.49	0.00	10.10
		Rhytimya	0.00	5.48	0.00	2.18	4.61	4.21	0.00	1.44
		Whiteavesia	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00
	Rostroconcha	*Technophorus*	2.73	0.00	7.30	0.00	0.00	0.00	0.00	0.00
Other		*Ancienta*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.33
		Conularia	0.00	0.00	0.00	0.36	0.00	0.77	0.00	1.44
		Cornulites	0.00	0.00	0.00	0.00	0.33	1.53	0.00	0.00
		Hyolithes	0.00	0.00	0.00	3.64	5.92	8.05	0.00	0.00
		Spatiopora	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.33
		Stromatocerium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Tetradium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
		Source:	Frey, 1987b	This study	This study	Guiseffi, 1982	Guiseffi, 1982	Guiseffi, 1982	This study	This study

* common elements of Guiseffi's (1982) assemblages, but no quantitative data available

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	East Fork Blue	Russell Middle	Bon Well Hill	Harpers Run	US Rt. 42	Russell Top	Hannah Creek	Liberty Clear Fork
	72.30	628.60	275.00	unknown	unknown	208.00	272.80	196.78
Genus								
Amphilichas	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.00
Flexicalymene	10.10	7.89	0.36	13.10	14.49	2.64	16.24	1.93
Homotelus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isotelus	4.15	0.00	0.00	6.05	11.59	0.48	2.93	0.00
Platycorphe	0.00	0.64	0.00	0.00	0.00	0.48	0.37	0.00
Hebertella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.54
Platystrophia	0.00	0.00	0.00	0.00	0.00	0.00	1.47	0.00
Plectorthis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rafinesquina	0.00	0.00	1.09	0.00	0.00	0.48	6.78	0.00
unidentified brach.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.52
Zygospira	4.15	0.16	0.00	0.00	0.00	0.00	4.40	65.05
lingulids	20.06	19.09	18.55	2.02	8.70	57.93	47.29	20.58
Trematis	2.77	1.03	1.45	0.00	0.00	0.00	2.02	0.00
Cincinnaticrinus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.26
Iocrinus	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00
Treptoceras	1.38	3.34	0.00	26.20	19.81	1.92	1.10	0.00
Trocholites	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
unidentified ceph.	0.00	0.00	0.00	0.00	0.00	0.00	1.10	0.00
Cyrtolites	0.00	0.00	0.00	0.00	0.00	0.48	1.10	0.00
Fusispira	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Liospira	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.00
Lophospira	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Loxoploxus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ruedemania	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sinuites	1.38	5.41	8.36	13.10	5.80	1.44	0.00	0.00
Sphenospira	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.02
unidentified gast.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.51
Ambonychia	8.99	16.47	13.82	2.02	5.80	4.33	2.20	0.76
Caritodens	1.38	2.23	0.00	0.00	2.90	0.24	1.10	2.29
Cleidophorus	2.07	0.56	5.82	0.00	5.80	0.48	0.00	0.00
Corallidomus	6.92	12.57	16.00	0.00	2.90	0.48	2.20	0.00
Cuneamya	4.84	1.11	2.91	11.34	11.59	4.33	2.02	0.00
Cycloconcha	0.00	0.00	1.82	0.00	0.00	0.00	0.00	0.00
Cymatonota	1.38	2.07	0.00	5.54	0.00	0.48	1.47	0.00
Cyrtodontula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Deceptrix	2.07	0.00	0.00	0.00	0.00	0.00	0.00	0.25
Eridonychia	0.00	0.00	2.55	0.00	0.00	0.00	0.00	0.00
Lyrodesma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Modiolopsis	0.00	0.00	2.55	0.00	0.00	0.00	0.73	0.00
Obalina	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00
Orthodesma	0.00	0.00	2.55	5.04	0.00	0.00	0.00	0.00
Pholadomorpha	0.00	0.32	3.27	10.08	8.70	0.00	1.47	0.00
Psiloconcha	12.45	13.28	11.64	1.01	0.00	16.11	0.18	2.29
Rhytimya	6.92	1.67	0.73	0.00	0.00	0.24	0.00	0.00
Whiteavesia	2.07	0.24	2.55	0.00	0.00	0.24	0.18	0.00
Technophorus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ancienta	6.92	5.41	3.27	0.00	0.00	5.77	0.73	0.00
Conularia	0.00	1.75	0.00	0.00	0.00	0.96	2.20	0.00
Cornulites	0.00	1.91	0.00	0.00	0.00	0.00	0.00	0.00
Hyolithes	0.00	0.00	0.36	0.00	0.00	0.00	0.00	0.00
Spatiopora	0.00	2.55	0.00	0.00	0.00	0.48	0.00	0.00
Stromatocerium	0.00	0.00	0.00	3.53	0.97	0.00	0.00	0.00
Tetradium	0.00	0.00	0.00	1.01	0.97	0.00	0.00	0.00
Source:	This study	This study	Guiseffi, 1982	Frey, 1987a	Frey, 1987a	This study	This study	This study

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1) Percentage abundances

Because of the wide range in sample sizes, absolute abundances are less informative than percentage abundances, which are simply the number of individuals divided by the total number of individuals found.

2) Life habits

Documentation of life habits, or trophic analysis, is a valuable tool both for interpreting environments and in evaluating temporal trends in community structure.

3) Diversity index

The best way to assess relative diversity in samples of varying size is rarefaction, which is examined in Chapter 5. Diversity indices, however, are useful because diversity can be summarized in a single number, allowing the samples to be ranked numerically. In this study, these results are generally consistent with patterns illustrated by rarefaction (see Chapter 5). Two indices were used in this study: The Shannon-Weaver Index (Shannon and Weaver, 1949), which measures overall diversity corrected for sample size, and the Pielou Index of Evenness (Pielou, 1966). The Shannon-Weaver Index H' is defined as

$$H' = \sum -p_i \log_n(p_i),$$

where p_i = percentage abundance of the ith genus in the sample. The Shannon-Weaver Index is sensitive to two factors: the number of genera found, and the evenness with which they are distributed. As evenness increases, H' approaches $H'\ max$:

$$H'\ max = \log_n(g),$$

where g is the number of genera. The Pielou Index of Evenness J (Pielou, 1966) simply measures the ratio of H' to $H'\ max$:

$$J = H' / H'\ max, \text{ or } J = H' / \log_n(g)$$

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4) Size

Size variations can be indicative of several environmental variables, including overall favorability for a given taxon, substrate stability (Guiseffi, 1982; Frey, 1983), or depth (Daley, 1993). At each site, *Flexicalymene* glabellar length and mollusk shell length were measured. Temporal size trends in common fauna will be considered in the following chapter. Below, only trilobite data have been included.

5) Taphonomy

Completeness, articulation, and other taphonomic characteristics of fossils can indicate a great deal about the environmental conditions under which burial and preservation occurred. Comparative taphonomy (Brett and Baird, 1986; Speyer and Brett, 1987) can be used to assess such aspects of a paleoenvironment as current strength and direction, storm-related winnowing and reworking of sediments, bioturbation, relative rate and episodicity of sedimentation, and oxygenation (Brett and Baird, 1986).

Given the relative abundance of fossil material and the lack of significant pyrite or lamination in the studied horizons, it is unlikely that anaerobic conditions or even dysaerobic conditions were ever present in these mudstones (Brett and Baird, 1986; Savrda and Bottjer, 1986). To assess energy of environment and characteristics of sedimentation, the most useful taphonomic attributes are articulation, orientation and distribution of fossils. Characteristics of orientation and distribution (i.e. condensed into layers or dispersed through the mudstone) will be described qualitatively in the sections below.

For comparison of articulation rates, the most useful fossil was the trilobite *Flexicalymene meeki*. Individual genera of pelecypods did not appear consistently enough, nor in sufficient abundance, to permit meaningful comparison of articulation rates between sites. *Flexicalymene*, however, appeared in moderate abundance in all sites, allowing for valid comparisons to be made. Trilobite taphonomy in Cincinnatian mudstones has been previously investigated by Brandt (1980; Brandt-Velbel, 1985).

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In analyzing completeness of trilobites, taphofacies models developed by Speyer and Brett (1986) and Speyer (1987) were used. Whole, prone individuals; enrolled individuals, intact molt ensembles, and disarticulated cephala, cranidia (cephala missing free cheeks), and pygidia were all counted. As in Speyer and Brett (1986), Articulation Percentage was calculated as the number of whole individuals plus intact molt ensembles divided by the total number of whole and disarticulated remains (i.e., the number of whole individuals plus the number of cranidia or pygidia, whichever is greater). Relatively high articulation ratios can be indicative of rapid burial by frequent and episodic sedimentation events, lower energy environments, and little disturbance by burrowing scavengers (Brett and Baird, 1986). Less articulation, on the other hand, could result from higher environmental energy, lower overall rates of sedimentation, or lower frequency of rapid-burial events.

6) Density

In each site excavated by the author, as well as those excavated by Guiseffi (1982), the amount of mudstone removed was recorded, which allowed for a calculation of the number of individuals found per liter. This information may be indicative of the rate of sedimentation or the capacity of the environment to support fauna.

7) Clay/quartz index

All of the sites excavated by the author, as well as other selected Cincinnatian mudstones, were analyzed for mineralogical content using x-ray diffraction. The following minerals were found in abundance: quartz, illite, chlorite, calcite, and dolomite.

X-ray diffraction data appears as a series of peaks, each of which have an amplitude, defined as a percentage of the highest peak. The clay/quartz index used here is equal to the combined amplitudes of the first illite and chlorite peaks divided by the quartz peak amplitude (Figure 12). Because these data were not calibrated to a known standard,

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Figure 12 - Graphical representation of method used to determine the clay/quartz index.

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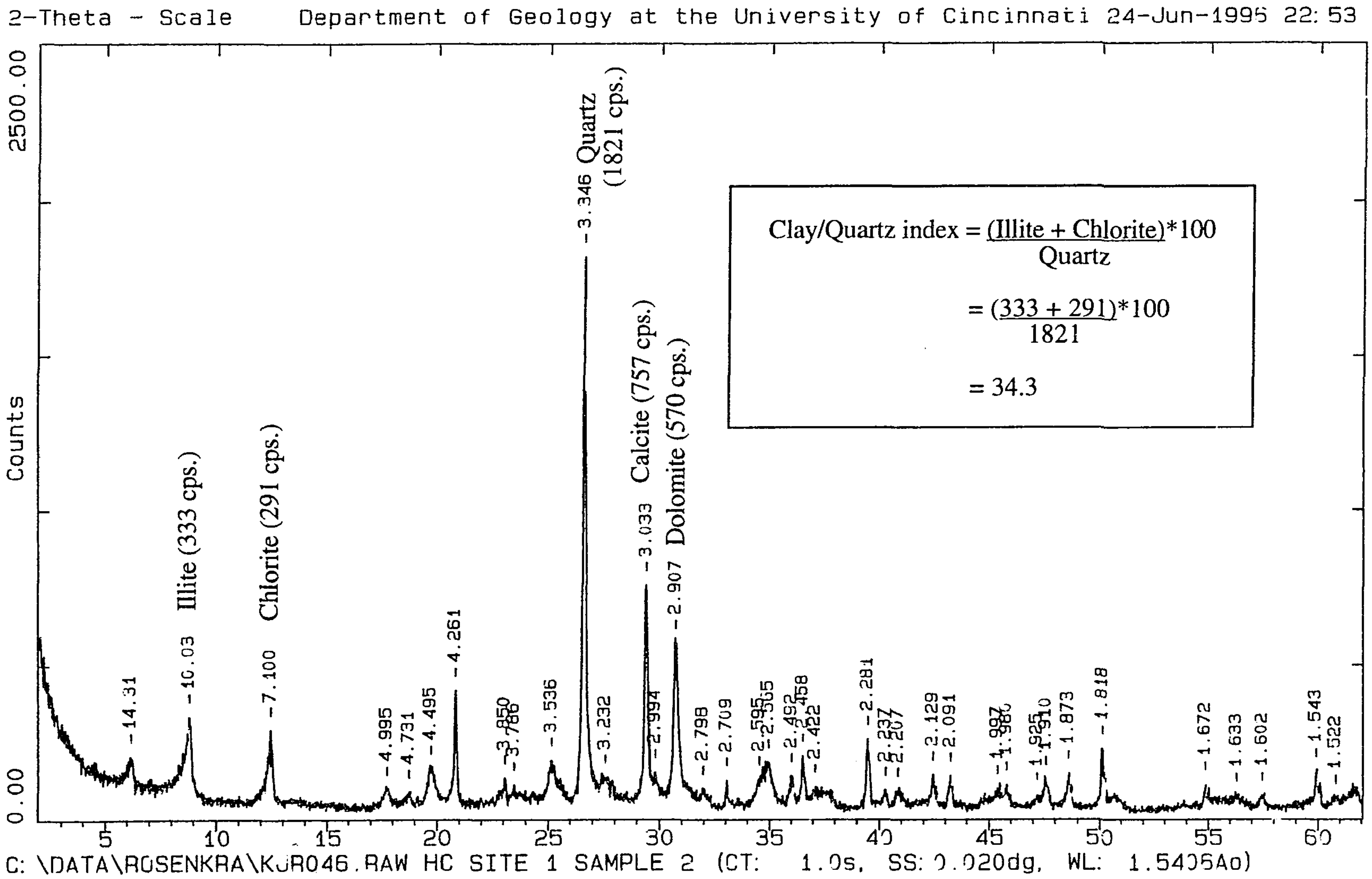

$$\text{Clay/Quartz index} = \frac{(\text{Illite} + \text{Chlorite})*100}{\text{Quartz}}$$

$$= \frac{(333 + 291)*100}{1821}$$

$$= 34.3$$

absolute percentages of quartz, illite and chlorite are not known. Data from Scotford (1965) indicate that mean percentages of illite, chlorite, and quartz are approximately 20%, 50%, and 10%, respectively in Cincinnatian mudstones.

Scotford (1965) showed that, along a single horizon, the percentage of clay increased to the west, while the percentages of sand and silt decreased. An elevated clay/quartz index, therefore, could indicate deeper, quieter, offshore conditions, while a lower clay/quartz index could indicate more turbulent, higher energy onshore conditions. Studies in modern (Sanders, 1958; Rhoads and Young, 1970) and ancient (Duff, 1975; MacQuaker and Gawthorpe, 1993) settings have effectively related community composition to the relative amounts of sand, silt and clay in the sediment.

8) Ichnofabric

Several authors (Brandt, 1980; Tobin, 1982; Frey, 1983; Brandt-Velbel, 1985) have described Cincinnatian mudstones as largely lacking in biogenic structures. R.G. Osgood, a pioneer in the study of Cincinnatian trace fossils, noted that

> Neither body fossils nor trace fossils are common in the lutites [mudstones], although brachiopods, trilobites, trilobite tracks, and irregular structureless burrows are sometimes encountered. (Osgood, 1970, p. 284)

A recent study of split cores and split slabs of Cincinnatian mudstones (Gaines et al. 1996) have demonstrated that, contrary to previous observations, the mudstones are in fact well bioturbated, with ichnofabric indices (Droser and Bottjer, 1993) ranging as high as I.I. 5 and 6. The use of these ichnofabric indices, however, is often problematic because of the lack of obvious bedding of the mudstones. As a result, it is very difficult to determine if the background ichnofabric of these mudstones is blank (I.I. 1) or completely homogenized due to bioturbation (I.I. 6). Therefore, the discussion of ichnofabrics will be limited to qualitative descriptions and burrow diameter measurements. Hughes and Cooper (1999) have provided a model for analysis of ichnofabric in Cincinnatian mudstones using thin sections, a technique not used in this study.

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Site by site results: Orphanage Road (Frey, 1987b)

Frey (1987b) described this unit as a "1.5 m thick mudstone unit exposed 18 m above road level, Kope Formation (Edenian)". Frey noted the small size of most pelecypods and monoplacophorans (less than 30 mm in length), relative to larger specimens found above in the Waynesville Formation. While the glabellar lengths of *Flexicalymene* are not available, Frey did measure cephalon widths, and found an average cephalon width of 10 mm, which is substantially smaller than the average widths of 19, 21, and 20 mm Frey measured at three Waynesville Formation sites. The Orphanage Road assemblage contained many genera not found at any other horizons in this study, including the gastropods *Lophospira*, *Ruedemannia*, and *Fusispira*; the pelecypod *Cyrtodontula*, the cephalopod *Trocholites*, the trilobite *Homotelus*, and the crinoid *Ectenocrinus* (Figure 13). In fact, nearly 50% of the genera found in this assemblage are not represented elsewhere in this study, and one additional genus, the rostroconch *Technophorus* was only found as a single individual in one other assemblage. On the other hand, this assemblage is similar to other older Cincinnatian assemblages in the abundance of *Sinuites*, the lack of *Pseudolingula*, and the relatively small size of most individuals.

Backbone Creek

Excavated by the author, this 1.5 m thick mudstone unit was located approximately 6 m below the Kope/Fairview contact, marked by a distinctive "two foot shale" at the base of a limestone rich interval (Tobin, 1980). It corresponds to the base of cycle 39 of Holland et al. (1997). The faunal assemblage here was similar to other Kope and Fairview samples: dominated by *Sinuites* and a diverse group of pelecypods, mostly infaunal suspension feeders (Figure 14). Abundant *Zygospira* accounted for most of the epifaunal suspension feeder fraction. The absence of epifaunal pelecypods such as *Ambonychia* and *Modiolopsis* may be related to instability of the substrate (Guiseffi, 1982; Daley, 1993), which in turn may be indicated by the enriched clay content of the sample. Sanders (1958)

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Figure 13 - Faunal composition and life habit distribution of Orphanage Road assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 3 - Indices for Orphanage Road.

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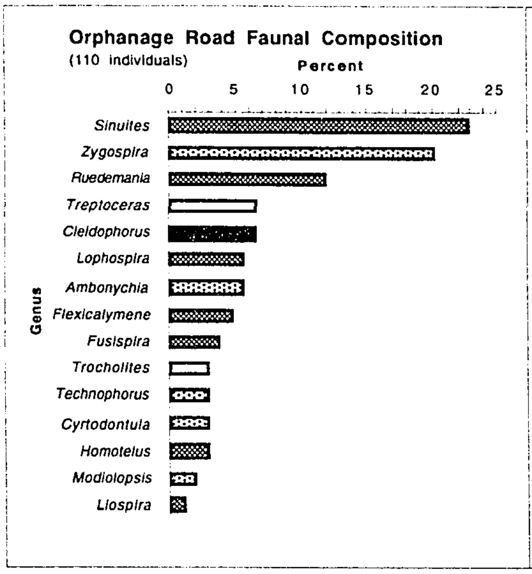

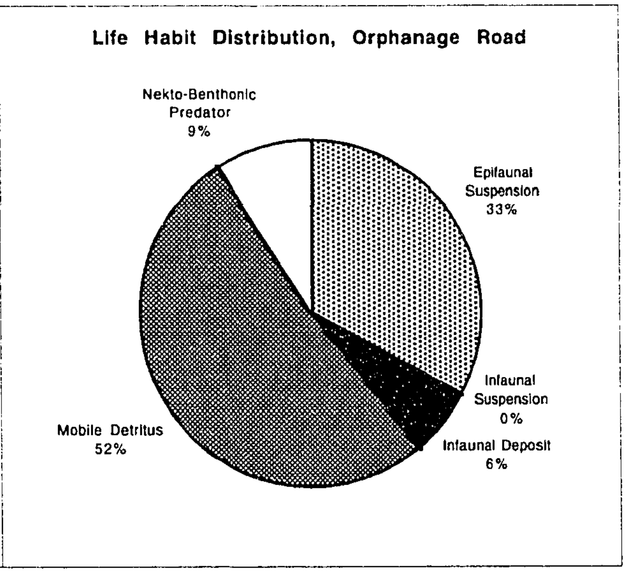

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.0199	7
Pielou Evenness *J*	0.8672	4
Average *Flexicalymene* cephalon width in mm (#individuals), standard deviation	10 (5)	3 (out of three)
Articulation% of *	No information	
Density (occurrences/liter)	No information	
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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Figure 14 - Faunal composition and life habit distribution of Backbone Creek assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 4 - Indices for Backbone Creek.

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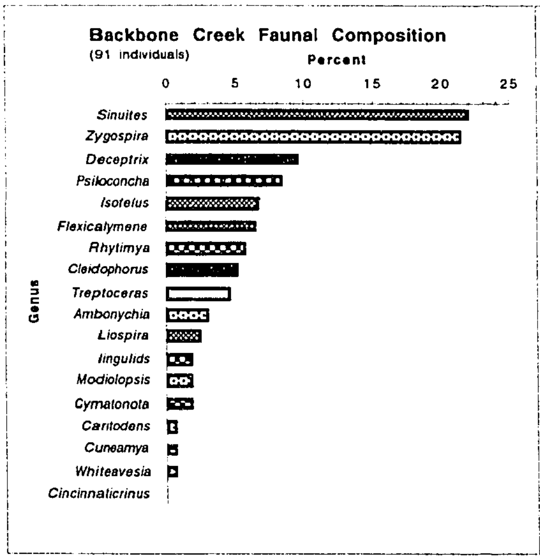

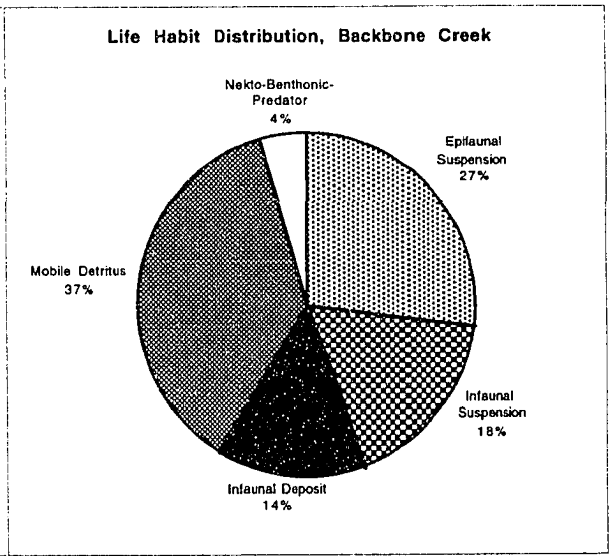

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.0251	6
Pielou Evenness *J*	0.8166	9
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	3.3 (20), 1.20	6 (out of 8)
Articulation% of *Flexicalymene*	20.0%	4 (out of 9)
Density (occurrences/liter)	11.1	3 (out of 12)
Clay/Quartz Index, standard deviation	37.4, 7.7	1 (out of 9)
Average burrow diameter in mm, standard deviation	1.53, 0.80	5 (out of 7)

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observed that deposit-feeding bivalves were more common in deeper, clay enriched substrates, and Rhoads and Young (1970) proposed that the lack of epifaunal filter feeders in these environments was due to the activity of deposit feeders, which produced a layer of unstable fecal material at the sediment-water interface. Consistent with this are the relatively large numbers of the deposit feeders *Cleidophorus* and *Deceptrix* in this sample. As at Orphanage Road, body sizes were relatively small for all taxa.

The ichnofabric of the Backbone Creek sample consisted of distinct burrows with dark and light infill. The dark-infill burrows were elliptical in cross-section, while the light-infill burrows were smaller, branching, and more complex in structure. Examples of possible *Teichnichus* and *Diplocraterion* burrows were also found here. The more fossiliferous intervals within the horizon were more intensely burrowed, and truncation of burrows was observed coincident with shell hash layers, consisting of disarticulated *Zygospira* shells and shell fragments. These can be interpreted as the basal shell-hash layers of graded event beds.

Articulation of *Flexicalymene* was close to the average of 18.8% (Table 4), and distribution of fossils varied through the layer. In the bottom 1/3 of this horizon, most fossils were found disarticulated and fragmented in shell-hash layers, indicating infrequent sedimentary events separated by relatively long periods of little or no sedimentation. In the top portion of the horizon, fossils were more evenly distributed through the mudstone, and several pelecypods were found in life position, possibly indicating a higher rate of sedimentation and less current energy, so that skeletal material was relatively undisturbed during deposition.

Backbone Creek Upper Exposure

Samples from this site were taken from a 1.8 m thick mudstone unit, the base of which is located approximately 3.5 m below the base of the Fairview Formation. Because of time constraints, only a small number of individuals were recovered from this sample. It

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was included, however, because of its interesting faunal composition, which contrasts with other assemblages from the Kope and Fairview. The fauna was dominated by beautifully preserved, large *Trematis crassipunctata* inarticulate brachiopods, along with the epifaunal filter-feeding pelecypods *Ambonychia* and *Modiolopsis* (Figure 15). Fragments of the trilobite *Isotelus* were also common. In contrast to the other Kope sites, body sizes were large and comparable to Waynesville samples (see Chapter 5). It is also interesting that this assemblage, dominated by epifaunal suspension-feeders, was excavated from a mudstone containing the lowest proportion of clay found in the sampled sites (Table 5). In this case, there may be a relationship between the proportion of silt in the substrate and its suitability for colonization by epifaunal organisms.

Reading Road (Guiseffi, 1982)

Guiseffi sampled two mudstone layers, designated A and B, at Reading Road. These layers lie 5.0 and 4.5 m above the base of the Fairview formation, respectively, and are separated by a thin limestone unit that grades laterally into a shell hash. *Sinuites* was the dominant faunal element of both layers, comprising nearly 40% of all individuals (Figure 16). There was an even distribution of infaunal and epifaunal suspension-feeding pelecypods, a few infaunal deposit-feeding pelecypods, and a small number of lingulids. Although no trilobite measurements were available from this site, other specimens were consistently small (see Ch. 5). Also noteworthy was the presence of ramose bryozoan colonies in this sample, in contrast to the samples described above.

A major difference between Guiseffi's (1982) three Fairview samples and the Kope sample from Backbone Creek is the lower fossil density, by an order of magnitude, in the Fairview beds (Table 6). This difference could reflect either a higher rate of sedimentation or a more hostile environment for colonization.

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Figure 15 - Faunal composition and life habit distribution of Backbone Upper assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 5 - Indices for Backbone Creek Upper.

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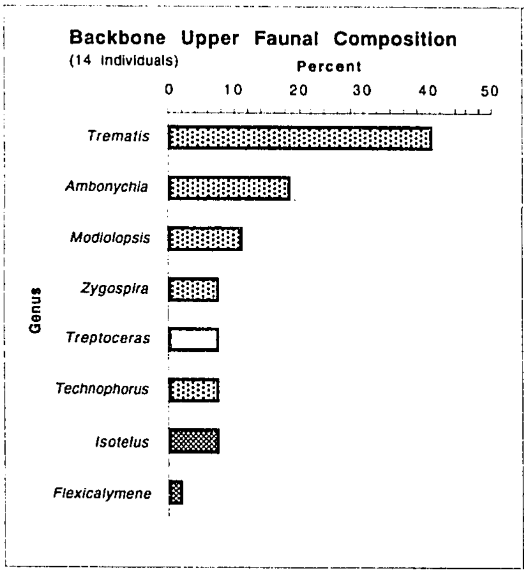

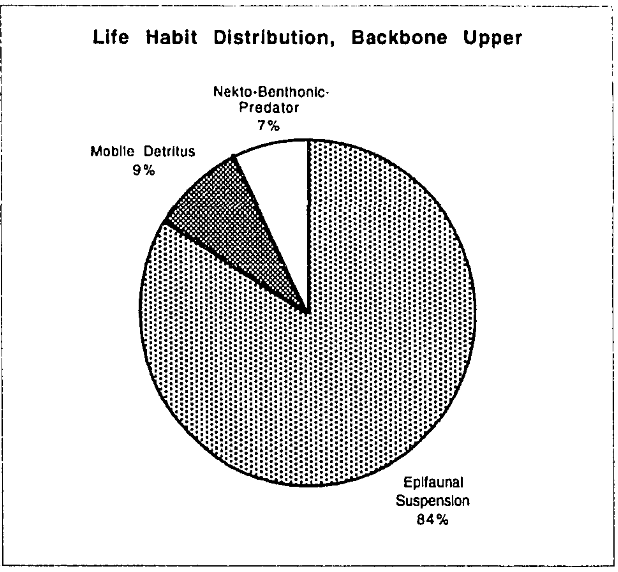

Index	Result	Rank (#Sites)
Shannon-Weaver Index H'	0.7578	13
Pielou Evenness J	0.8391	6
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	No information	
Articulation% of *Flexicalymene*	0.0%	9 (out of 9)
Individuals/Liter	No information	
Clay/Quartz Index	23.29	9 (out of 9)
Average burrow diameter (mm), standard deviation	No information	

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Figure 16 - Faunal composition and life habit distribution of Reading Road assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 6 - Indices for Reading Road.

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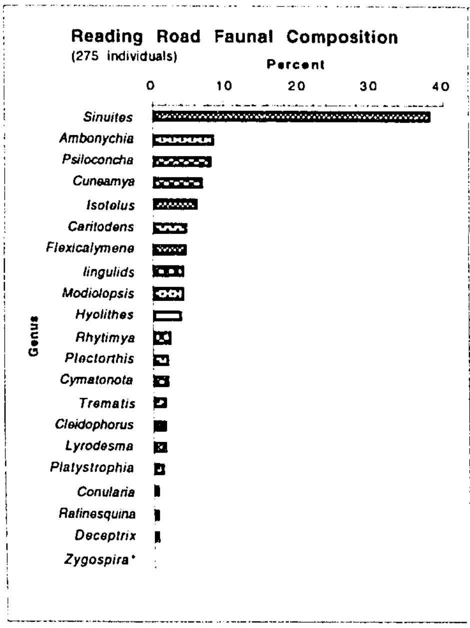

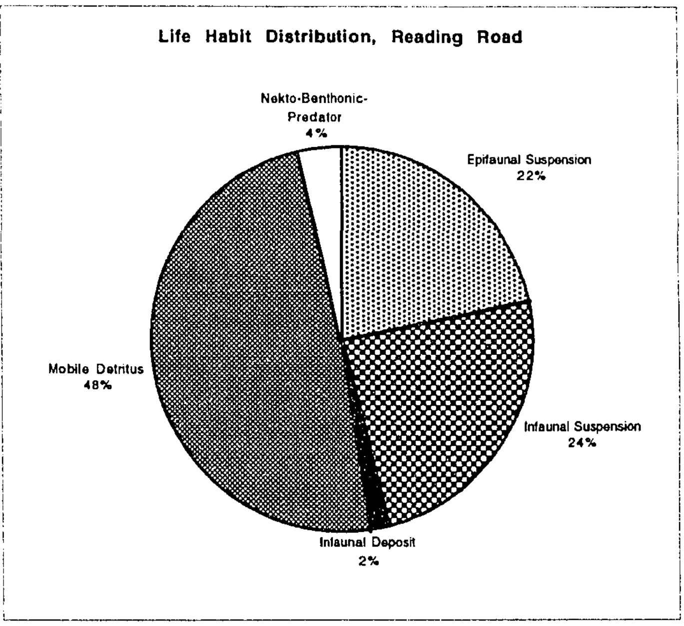

Index	Result	Rank (#Sites)
Shannon-Weaver Index H'	1.0002	9
Pielou Evenness J	0.7688	11
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	No information	
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	1.20	11 (out of 12)
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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Springdale (Guiseffi, 1982)

Two mudstone layers (A and B), approximately 9.0 m above the base of the Fairview Formation, were sampled at this outcrop. Mudstone layer A was 15-17 cm thick and layer B was of variable thickness. The two layers were separated by a thin limestone lens, and contained a highly comparable fauna. *Sinuites* was followed in abundance by the infaunal suspension-feeding pelecypods *Cuneamya* and *Psiloconcha* and the epifaunal suspension-feeding pelecypod *Ambonychia* (Figure 17). Typically small body sizes (see Ch. 5) and low density (Table 7) characterize this sample.

Harrison (Guiseffi, 1982)

Two layers were excavated at this outcrop, both approximately 4.5 m above the base of the Fairview Formation. As in other Fairview/Kope samples, the most common genus was *Sinuites*. Other common genera included the infaunal suspension-feeder *Psiloconcha*, the trilobite *Isotelus*, and the problematic *Hyolithes* (Figure 18). This locality had the highest ranking Shannon-Weaver index in the database (Table 8), although its genus richness is quite comparable to most others in this study, with around 20 genera represented. The high Shannon-Weaver value therefore reflects a greater evenness in abundances of constituent genera, which is apparent when comparing the histogram in Figure 18 to those from other samples.

Dornbusch

The sampled horizon occurs within the Corryville Member, 10 m above the base of the measured section (see Appendix 2) and most likely within Zone 2 of Goldman (1993). Although the mudstone exhibited a typical blocky parting and lack of bedding, it was considerably less fossiliferous than other sites, ranking last in density and diversity (Table 9). The fossils found were almost exclusively lingulids, many of which were found in life position, indicating a lack of disturbance by currents and/or burrowing infauna. This

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Figure 17 - Faunal composition and life habit distribution of Springdale assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 7 - Indices for Springdale.

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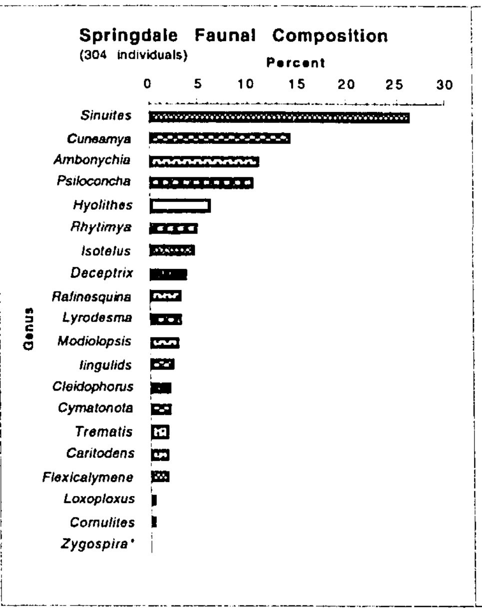

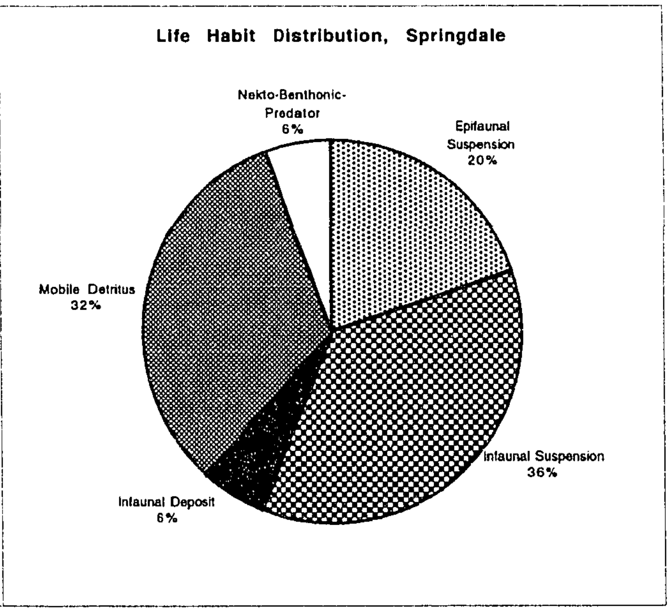

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.0644	5
Pielou Evenness *J*	0.8324	7
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	No information	
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	1.65	10 (out of 12)
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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Figure 18 - Faunal composition and life habit distribution of Harrison assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 8 - Indices for Harrison.

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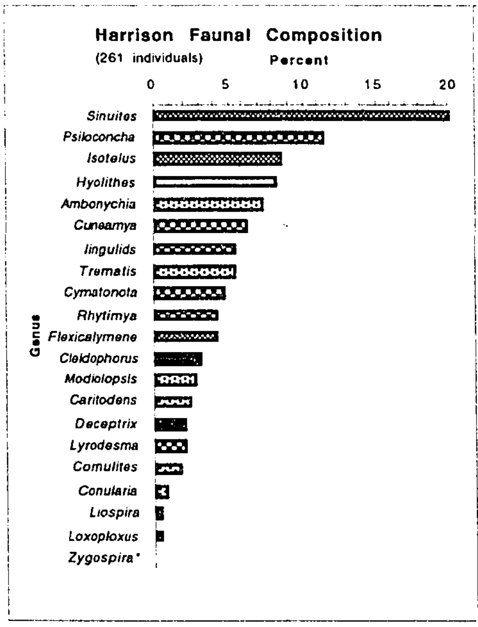

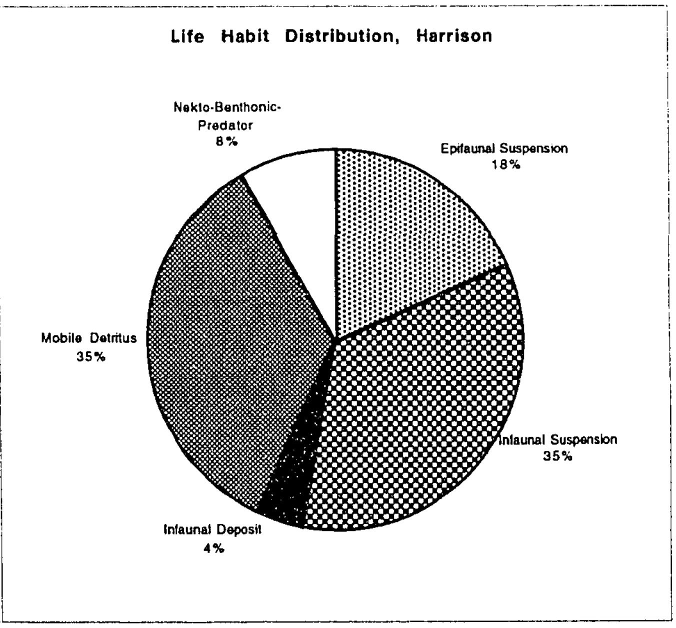

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.1516	1
Pielou Evenness *J*	0.8852	3
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	No information	
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	2.01	9 (out of 12)
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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Figure 19 - Faunal composition and life habit distribution of Dornbusch assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 9 - Indices for Dornbusch.

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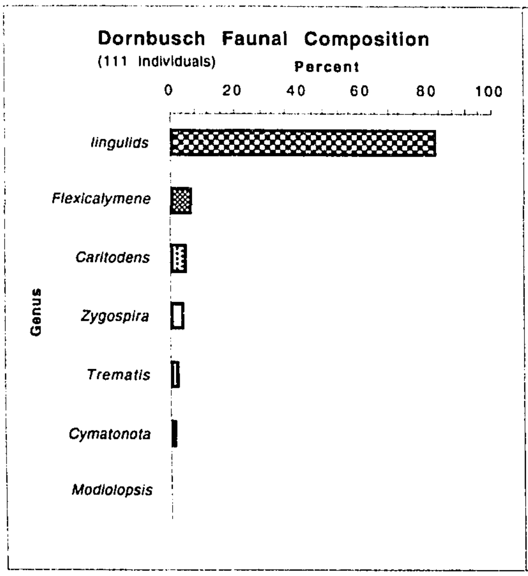

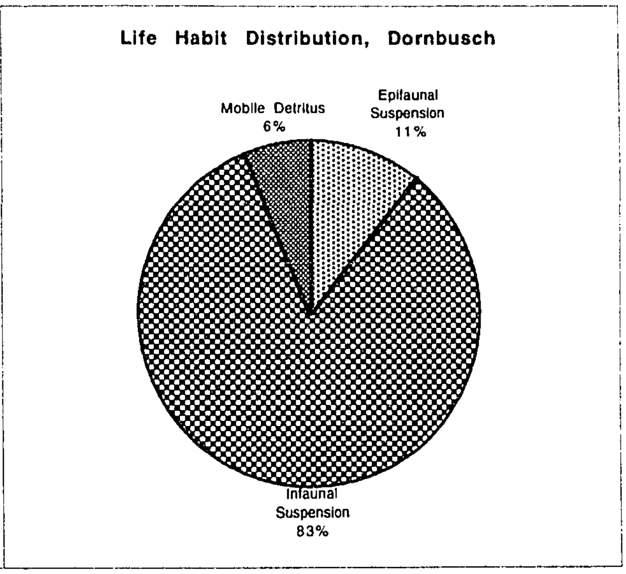

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.3270	16
Pielou Evenness *J*	0.3870	16
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	3.2 (3), 0.6	7 (out of 8)
Articulation% of *Flexicalymene*	38.5%	1 (out of 9)
Density (occurrences/liter)	0.65	12 (out of 12)
Clay/Quartz Index, standard deviation	23.30	8 (out of 9)
Average burrow diameter (mm), standard deviation	0.98, 0.40	7 (out of 7)

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observation is corroborated by the high articulation ratio of the trilobites (Table 9). Relatively high rates of sedimentation and a lack of current related winnowing of skeletal material could account for the sparse but well preserved fauna. Body sizes of the fauna were inconsistent. The trilobites found were small, as were the examples of *Caritodens* found here. On the other hand, a single very large *Modiolopsis* was found here, and the examples of lingulids were average to large in size (up to 32 mm in length).

Examination of the mudstone slabs in cross-section showed a much less bioturbated sediment than most other samples. Whereas many other mudstones appear quite homogenized by bioturbation, in this mudstone event-beds could be discerned, including at least one graded bed. Overall, this horizon appears to have been less hospitable to colonization and community diversification than many other mudstones examined in this study, which again could be related to high rates of sedimentation.

Russell Lower Exposure

The sampled mudstone at this locality is 40 cm thick, and is located approximately 3-4 m above the base of the Waynesville Formation. It contained an unusual fauna of lingulids, the infaunal suspension-feeding *Psiloconcha*, abundant individuals of the deposit feeder *Cleidophorus*, and the cephalopod *Treptoceras* (Figure 20). Specimens of *Treptoceras* were found encrusted on all sides with the bryozoan *Spatiopora*, suggesting a living association. Also present were sclerites of the rare trilobite *Platycorphe*. Important faunal elements not included in the quantitative sample included thin layers of numerous *Onniella* and abundant fragments of delicately branching bryozoans. Body sizes of all fauna but *Treptoceras* were relatively small, as were burrow diameters (Table 10) observed in ichnofabric. These burrows were delicate, branching and clearly visible. The small, delicate nature of the fauna here suggests a quiet, protected environment and relatively low rates of deposition. Infrequency of depositional events is suggested by the articulation ratio of trilobites and the presence of abundant articulate brachiopods and bryozoans, which

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Figure 20 - Faunal composition and life habit distribution of Russell Lower assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 10 - Indices for Russell Lower.

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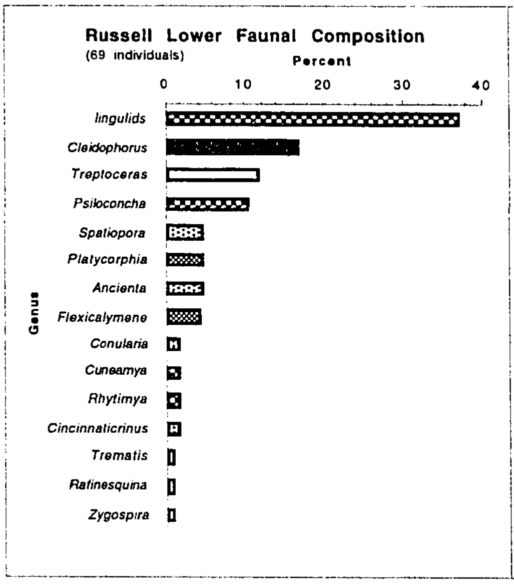

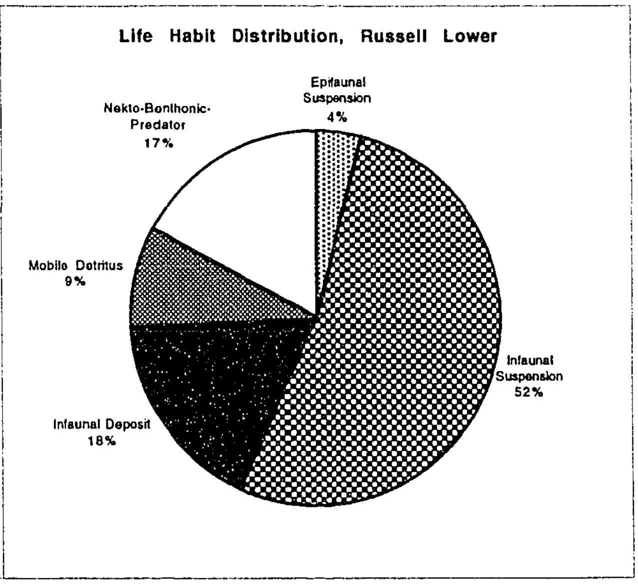

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.8840	11
Pielou Evenness *J*	0.7517	12
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	3.7 (5), 1.5	5 (out of 8)
Articulation% of *Flexicalymene*	11.1%	7 (out of 9)
Density (occurrences/liter)	12.36	2 (out of 12)
Clay/Quartz Index, standard deviation	29.70	6 (out of 9)
Average burrow diameter (mm), standard deviation	1.30, 1.11	6 (out of 7)

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probably preferred clear water to turbid conditions. *Onniella* has been interpreted as a deep water genus (Daley, 1993; Holland, 1996), although a deeper water environment is not supported by the clay/quartz index.

East Fork Blue Creek

The sampled mudstone at this site was poorly exposed on the bank of a small creek, and its stratigraphic position within the Waynesville Formation could not be determined. Based on the distance above the Arnheim/Waynesville boundary, which could be identified on the East Fork of Blue Creek nearby, it is certain that this horizon is in the lower portion of the Waynesville Formation, most likely between the Russell Lower and Russell Middle horizons. The fauna found in this horizon was a typical Waynesville assemblage, including lingulids, *Psiloconcha*, *Flexicalymene*, *Ambonychia*, and *Corallidomus* (Figure 21). Also present in small numbers (but, as in other sites, not included in the quantitative sample) was the brachiopod *Onniella.* Notably absent from this assemblage, as at Russell Lower, was *Sinuites* (only one found). Body sizes here were generally larger than at Russell Lower but smaller than at Russell Middle. Because the mudstone here was highly weathered, trace fossil data and clay/quartz indices were not measured for this horizon.

Russell Middle

Exposed on the bank of Russell Branch is an impressively thick (1.8 m) Waynesville mudstone that marks the top of the Fort Ancient Member, approximately 11 m above the base of the Waynesville Formation. This horizon corresponds to the "Trilobite Shale" of Frey (1983, 1987a) and correlates to the *Treptoceras duseri* Shale (Frey, 1983, 1987a) in southwest Ohio. This unit also correlates to the famous "Butter Layer" at Boudinot Avenue in Cincinnati (Schweinfürth, 1958) which yielded literally thousands of *Flexicalymene* specimens to local collectors and museums. Fossils found in this unit were generally large and robust (the largest *Flexicalymene* were found here), and the fauna was

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Figure 21 - Faunal composition and life habit distribution of East Fork Blue Creek assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 11 - Indices for East Fork Blue Creek.

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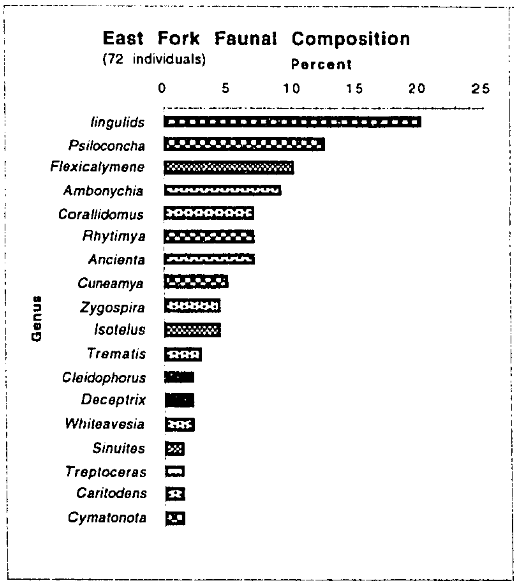

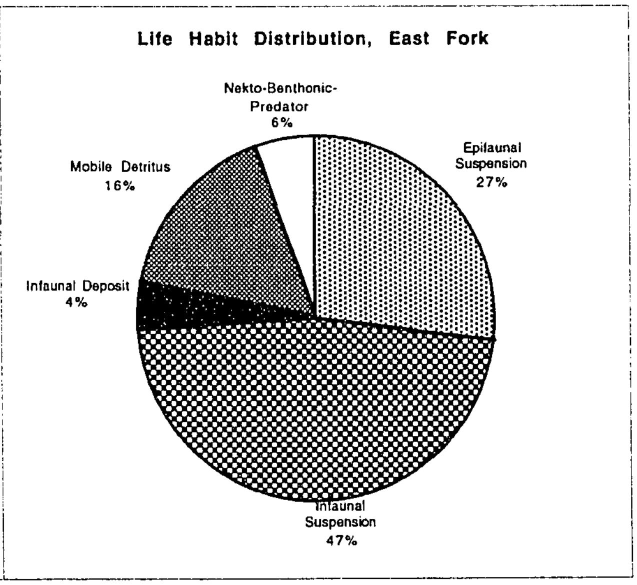

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.1170	2
Pielou Evenness *J*	0.8898	2
Average *Flexicalymene* glabella length in mm (#individuals), standard deviation	3.9 (15), 1.7	4 (out of 8)
Articulation% of *Flexicalymene*	14.7%	6 (out of 9)
Density (occurrences/liter)	11.06	4 (out of 12)
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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dominated by lingulids, *Ambonychia*, *Psiloconcha*, and *Corallidomus* (Figure 22). From the bottom to the top of this unit, a transition was observed in pelecypods, with the infaunal *Psiloconcha* dominating at the bottom and the epifaunal *Corallidomus* and *Ambonychia* the most abundant pelecypods at the top (Figure 23). While not as abundant as in the Kope and Fairview samples, the individuals of *Sinuites* recovered here were significantly larger than their Kope and Fairview counterparts.

There were several indicators of current energy and stable substrates at the top of this unit, including a crinoid, some bryozoan material and, most notably, a lensing shingled *Rafinesquina* layer in the upper third of the unit. The bottom portion of this unit also contained evidence of event beds, including a rippled calcisiltite storm bed and a thin shell-hash layer that may mark the bottom of a smaller event-bed. The entire unit lies on a thick, rippled limestone bed. The interpretation of this unit as relatively high energy compared to other studied mudstones is supported by the low articulation ratio of *Flexicalymene* (Table 12).

In contrast to the robust shelly fauna, ichnofossils preserved in rock samples from this site were inconsistent and very poorly preserved. Rather than a lack of ichnofauna, however, this may reflect the essential difficulty of interpreting ichnofabric in these mudstones. The lack of regular bedding makes it very difficult to distinguish an undisturbed area (I.I. 1) from a completely homogenized one (I.I. 6), although this issue could probably be resolved using thin sections. Four of the eight samples studied from this horizon contained virtually no distinguishable burrows, although a vague wavy pattern was observed that could indicate bioturbation. The ichnofabric in these samples was further obscured by a tendency of the rock surface to break up into a web of fine cracks after it was split.

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Figure 22 - Faunal composition and life habit distribution of Russell Middle assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 12 - Indices for Russell Middle.

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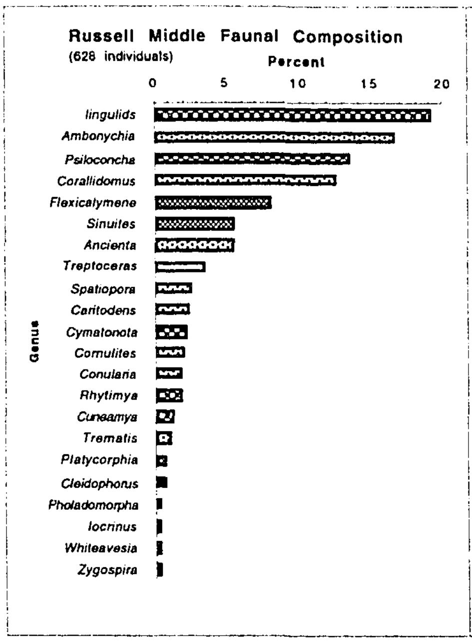

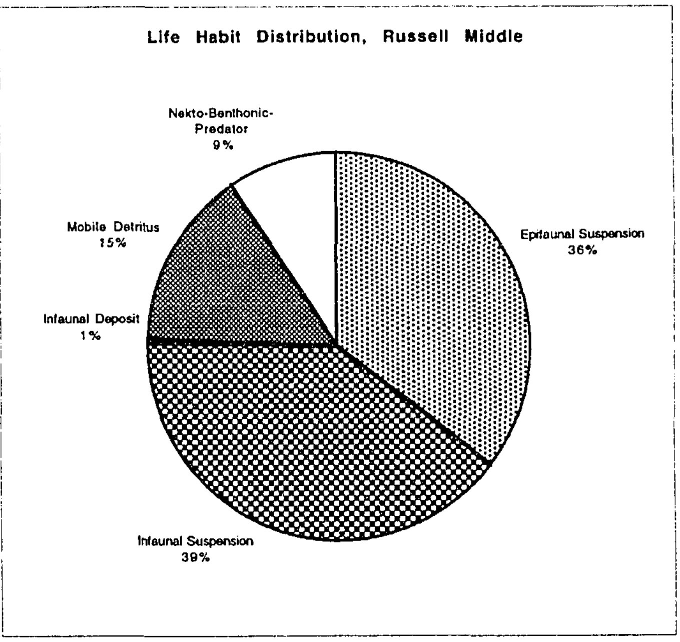

Index	**Result**	**Rank (#Sites)**
Shannon-Weaver Index *H'*	1.0702	4
Pielou Evenness *J*	0.7972	10
Average *Flexicalymene* glabella length (#individuals), standard deviation	5.9 (95), 1.7	1 (out of 8)
Articulation% of *Flexicalymene*	9.6%	8 (out of 9)
Density (occurrences/liter)	8.51	6 (out of 12)
Clay/Quartz Index, standard deviation	35.12, 2.82	2 (out of 9)
Average burrow diameter (mm), standard deviation	2.09, 1.24	4 (out of 7)

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Figure 23 - Faunal trends in Russell Middle, from bottom to top of unit.

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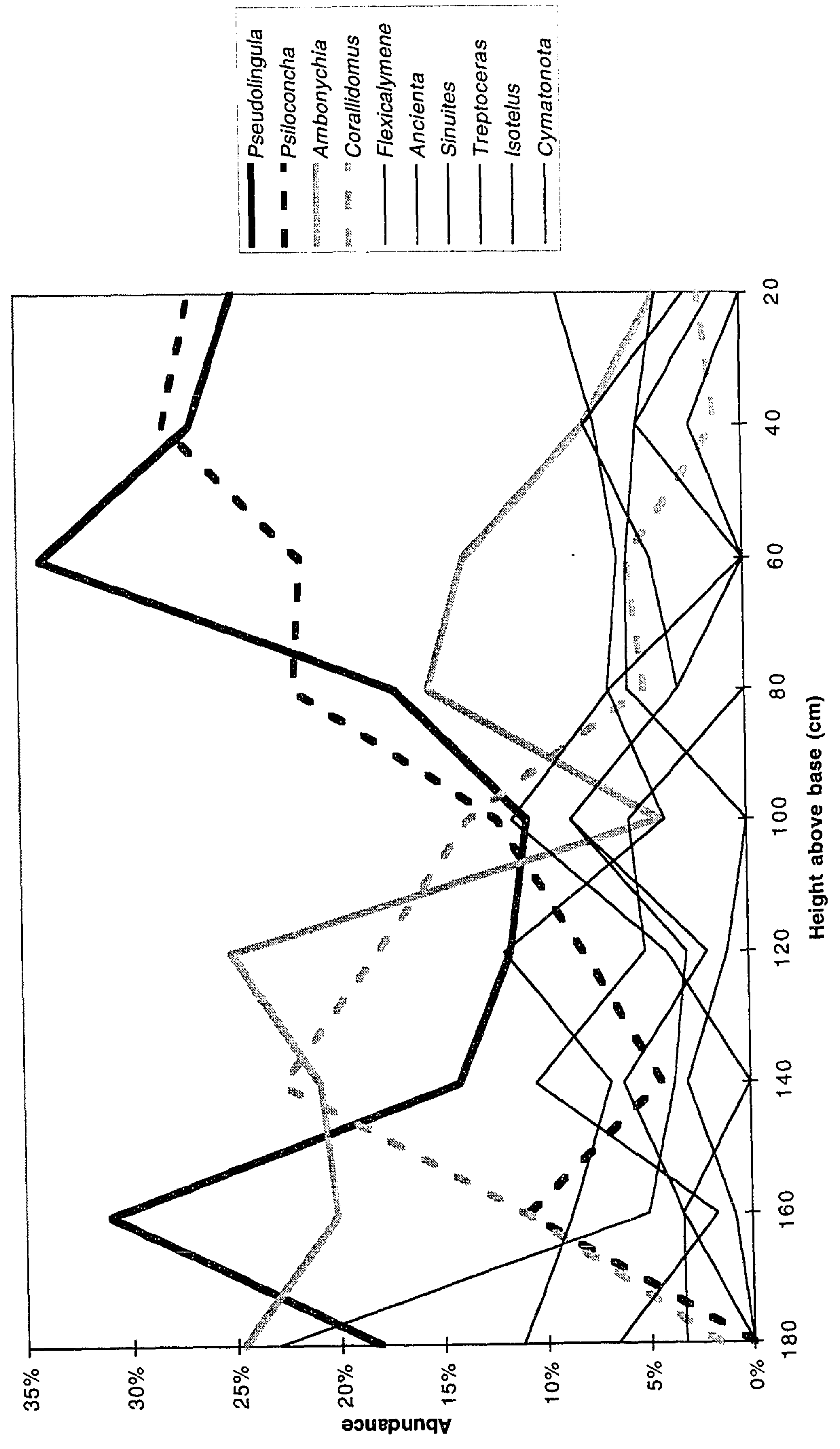

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Bon Well Hill (Guiseffi, 1982)

This site was excavated by Guiseffi (1982); it was also sampled by Frey (1987a, b), Miller (1989), and Brandt (1980). This is an additional exposure of the Waynesville "trilobite shale" (Frey, 1983) and, therefore, correlative to Russell Middle and the *Treptoceras duseri* shale samples Harper's Run and US Rt. 42. The fauna was similar to the Russell Middle locality with a few exceptions. Guiseffi discovered only small numbers of the trilobite *Flexicalymene* (although this is contradicted by Frey, 1987a, who recorded 17% *Flexicalymene* at this location), and higher percentage of the pelecypods *Cleidophorus* and *Pholadomorpha* than were discovered at Russell Middle (Figure 24). As with Russell Middle mudstones, ichnofabric was difficult to distinguish through the fine cracks that appeared on the split surfaces.

Harper's Run (Frey, 1987a)

This site was excavated by Frey (1987a; also described in Frey, 1987b; 1983). It is a thick (1.5 m) mudstone that unit represents the *Treptoceras duseri* shale of Southwest Ohio and is correlated to US Rt. 42, Bon Well Hill, and Russell Middle. While the faunal composition was similar to the latter two sites, relative abundances of genera were very different here. The cephalopod *Treptoceras duseri* dominated, followed in abundance by *Sinuites*, *Flexicalymene*, the infaunal suspension-feeding pelecypod *Cuneamya*, and the epifaunal suspension-feeding pelecypod *Pholadomorpha* (Figure 25). Unusual for a Waynesville assemblage, lingulids in this sample comprised only 2% of the recovered fauna. Other unusual features of this assemblage were the presence of a stromatoporoid (*Stromatocerium*) and a coral (*Tetradium*).

The original faunal list (Frey, 1987a) actually included many more genera than are listed here; fourteen additional non bryozoan genera (including seven cephalopods not recorded elsewhere) were listed, each of which made up less than 1% of the total fauna.

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Figure 24 - Faunal composition and life habit distribution of Bon Well Hill assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 13 - Indices for Bon Well Hill.

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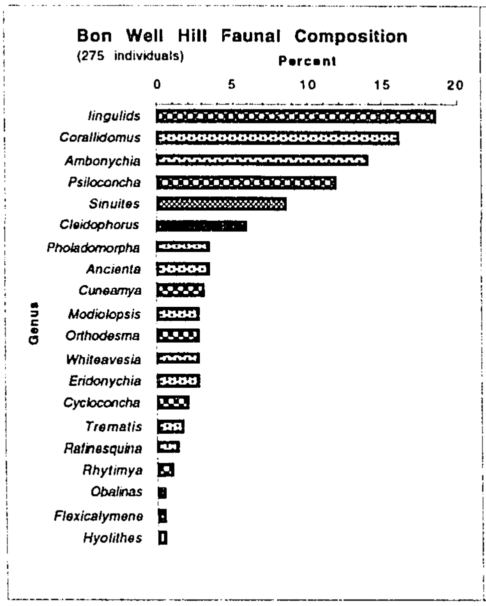

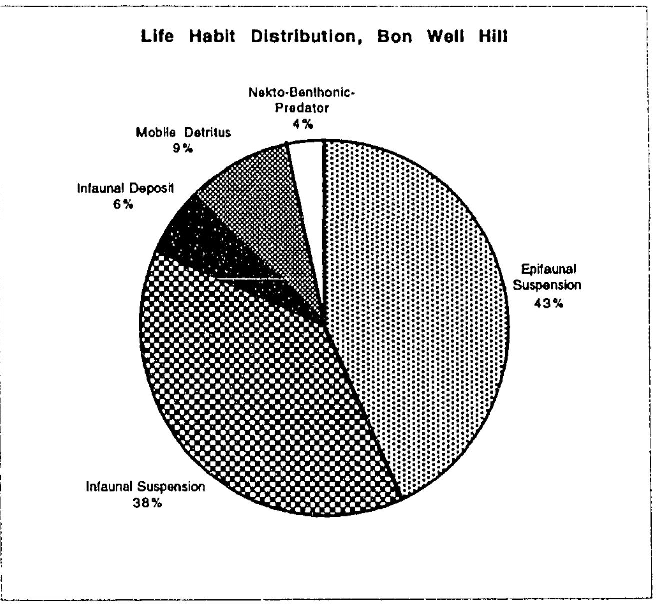

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.0787	3
Pielou Evenness *J*	0.8291	8
Average *Flexicalymene* glabella length (#individuals), standard deviation	No information	
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	6.66	7 (out of 12)
Clay/Quartz Index, standard deviation	31.46, 3.89	3 (out of 9)
Average burrow diameter (mm), standard deviation	No information	

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Figure 25 - Faunal composition and life habit distribution of Harper's Run assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 14 - Indices for Harper's Run.

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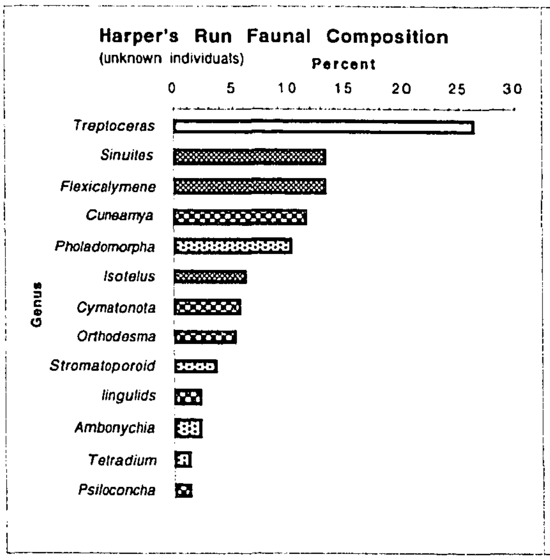

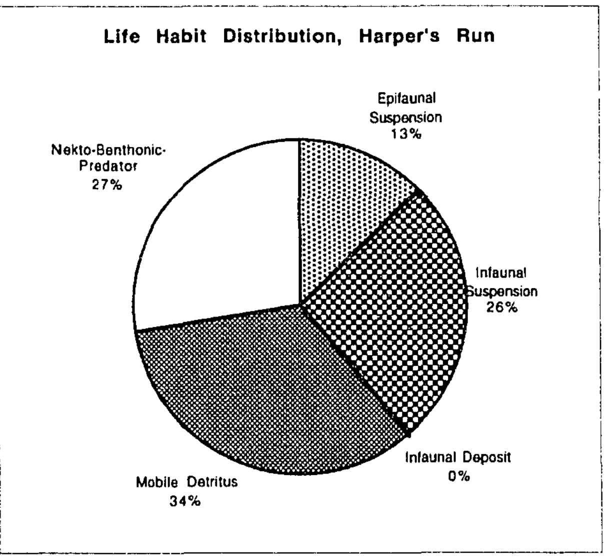

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.9597	10
Pielou Evenness *J*	0.8616	5
Average *Flexicalymene* cephalon width (#individuals)	19 (12)	2 (out of 3)
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	No information	
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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The documentation of so many rare taxa in this sample was most likely due to the intensity of collecting here, rather than any kind of fundamental ecological difference from other samples. The presence of a single sample with so many rare taxa could distort the calculations of persistence and turnover in the overall fauna and bias the test of coordinated stasis for this interval. Therefore, it was decided to exclude the rare taxa (those that make up less than 1% of the sample), to make this sample more comparable to other quantitative samples in this database, which are based on smaller collections with fewer rare taxa. Based on the same argument, this was done for the US Rt. 42 sample as well. An unintended result of eliminating the rare taxa was that diversity indices for these samples were also reduced. This is an artifact of excluding too many rare taxa and does not reflect a real diversity difference.

While information on *Flexicalymene* glabellar length was unavailable for this site, Frey (1987b) did measure cephalon widths and found a mean of 21 mm (Table 14), which is significantly larger than the mean of 10 mm measured at Orphanage Road. Cephalon widths recorded at Bon Well Hill and US Rt. 42 (Frey, 1987b) were similar to the Harper's Run results.

US Rt. 42 (Frey, 1987a)

This site was excavated by Frey (1987b, also described in Frey, 1987a, 1983). It is another example of the thick (1.5 m) Waynesville *Treptoceras duseri* shale, which is correlative to the horizon sampled at Bon Well Hill and Russell Middle. The fauna here was similar to the Harper's Run assemblage, except that there were increased abundances of *Isotelus*, lingulids, *Ambonychia*, and *Cleidophorus* and a decrease in *Sinuites*, *Treptoceras*, *Cymatonota*, and *Orthodesma* (Figure 26). In these ways, this assemblage appears to be intermediate in composition between the Harper's Run and Bon Well Hill faunas. Note that as in Harper's Run sample, many rare genera were excluded from the above list.

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Figure 26 - Faunal composition and life habit distribution of US Rt. 42 assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 15 - Indices for US Rt. 42.

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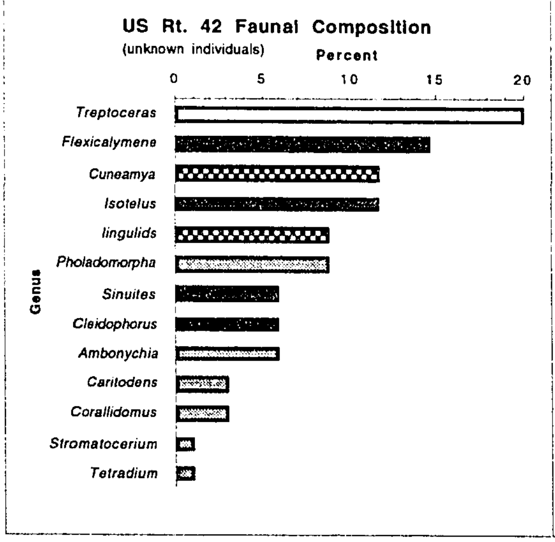

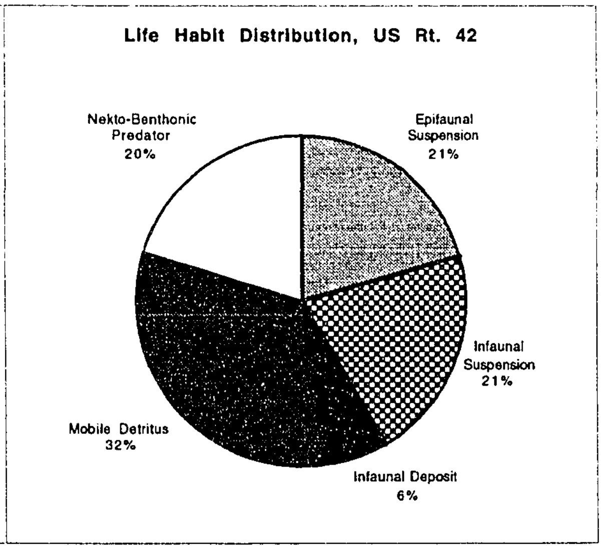

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	1.0055	8
Pielou Evenness *J*	0.9026	1
Average *Flexicalymene* cephalon width (#individuals)	21 (6)	1 (out of 3)
Articulation% of *Flexicalymene*	No information	
Density (occurrences/liter)	No information	
Clay/Quartz Index, standard deviation	No information	
Average burrow diameter (mm), standard deviation	No information	

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Russell Top

At this locality, the sampled unit was a thin mudstone bed (13 cm thick) located approximately 1 m above the Russell Middle unit and 14 m above the base of the Waynesville Formation. This unit is separated from the Russell Middle unit by 2-3 thick, closely spaced limestone beds. The sampled mudstone lies immediately atop an *Onniella* rich limestone, and there are two single shell thick *Onniella* beds within the unit. The fauna of Russell Top was dominated by large, well preserved (mostly whole) lingulids, as well as smaller numbers of *Psiloconcha*, *Ambonychia*, and *Cuneamya* (Figure 27). A faunal transition was observed within this thin unit. In the middle portion of the unit, which consisted of a clean, blocky mudstone, *Pseudolingula*, *Psiloconcha*, and *Cuneamya* predominated to the exclusion of almost all other taxa. At the top of the unit, just below another *Onniella* rich limestone layer, a slightly more diverse pelecypod assemblage was found, including more *Ambonychia*, a few *Corallidomus*, two *Conularia* specimens, and numerous *Onniella*.

The faunal structure suggests that the upper half of this unit is an event bed, with infaunal taxa appearing within the unit and epifaunal taxa at the top. As the substrate was stabilized, a takeover by *Onniella* ensued (see Figure 4). The high density of fossil occurrences (Table 16) and the large, well preserved ichnofossils indicate that environmental conditions were highly favorable to colonization.

Hannah Creek

The sampled unit exposed at Hannah Creek is a moderately thick (0.5 m) mudstone unit in the upper portion of the Waynesville Formation, approximately 27 m above its base. Most fossils were recovered below a thin, lensing limestone bed located 35 cm above the base of the unit. One shell thick *Rafinesquina* and *Onniella* layers were observed in the bottom one-fourth of the unit. As in the Russell Upper assemblage, lingulids were the most dominant taxa, followed in abundance by relatively large individuals of

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Figure 27 - Faunal composition and life habit distribution of Russell Top assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 16 - Indices for Russell top.

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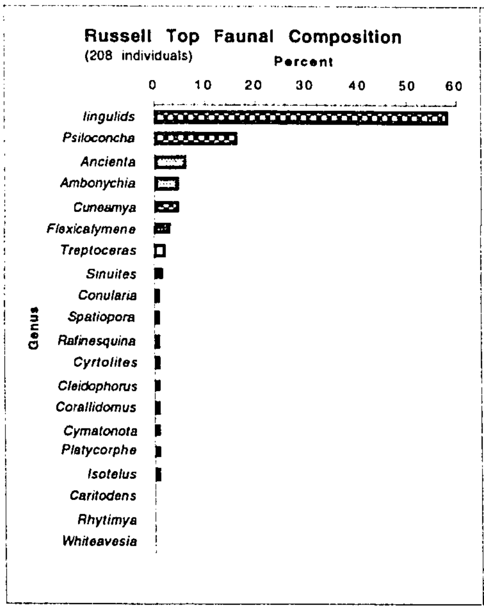

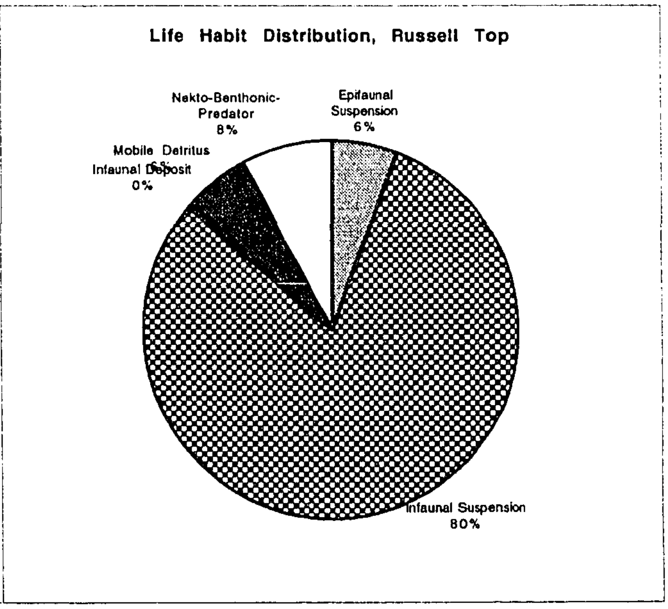

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.6833	14
Pielou Evenness *J*	0.5252	14
Average *Flexicalymene* glabella length (#individuals), standard deviation	5.6 (13), 1.5	2 (out of 8)
Articulation% of *Flexicalymene*	15.4%	5 (out of 9)
Density (occurrences/liter)	13.58	1 (out of 12)
Clay/Quartz Index, standard deviation	30.13, 2.67	4 (out of 9)
Average burrow diameter (mm), standard deviation	1.89, 2.79	2 (out of 7)

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Flexicalymene. The remaining fauna consisted of much lower abundances (<3%) of various pelecypods, *Conularia*, and the articulate brachiopods *Zygospira* and *Rafinesquina* (Figure 28). Densities were relatively low compared to other Waynesville sites (Table 17). Other elements of the Hannah Creek assemblage included occasional large, well preserved, bryozoan colonies, one of which was preserved upside-down, indicating that it had been toppled.

While body fossils were not particularly abundant in this unit, the mudstone samples collected here illustrated the highest degree of bioturbation and the greatest diversity of trace fossils of any sample. In some cases, three generations of burrows were observed, one imprinted upon the other. Burrows with light and dark infill were observed, as well as several examples of lined burrows, containing a white lining and a dark infill. Burrow diameters ranged from less than 1 mm to a maximum of over 4 mm.

The contrasting lines of evidence at Hannah Creek make interpretation of depositional environment difficult. The relatively low fossil density and high articulation ratio of trilobites suggest rates of sedimentation and frequency of depositional events were higher here than at Russell Middle, in which a similar fauna was preserved, although probably not as high as at Dornbusch. The articulate brachiopod beds and bryozoans, however, indicate significant periods of substrate stability and low turbidity. The bryozoan colony may have been toppled during a particularly strong storm event. The dense ichnofabric and large body size of fossils suggests a relatively shallow, well oxygenated environment.

As in several other sites (notably Russell Lower), the clay/quartz index ranking (5 out of 9) does not appear to reinforce the environmental interpretation of Hannah Creek as a relatively onshore environment. This may be an indication that, at the resolution of individual hand samples, the proportions of clay and quartz are variable and may not reflect the environment of deposition in any meaningful way (see Chapter 5).

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Figure 28 - Faunal composition and life habit distribution of Hannah Creek assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 17 - Indices for Hannah Creek.

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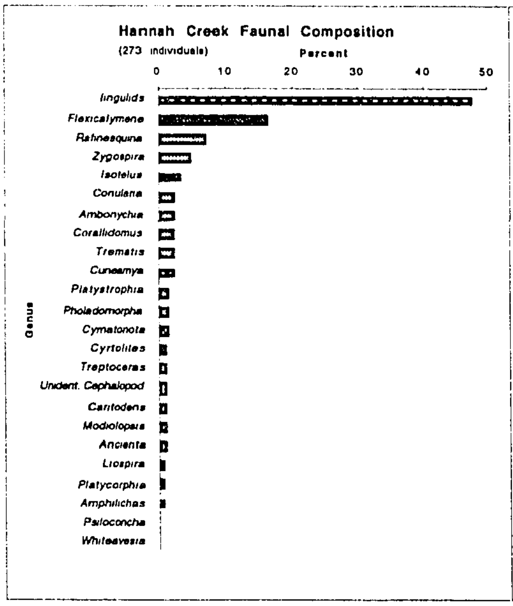

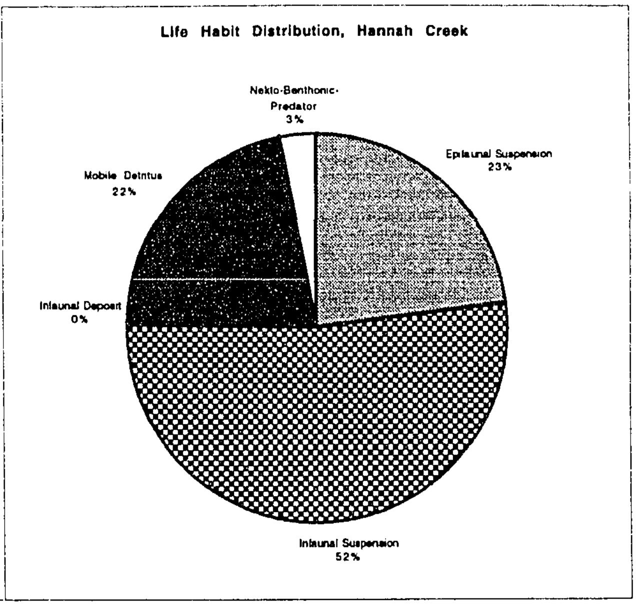

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.8786	12
Pielou Evenness *J*	0.6366	13
Average *Flexicalymene* glabella length (#individuals), standard deviation	5.0 (25), 1.6	3 (out of 8)
Articulation% of *Flexicalymene*	33.0%	2 (out of 9)
Density (occurrences/liter)	2.91	8 (out of 12)
Clay/Quartz Index, standard deviation	30.12, 3.77	5 (out of 9)
Average burrow diameter (mm), standard deviation	2.13, 1.27	3 (out of 7)

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Clear Fork

The sampled horizon at Clear Fork lies just below the base of the Liberty Formation, approximately 37 m above the base of the Waynesville Formation, and corresponds to the "pea-size flexi" layer known to local collectors. It also corresponds to the "*Loxoplocus bowdeni*" zone identified by Frey (1978), although the fauna recorded in this locality is quite different from that described by Frey (1978). The sampled horizon consists of 60 cm of mudstone divided by three thin limestone beds and numerous limestone nodules. The dominant genus in this unusual assemblage was the articulate brachiopod *Zygospira*, which occurred as numerous tiny (~4 mm) articulated individuals (Figure 29). Next in importance were lingulids, many of which occurred in life position. The remaining fauna consisted of tiny *Flexicalymene* trilobites, the articulate brachiopod *Hebertella* (which, along with *Deceptrix*, was associated with the limestone nodules and lenses), and, in the upper 10 cm of the horizon, the crinoid *Cincinnaticrinus*. Although the density was relatively high, this is mostly related to the presence of numerous tiny *Zygospira*--other fossils were considerably less abundant. As the term "pea-size flexi" implies, body sizes of all fauna, especially trilobites, were very small. The low diversity and small body size that characterize this community may indicate a relatively hostile environment for colonization and growth. Taphonomic characteristics, including a high rate of articulation of trilobites, the articulation of *Zygospira*, and the occurrence of many *Pseudolingula* in life position all indicate that, as in the Dornbusch sample, it is likely that energy of environment was low and rates of sedimentation, or at least frequency of deposition, was high. The cause of the small body sizes is unknown, but is probably not produced by the smothering of a single "juvenile" community, as the small body sizes were found in multiple mudstone horizons separated by thin limestones. Rather, an environmental explanation such as low oxygen or unusual salinity is more likely.

As in several other samples, the trace fossil record appears to contradict the body fossil record. Although the mudstone was not densely bioturbated, burrows were not

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Figure 29 - Faunal composition and life habit distribution of Clear Fork assemblage. Symbols in left chart correspond to life habits on the pie chart at right.

Table 18 - Indices for Clear Fork.

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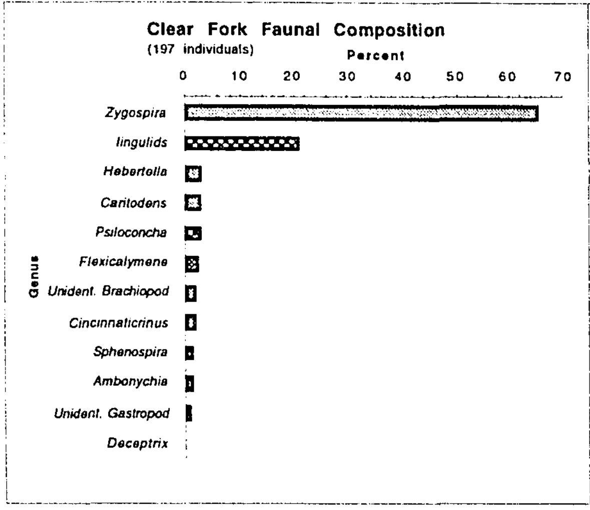

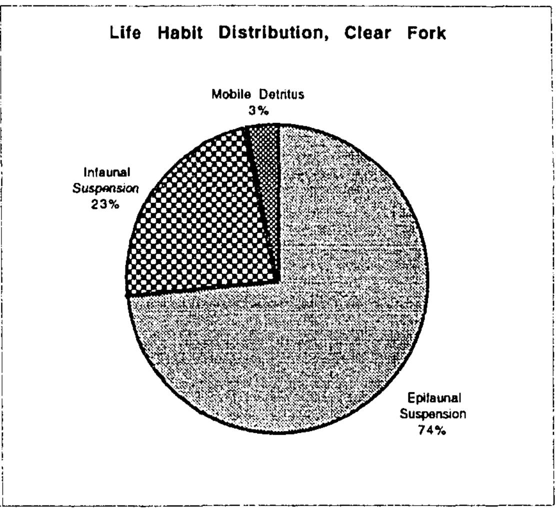

Index	Result	Rank (#Sites)
Shannon-Weaver Index *H'*	0.5177	15
Pielou Evenness *J*	0.4798	15
Average *Flexicalymene* glabella length (#individuals), standard deviation	2.4 (12), 0.6	8 (out of 8)
Articulation% of *Flexicalymene*	27.3%	3 (out of 9)
Density (occurrences/liter)	10.15	5 (out of 12)
Clay/Quartz Index, standard deviation	28.50	7 (out of 9)
Average burrow diameter (mm), standard deviation	3.93	1 (out of 7)

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uncommon, and many burrow diameters were surprisingly large, given the small size of body fossils. As in several other layers (most notably Backbone Creek but also possibly Dornbusch, Russell Branch Lower and Russell Branch Upper), evidence for event bed deposition included burrows truncated by a basal shell hash layer.

Other fossiliferous mudstones

Richly fossiliferous mudstones in the Cincinnatian are not limited to the horizons described above. Local collectors have discovered many mudstone localities rich in trilobites and other fauna. Dan Cooper, an amateur collector who has often cooperated and collaborated with local paleontologists, has excavated sites at Oldenberg (Franklin Co., Indiana), Monroe (Butler Co., Ohio), and near Mt. Orab (Highland Co., Ohio). The Oldenberg site, stratigraphically positioned in the upper Waynesville Formation above the Hannah Creek site and below the Clear Fork site, contains a densely fossiliferous fauna containing trilobites (*Flexicalymene* and *Isotelus*), brachiopods (lingulids, *Trematis*, *Rafinesquina*, *Zygospira*, and *Platystrophia*), mollusks (cephalopods, *Ambonychia*) and large bryozoan colonies. Unfortunately, I was unable to gain permission to do a quantitative sample of this horizon. The Monroe locality exposed a Corryville mudstone that contained trilobites and bryozoan encrusted cephalopods. Although this site has since been covered over by construction, samples of the fossils and enclosing mudstones were made available at the Cincinnati Museum Center. The Mt. Orab site, in the Sunset Member of the Arnheim Formation, was studied by Ferree (1993). Because of the lack of detail in identification of taxa, especially pelecypods, I was unable to include this data in the database. However, Ferree did document an interesting assemblage dominated by lingulids and *Flexicalymene* but also containing large numbers of *Rafinesquina*, various pelecypods (mostly *Modiolopsis*), and, surprisingly, abundant graptolites. Guiseffi (1982) described a Corryville mudstone designated "Bushelman's" (Hamilton Co., Ohio) that was described as containing *Ambonychia*, *Corallidomus*, and other typical mudstone community

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members. The presence of *Corallidomus* in this sample is surprising, because it has been listed as a "Richmondian invader" by Holland (1996a: Frey (1983) noted the occurrence of *Corallidomus versaillensis* in Indiana in strata equivalent to the Corryville Member). Dattilo (1994) documented faunas rich in gastropods, deposit-feeding pelecypods, trilobites and other organisms in the Miamitown shale. As with Ferree's data, differences in methods of collection and levels of identification precluded the use of this data for this study. Finally, Hughes and Cooper (1999) excavated a unique cluster of articulated *Flexicalymene granulosa* in the Kope Formation

Mudstone samples from the Oldenberg, Monroe and Mt. Orab formations were available for x-ray diffraction and ichnofabric analysis. I was unable to obtain mudstone samples from Bushelman's, as the exposure has since been covered over.

Summary

With some exceptions, the following observations can be made about the mudstone faunas described above:

1) While samples were generally rich in mollusks, inarticulate brachiopods, and trilobites, several variations were present. The compositional variability is analyzed further in the following chapters.

2) *Sinuites* was the most abundant genus in the Edenian/Maysvillian samples, while lingulids were the most common taxa in the Richmondian samples.

3) The trace fossil record often did not correspond well to the body fossil record. Some of the largest burrows were found at the site with the smallest body fossils (Clear Fork), and the most diverse assemblage of trace fossils was found in a locality with a relatively low density of body fossils (Hannah Creek). The Russell Branch Middle and Bon Well Hill

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localities, which contained a robust and diverse fauna, contained very few distinguishable trace fossils.

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Chapter 5: Analysis of Faunal Trends and Comparison to Unfossiliferous Mudstones

In the preceding chapter, data were presented on a site by site basis to familiarize the reader with the important faunal elements of these samples, and to identify any trends, patterns, or relationships to be analyzed in greater depth. In the first part of the current chapter, trends from older to younger samples are examined with respect to diversity, body size, dominant taxa, and life habit distribution. In the second part, characteristics of fossiliferous and unfossiliferous mudstones are compared with respect to stratigraphic position, lateral continuity, sedimentological composition, and ichnofabric.

To facilitate the analysis of trends, the study interval was divided into "Lower Cincinnatian" and "Upper Cincinnatian" sections. The Lower Cincinnatian includes all Edenian and Maysvillian samples. The Upper Cincinnatian includes all Richmondian samples. This division was made here because (1) it splits the data approximately in half (seven samples below, nine samples above), (2) there is a full range of facies from offshore to onshore represented in each section, and (3) there was an invasion of fauna into the study region at the base of the Richmondian (Holland, 1996a). The effect of this invasion on the mudstone communities is a key component of this study.

Rarefaction

Rarefaction is a method developed initially by Sanders (1968) to compare the diversity of differently sized samples. The goal of rarefaction is to answer the question: if samples were scaled down to the same size, which would contain more taxa? This method is highly effective in illustrating diversity because it allows for comparison of samples with different degrees of evenness.

Conceptually, rarefaction works by simulating a collection of fossils from a locality. As individuals are selected without replacement from a sample, a running tally can be kept of the number of taxa recorded as selection continues until every individual is

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accounted for. The result is a curve plotting number of taxa represented vs. number of individuals sampled. In this study, an analytical method (from Raup, 1975) was used to produce a similar result.

Rarefaction curves can indicate several characteristics of an assemblage, the most useful of which is the comparison of diversity in samples scaled to the same size. The shape of rarefaction curves can also reflect the evenness and completeness of the sample. Highly convex curves indicate a well balanced community, where many taxa are common and are therefore “found” relatively quickly. If the abundance distribution is highly skewed toward one or two dominant taxa, the result will be a more gently sloping rarefaction curve because more individuals will have to be counted before the uncommon taxa are recorded. A rarefaction curve that flattens out as the number of individuals rises can indicate that most taxa to be found in a community have actually been sampled. If the curve does not flatten out, it is likely that more taxa are present and the sample is most likely incomplete. It should be emphasized, however, that rarefaction curves cannot be extrapolated (Sanders, 1968; Raup, 1975), and therefore one cannot make assumptions about the total number of taxa present in samples larger than those actually collected.

Rarefaction analysis was performed on eleven of the sixteen mudstone samples. Only one sample was included from Guiseffi’s (1982) three Fairview samples, all of which were comparable in diversity and overall dominance structure. I was unable to rarefy Frey’s (1987a) US Rt. 42 and Harper’s Run samples because only percentage abundance data were available. Backbone Upper was not included because of its extremely small sample size. Because there is a significant faunal transition that occurs within the Russell Middle mudstone layer (see below) which could increase diversity by essentially including two overlapping communities, the sample used in this analysis was taken from a smaller interval within the total thickness of this unit.

Results of rarefaction are shown in Figure 30. Rarefied to a common sample size of approximately 60 individuals, there is essentially no diversity difference within a group

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Figure 30 - Rarefaction of mudstone samples.

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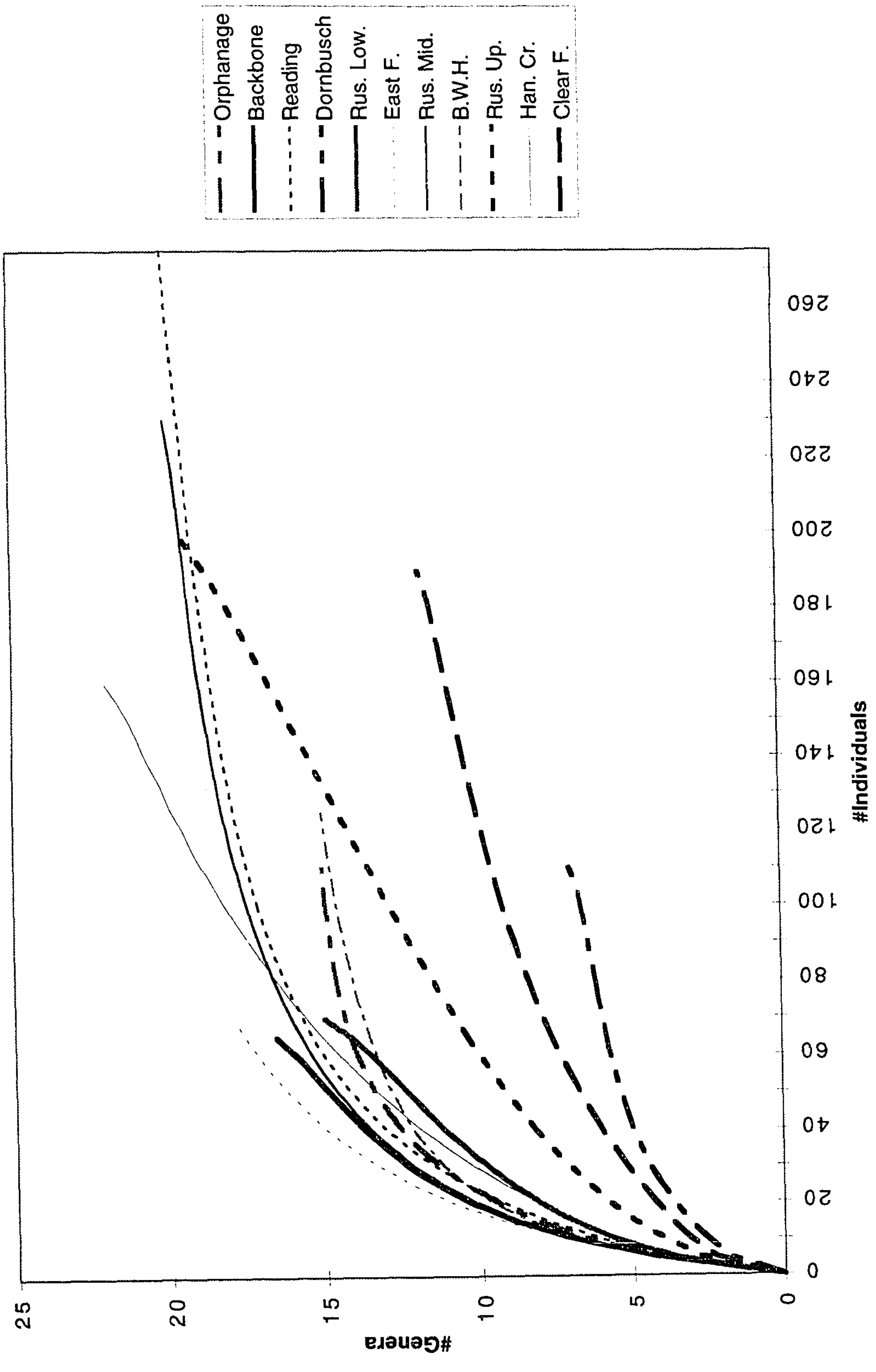

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that includes Edenian, Maysvillian, and Richmondian samples. The two largest samples in this group, Reading Road (Maysvillian) and Russell Middle (Richmondian), have virtually identical diversity curves. There is no evidence that overall diversity of communities changes from the Lower to Upper Cincinnatian samples.

The three outliers all have lower diversities at 60 individuals. This includes the Dornbusch, Clear Fork, and Russell Upper samples. In addition to low diversity, the Dornbusch sample showed a low density of occurrences and a relatively low intensity of bioturbation. Because the fauna present here shows excellent preservation (including specimens in life position), the relative lack of fossils cannot be attributed to taphonomic artifact. It is possible that high rates of sedimentation, as indicated by the articulation ratio of trilobites here, may have discouraged colonization by filter feeding and grazing (e.g., *Sinuites*) mollusks at this locality. Alternatively, a lack of time averaging in a sequence of obrution deposits could also account for the relatively low genus richness here.

As at Dornbusch, the Clear Fork assemblage lacked many of the common mollusks that characterized most other samples. The dwarfed nature of the fauna at this locality suggest unfavorable environmental conditions were responsible for the lack of diversity here. In contrast, the lack of genus richness at 60 individuals in Russell Upper can be attributed to the dominance of lingulids. As the number of individuals counted approaches 200, the generic richness in this sample is comparable to other samples.

Size trends

In general, body sizes were consistent in each site. Consequently, samples contained individuals that were either large, average, or small for a given genus. A significant body size difference was observed between Lower and Upper Cincinnatian samples (Table 19), as was noted by Guiseffi (1982) and Frey (1987b). Figures 31 through 40 illustrate size trends and size-frequency histograms for *Sinuites*, *Ambonychia*, *Cuneamya*, *Psiloconcha*, and *Flexicalymene*.

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Table 19 - Test for statistical significance of size differences in Edenian/Maysvillian and Richmondian taxa. A $P(Z \leq z)$ of less than 0.05 indicates greater than 95% confidence that mean lengths of the two populations are different.

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Genus	**Mean Length (mm), Variance** (Edenian/Maysvillian)	**Mean Length (mm), Variance** (Richmondian)	**z**	**z Critical** (two-tail)	**P(|Z|≤|z|)** (two-tail)
Sinuites	15.26, 24.76	28.42, 48.37	-8.49	1.96	0.00
Ambonychia	15.16, 40.85	38.23, 161.08	-12.13	1.96	0.00
Cuneamya	10.49, 13.4	26.94, 96.59	-7.87	1.96	$9.44*10^{-16}$
Psiloconcha	8.84, 17.85	19.53, 61.43	-8.48	1.96	0.00
Flexicalymene	3.36*, 1.24	4.82*, 3.88	-5.17	1.96	$5.96*10^{-8}$

**Flexicalymene* mean glabella length

Figure 31 - *Sinuites* measurements. Orphanage-Harrison samples from Lower Cincinnatian (Edenian/Maysvillian), East Fork-Russell Upper samples from Upper Cincinnatian (Richmondian).

Figure 32 - *Sinuites* size frequency.

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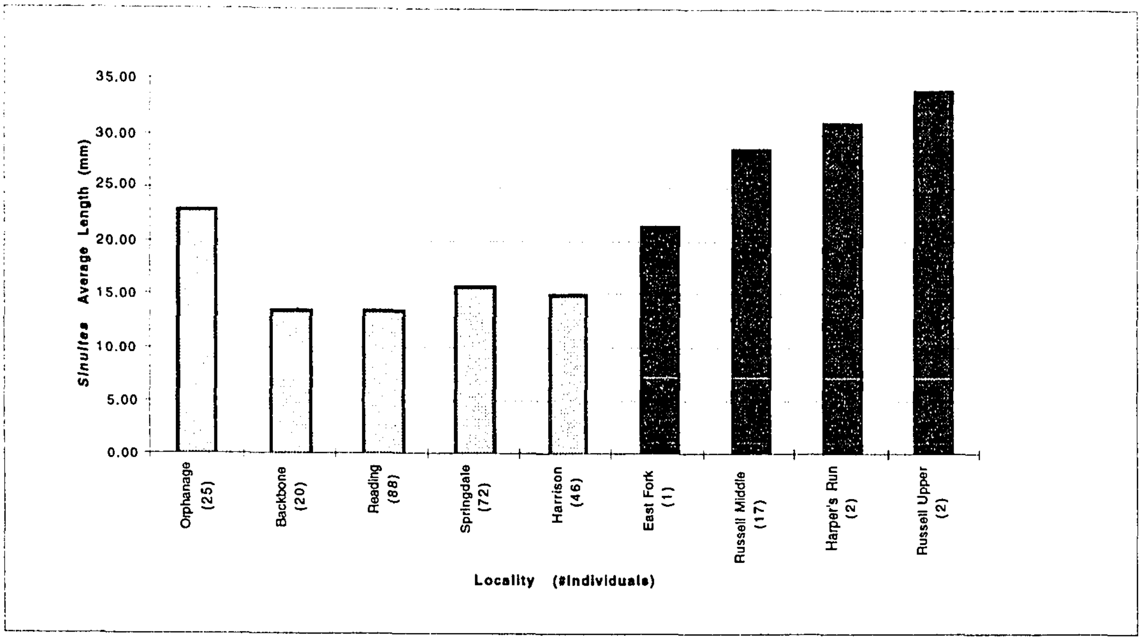

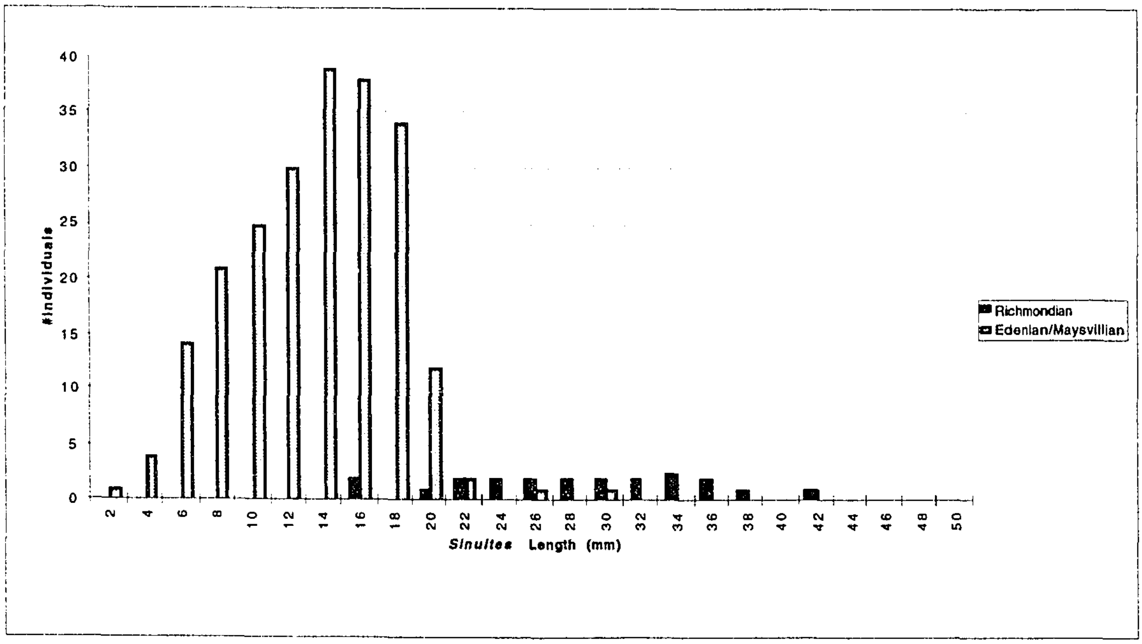

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Figure 33 - *Ambonychia* measurements. Orphanage-Harrison samples from Lower Cincinnatian (Edenian/Maysvillian), East Fork-Hannah Creek samples from Upper Cincinnatian (Richmondian).

Figure 34 - *Ambonychia* size frequency.

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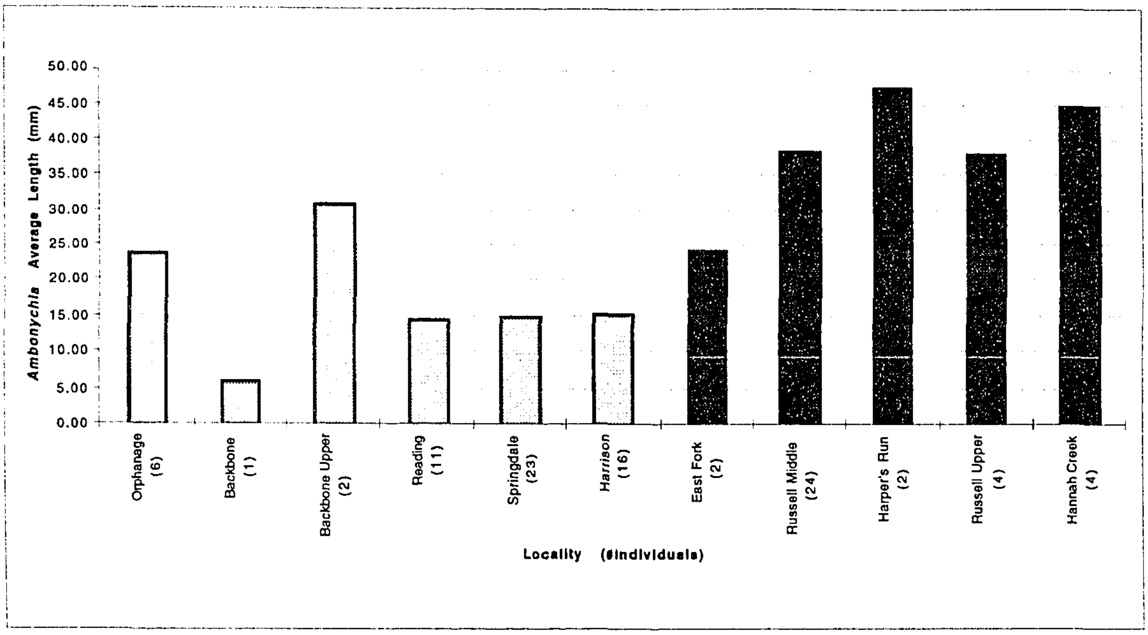

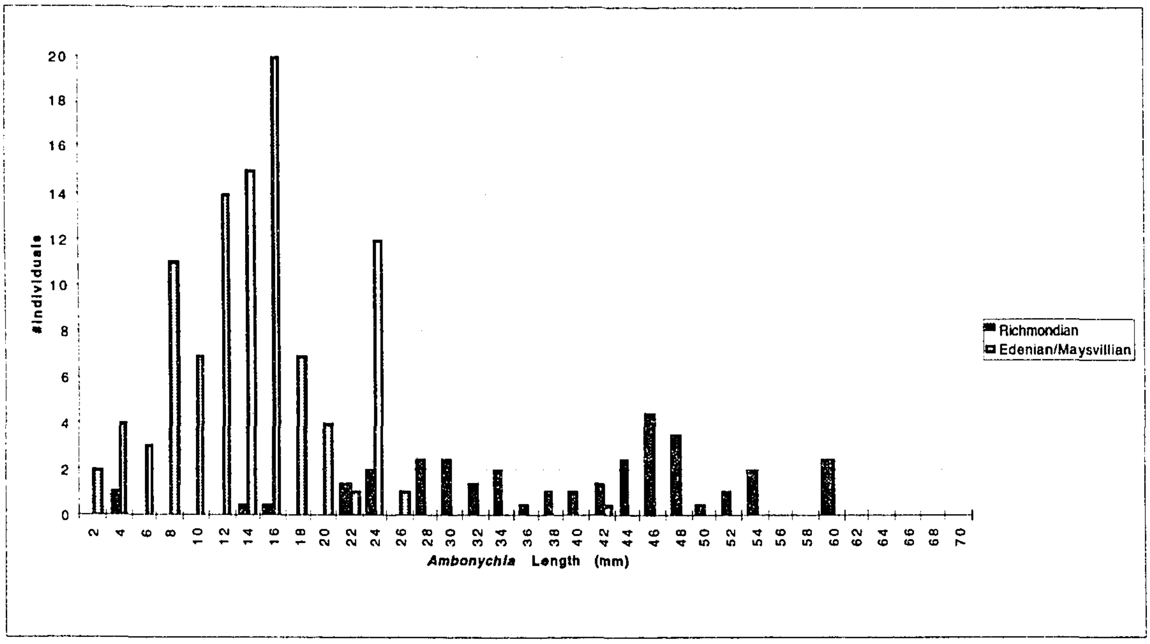

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Figure 35 - *Cuneamya* measurements. Reading-Harrison samples from Lower Cincinnatian (Edenian/Maysvillian), Russell Lower-Hannah Creek samples from Upper Cincinnatian (Richmondian).

Figure 36 - *Cuneamya* size frequency.

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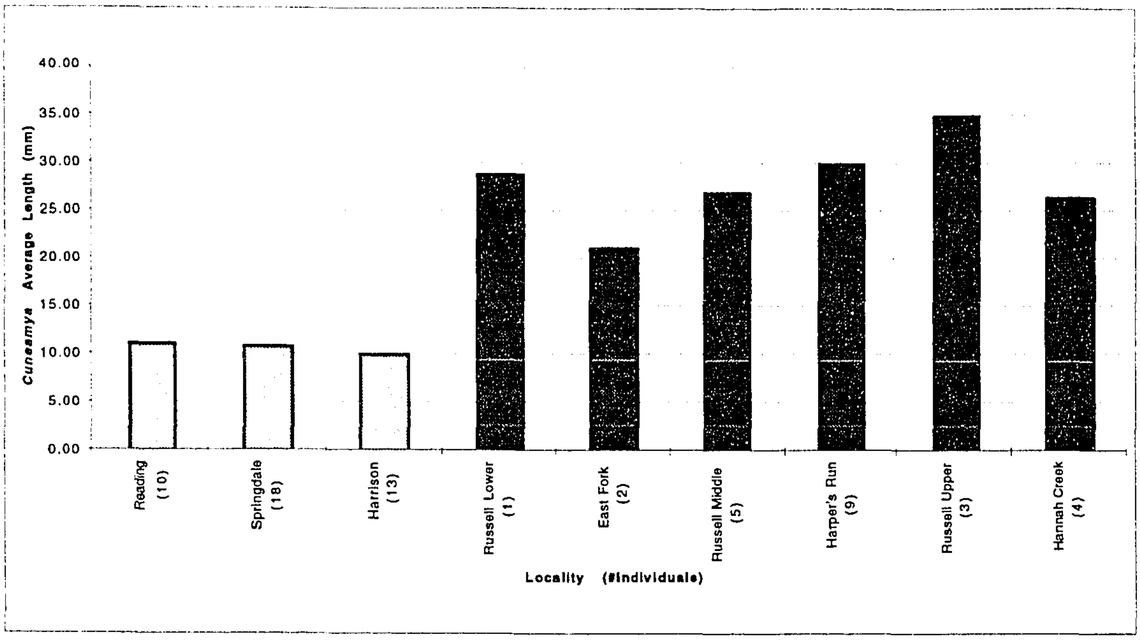

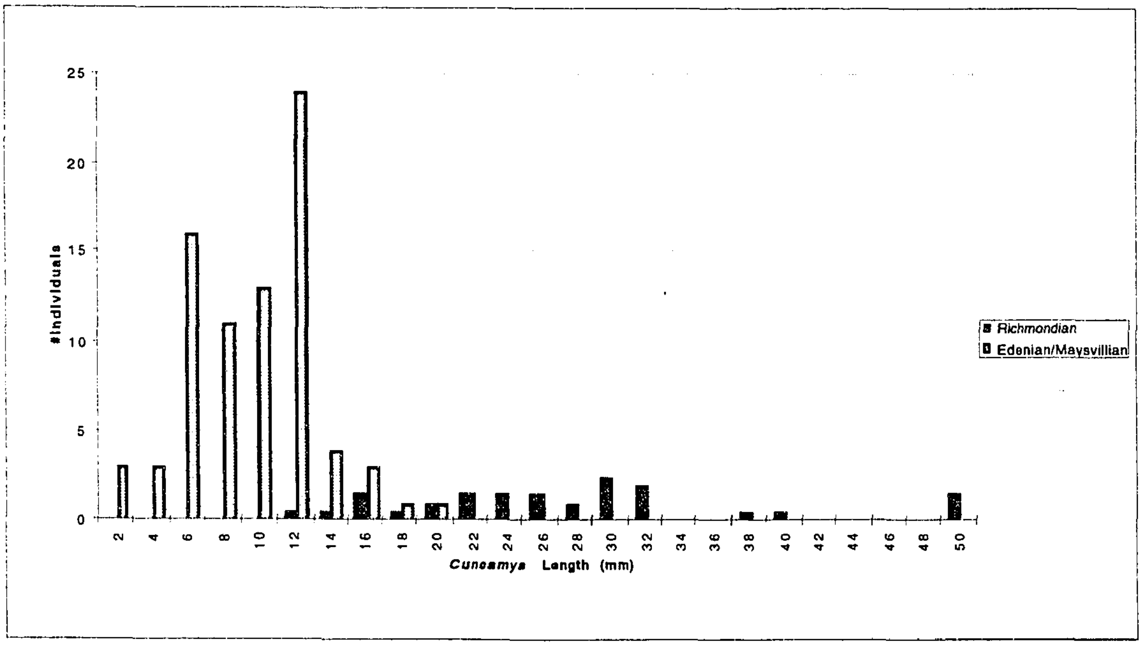

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Figure 37 - *Psiloconcha* measurements. Backbone-Dornbusch samples from Lower Cincinnatian (Edenian/Maysvillian), Russell Lower-Clear Fork samples from Upper Cincinnatian (Richmondian).

Figure 38 - *Psiloconcha* size frequency.

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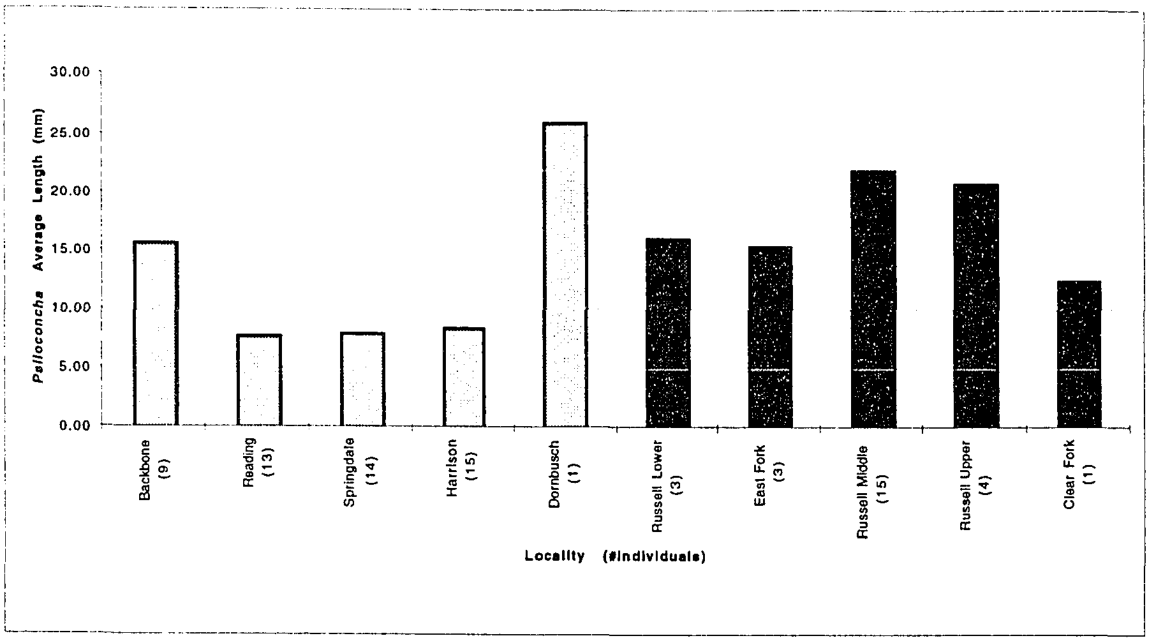

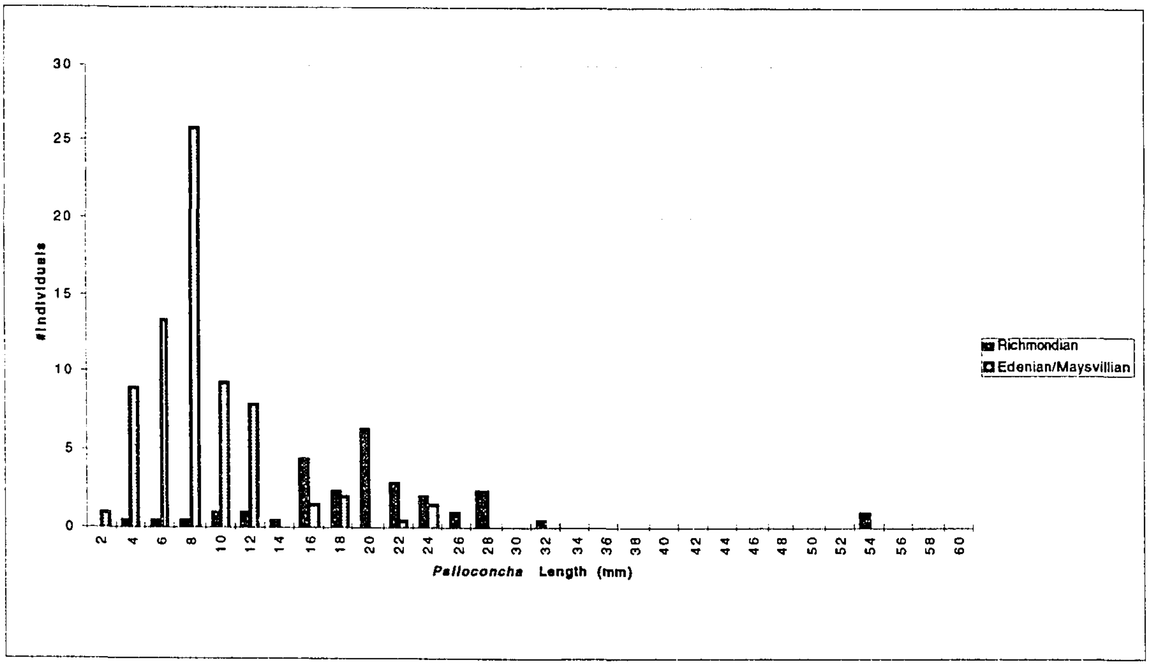

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Figure 39 - *Flexicalymene* measurements. Backbone and Dornbusch samples from Lower Cincinnatian (Edenian/Maysvillian), Russell Lower-Clear Fork samples from Upper Cincinnatian (Richmondian). St. Leon sample was obtained from a mudstone unit exposed at the Indiana Rt. 1 roadcut, and is correlative to the Clear Fork beds.

Figure 40 - *Flexicalymene* glabellar size frequency.

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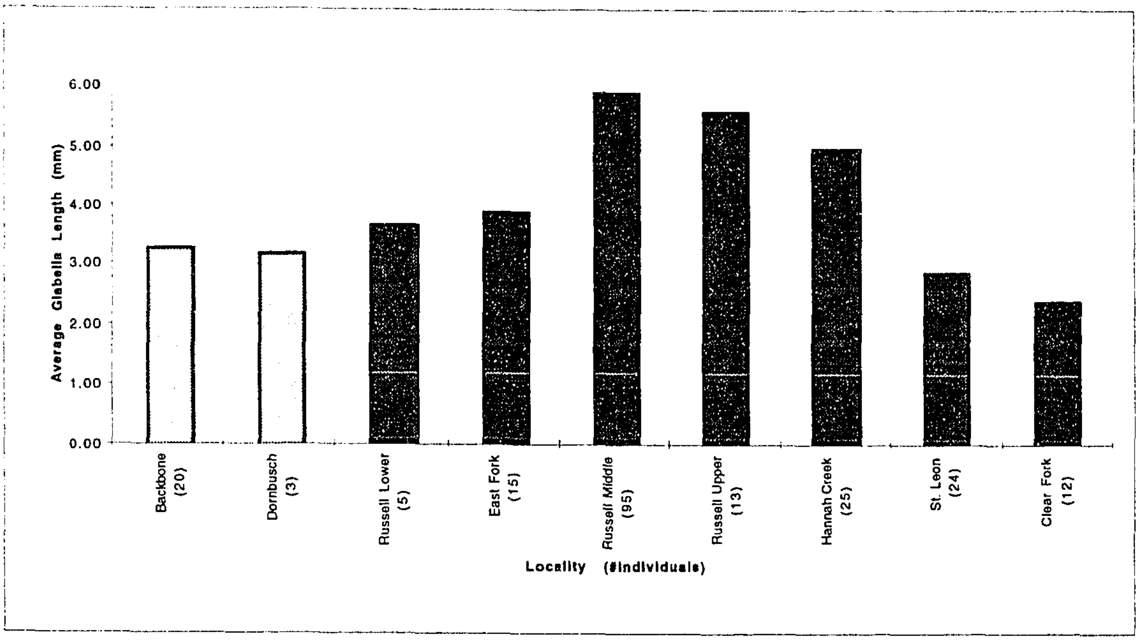

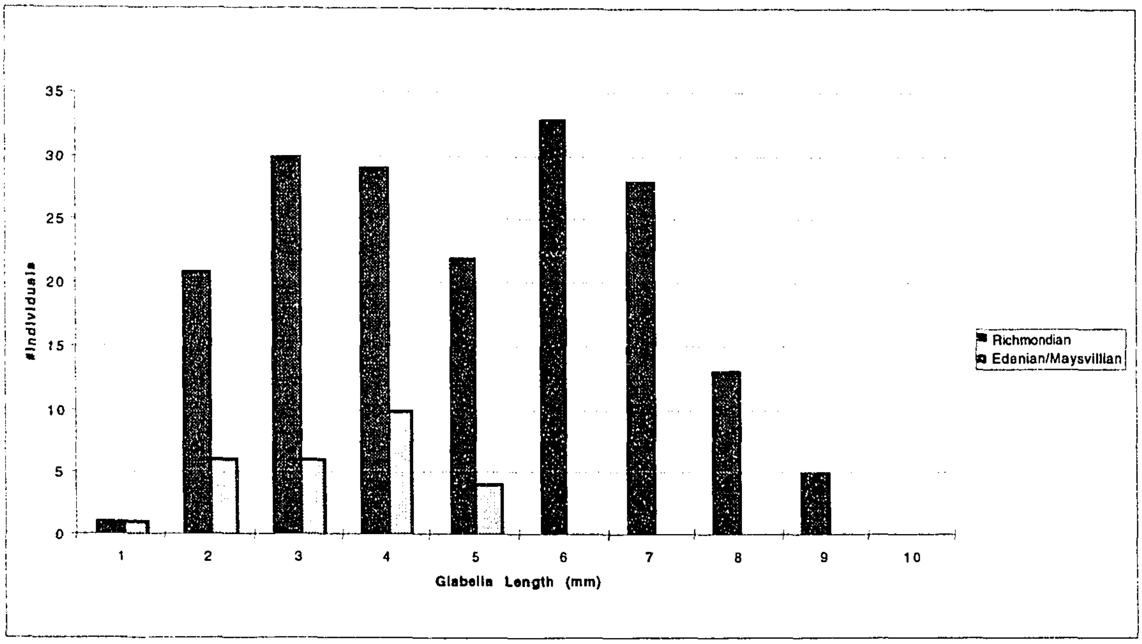

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Figure 41 - Relationship of *Ambonychia* shell-size to sequence stratigraphy (from Daley, 1993).

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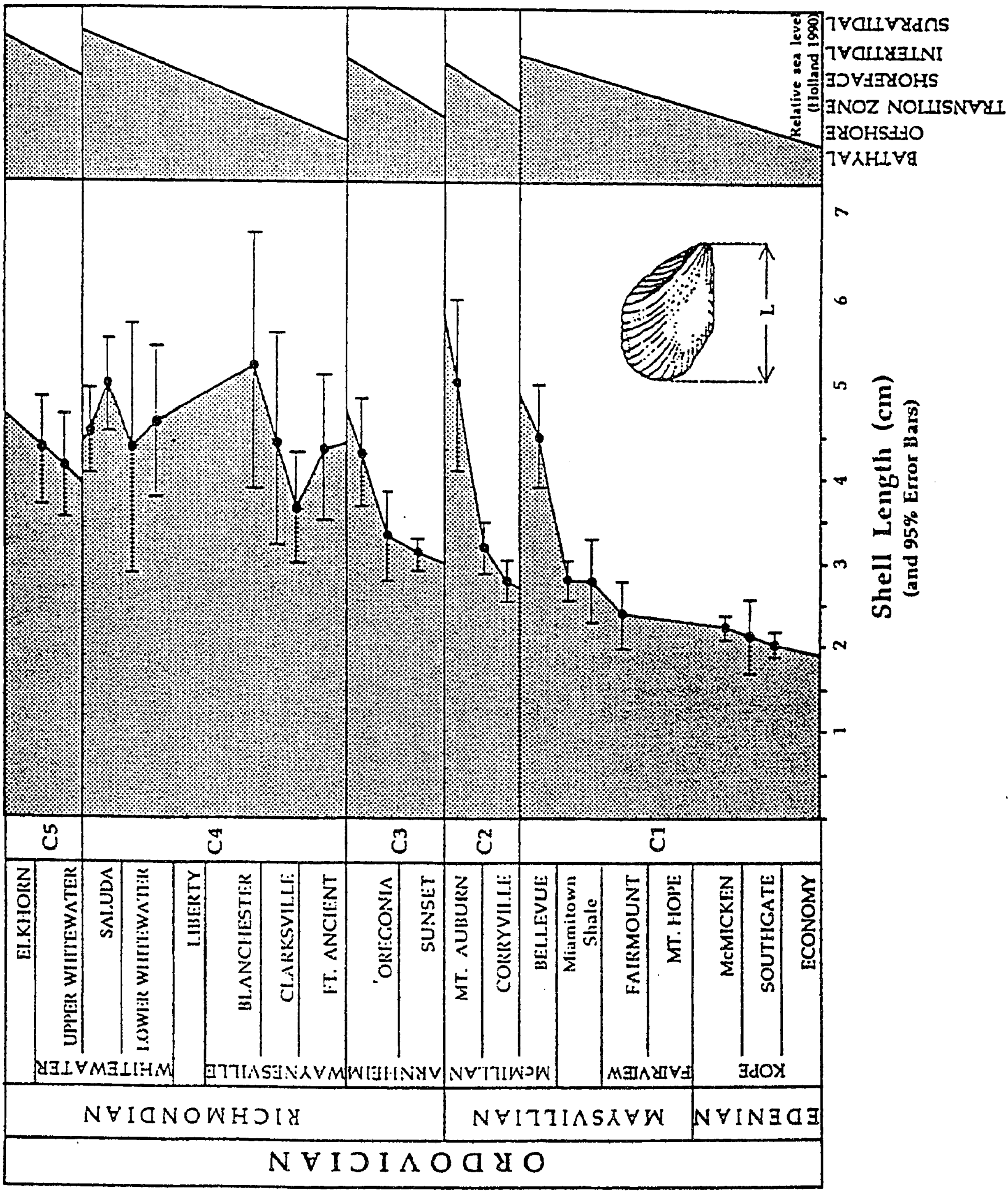

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There are three notable exceptions to the general trend. First, the Richmondian samples from Clear Fork and Russell Lower were both composed of very small individuals, especially trilobites. Second, Backbone Upper (Edenian) contained large individuals of *Ambonychia* and *Trematis crassipunctata*. The existence of these counterexamples is significant, because they indicate that the size trends were not monotonic, and, therefore, most likely were related to environmental variables rather than evolutionary change. Daley (1993) demonstrated that body size of *Ambonychia*, at least in limestones, could be correlated to the stratigraphic position of samples within shallowing upward sequences (Figure 41), with smaller mean size in deeper facies and larger mean size in onshore facies. From the Kope through the Arnheim, the average sizes track proposed sea level changes well. In the Waynesville through Saluda sequence, however, sizes were large throughout. Pojeta (1961) also noted the large size of Richmondian *Ambonychia*, which he attributed to the evolutionary development of a keel, allowing individuals to remain stable in soft muds at larger sizes. The fact that nearly *all* taxa appear to be larger in these Waynesville samples, however, is evidence that this explanation is not solely responsible for the pattern.

Lingulids vs. *Sinuites*

The previous chapter showed that most Lower Cincinnatian samples contained abundant *Sinuites*, while most Upper Cincinnatian samples (as well as the Dornbusch sample) were rich in lingulids. Of the persistent taxa, only these showed a consistent abundance shift from the Lower Cincinnatian to the Upper Cincinnatian (Figure 42). As exceptions to this trend (e.g. Backbone Upper and Harper's Run) can be found, it is inferred that the increasing dominance of lingulids was related to a prevalence of favorable environments in the younger samples.

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Figure 42 - Percent abundances of Lingulids and *Sinuites*.

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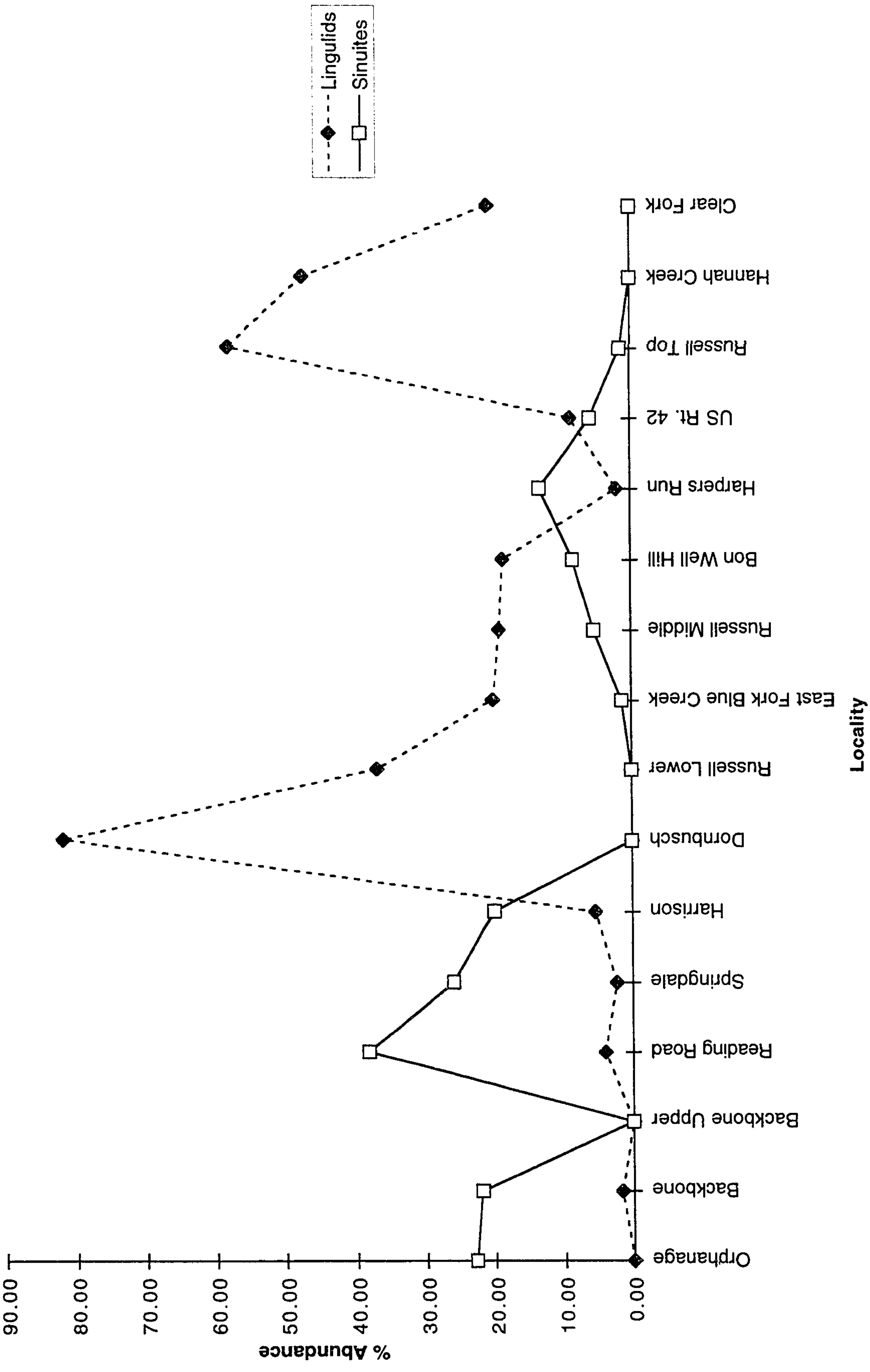

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Life habits

Aside from those caused by the changing populations of the dominant taxa *Sinuites* (a grazer) and lingulids (infaunal suspension-feeders), no significant trends in life habit distribution were detected (Figure 43). Examples of communities dominated by each life habit were found in Lower and Upper Cincinnatian samples.

Summary of faunal trends

Lower and Upper Cincinnatian mudstone communities can be distinguished by the following characteristics:

1) The appearance of new genera (*Corallidomus*, *Pholadomorpha*, and *Ancienta*) in moderate abundances in Upper Cincinnatian samples.

2) Larger sizes of common genera in most (but not all) Upper Cincinnatian samples.

3) Dominance by *Sinuites* in Lower Cincinnatian samples, and by lingulids in Upper Cincinnatian samples.

Based on the predominance of lingulids, the Corryville sample (Dornbusch) was more similar to the Upper Cincinnatian samples than to the other Lower Cincinnatian samples. Overall diversity and life habits, while highly variable, showed no consistent trends from Lower to Upper Cincinnatian assemblages. Faunal abundance patterns will be further analyzed in the following chapters.

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Figure 43 - Relative proportions of most common life habits in all samples.

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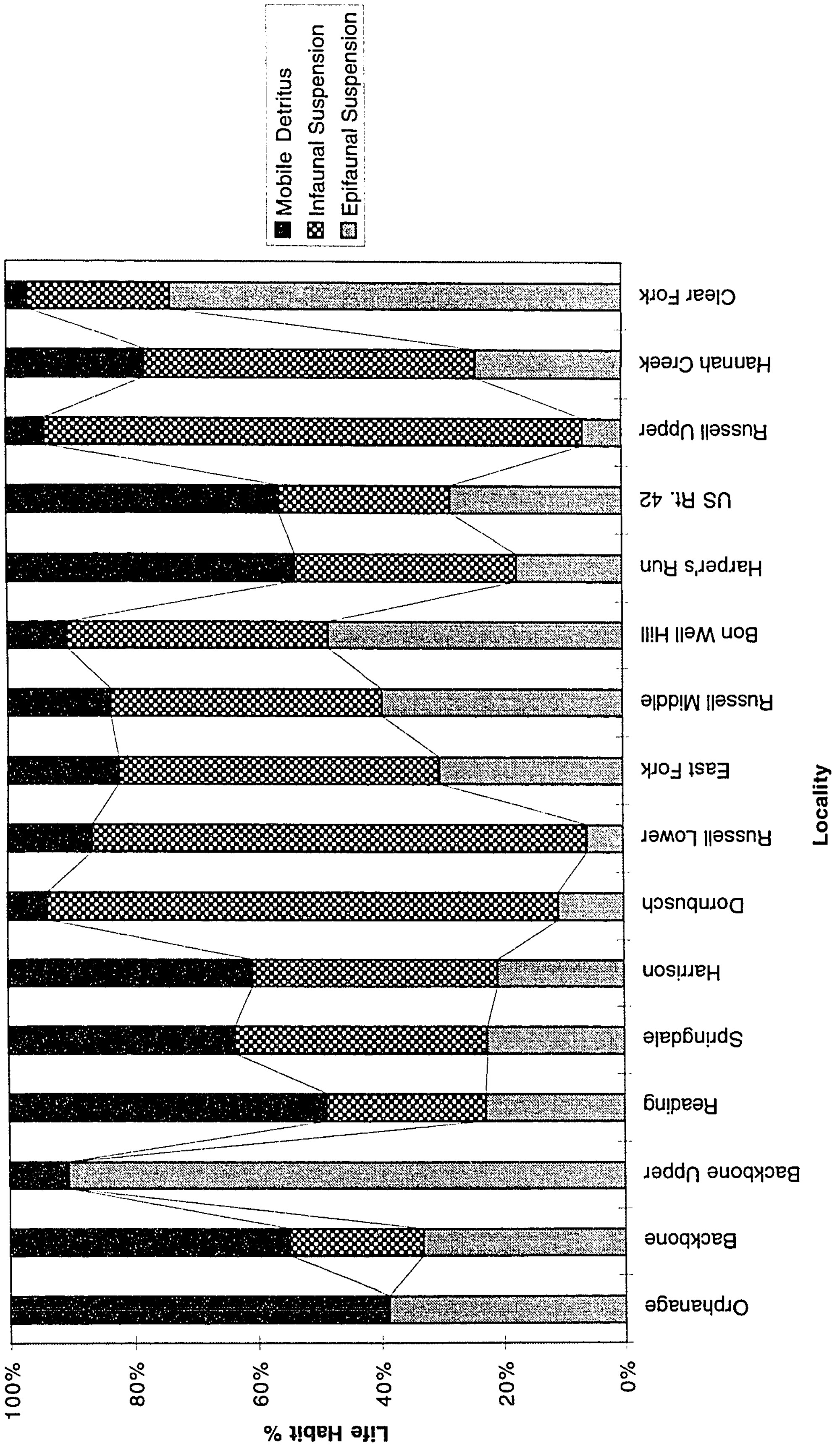

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Comparison to other mudstones

In the course of searching for horizons containing well preserved and abundant fossils, many additional mudstones were observed and sampled qualitatively. Most Cincinnatian mudstones observed by the author contained few fossils, and where fossils did occur, they most often appeared as thin layers of disarticulated shells, usually of the brachiopods *Zygospira* or *Onniella*. Such mudstone horizons were observed in the Fairview, Corryville, Arnheim, Waynesville and Liberty formations. Kope mudstones were usually nearly entirely unfossiliferous except for occasional graptolites, trilobite sclera, and thin packstones.

This leads to an interesting question: why do some Cincinnatian mudstones contain a diverse, unique and *in situ* fauna, while others are almost entirely barren? While this study was not designed specifically to address this question, the observations and data discussed below may help to identify patterns to be investigated further.

Lateral continuity

An important component of this problem is the degree to which the mudstone horizons and constituent communities could be traced and recognized laterally. If these communities only existed and were preserved on isolated patches of a muddy seafloor, then the lack of fossils in some mudstones could be attributed to this intermittent colonization. The existence of communities continuously present and traceable for large distances on the same horizon, on the other hand, would argue against this explanation.

The degree to which these communities and horizons could be traced laterally was variable. In the Waynesville Formation, the "Trilobite shale" in Indiana and the "Treptoceras duseri shale" in Ohio (Frey, 1983) represent the same horizon, which is laterally traceable for more than 90 km. The "pea-size flexi" bed represented by the Clear Fork sample can also be found at the Caesar Creek spillway, over 80 km away. Although a quantitative sample was not taken at the latter, the association of tiny *Flexicalymene*

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trilobites, *Cincinnaticrinus* columnals and *Zygospira* valves was easily recognized at Caesar Creek. The layers yielding the deposit-feeder rich sample at Russell Lower were also recognized at an outcrop on Indiana Rt. 1, several kilometers away.

Other sampled horizons could not be traced laterally from one outcrop to another. The thick mudstone at Hannah Creek was located just below a distinctive series of thick, shelf forming limestones. In the limestone beds within this interval, a faunal transition occurs, with *Onniella* and *Rafinesquina* below, and *Strophomena* above. While the limestone interval could be identified at a large roadcut on Indiana Rt. 1, the thick mudstone sampled at Hannah Creek could not be identified. The thick mudstone unit at Dornbusch was also not recognized at any other outcrop, including the Stone Lick Creek section proposed as the type section for the Corryville (Goldman, 1994). In the Fairview samples, Guiseffi (1982) observed that the fossil rich horizons sometimes were not continuous in a single outcrop, stating that “not only did the limestone layers pinch out and thicken, but that the fossil shell layers within the shales varied also in a similar manner” (Guiseffi, 1982, p. 30). The fact that Guiseffi did not obtain his three samples from the same horizon in the Fairview may indicate that these horizons/ communities could not be identified and correlated accurately across the three widely separated outcrops.

Clay/quartz index

Mudstone samples from sites (excluding Backbone Upper and East Fork) excavated in this study were taken for x-ray diffraction analysis. Additional samples were taken from unfossiliferous horizons in the Kope (Kentucky Rt. 17), Fairview (Backbone Creek), Corryville (Second Creek), Arnheim (Second Creek), and Waynesville (Salt Creek, Hannah Creek Upper) Formations.

As mentioned earlier, the clay/quartz index is not an absolute measure of percentage composition, but it can be used to compare samples within this database. A t-test of clay/quartz index for fossiliferous and unfossiliferous mudstones shows a significant

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difference in mean values (Table 21). The more argillaceous composition of the fossiliferous mudstones may explain the use of the term "butter shale" to describe some of these beds. However, while the compositional difference is significant, there is considerable overlap. The Backbone Upper and Dornbusch samples both contain a relatively low proportion of clay, while the Kentucky Rt. 17 sample has a relatively high clay/quartz index. Also, it should be emphasized that the division of samples into "fossiliferous" and "unfossiliferous" mudstones is somewhat artificial. Rather than a sharp distinction, there appears to be a gradation from nearly barren mudstones to mudstones containing a low density of fossils (such as Dornbusch, Reading Road, Springdale, and Harrison) to mudstones containing an abundant, robust, and diverse fauna.

Within the fossiliferous shales, clay/quartz index shows a positive correlation to diversity (Figure 44), although the R^2 value of 0.59 is not particularly high. There are two plausible explanations for this relationship. The first is that clay rich samples represented more offshore communities (Scotford, 1965), which in turn supported a greater diversity and abundance of organisms. Watkins (1978) documented a diversity increase in Silurian bivalves from nearshore to deeper shelf biofacies. It is also possible that the amount of clay in the mud affected the stability of the substrate, which in turn could have influenced colonization by infaunal and epifaunal organisms.

Highlighted in Figure 44 is one anomalous sample in which a relatively silty mudstone (low clay/quartz index) contained a diverse fauna. This sample was Backbone Upper, which contained epifaunal suspension feeders (*Trematis*, *Ambonychia*, *Modiolopsis*) and mobile detritus feeders (*Isotelus*, *Flexicalymene*). The lack of infaunal organisms here could be an indication that the silty substrate was not favorable to burrowing lifestyles. However, this relationship does not hold for other samples. No correlation was found between clay/quartz index and the proportion of epifaunal or infaunal taxa (Figures 45 and 46).

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Table 20 - Average clay/quartz indices for all samples, in stratigraphic order. Sites used for quantitative faunal samples in **bold**.

Table 21 - T-Test for significance in difference of mean clay/quartz indices of fossiliferous and unfossiliferous mudstones. A $P(T \leq t)$ less than 0.05 indicates a greater than 95% probability of a difference in mean clay/quartz index.

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Locality Name (Formation)	**Average Clay/Quartz Index**	**Standard Deviation**
Kentucky Rte. 17 (Kope)	30.31	5.43
Backbone Creek (Kope)	37.43	7.72
Backbone Upper (Kope)	23.29	--
Other Backbone Mudstones (Fairview)	25.37	4.98
Dornbusch (Corryville)	23.30	2.11
Second Creek (Corryville)	22.97	4.99
Russell Lower (Waynesville)	29.70	3.12
Russell Middle (Waynesville)	35.12	2.82
Bon Well Hill (Waynesville)	31.46	3.89
Russell Upper (Waynesville)	30.13	2.67
Salt Creek (Waynesville)	23.41	1.52
Hannah Creek (Waynesville)	30.12	3.77
Hannah Upper Mudstone (Waynesville)	20.81	--
Clear Fork (Liberty)	28.50	4.01

Mean clay/quartz index, #samples (Fossiliferous mudstones)	**Mean clay/quartz index, #samples** (Unfossiliferous mudstones)	**t**	**t Critical** (two-tail)	**P(T≤t)** (two-tail)
30.85, 42	25.19, 17	3.50	2.00	0.000917

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Figure 44 - Diversity index (H') vs. average clay/quartz index (with best fit line, R^2=0.59). Backbone Upper sample appears as a black square (see text).

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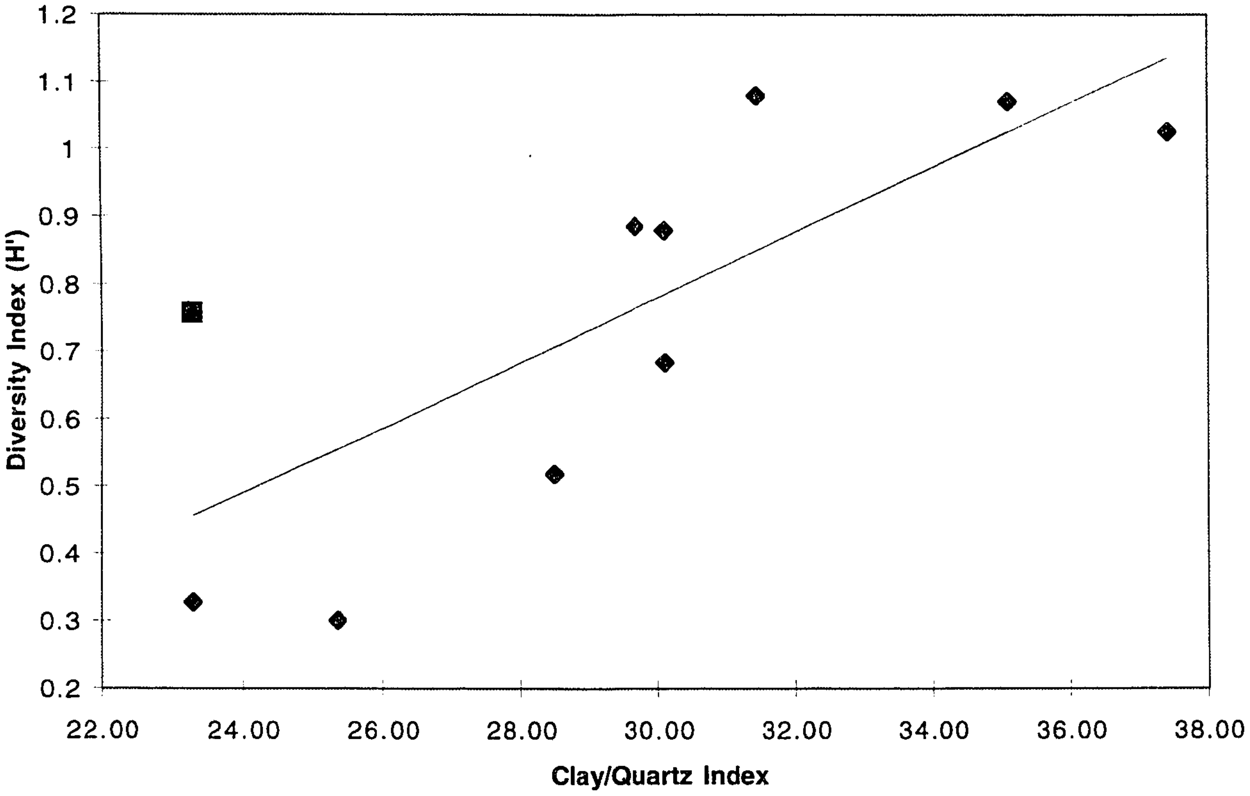

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Figure 45 - Percent epifaunal suspension feeding vs. average clay/quartz index.

Figure 46 - Percent infaunal suspension feeding vs. average clay/quartz index.

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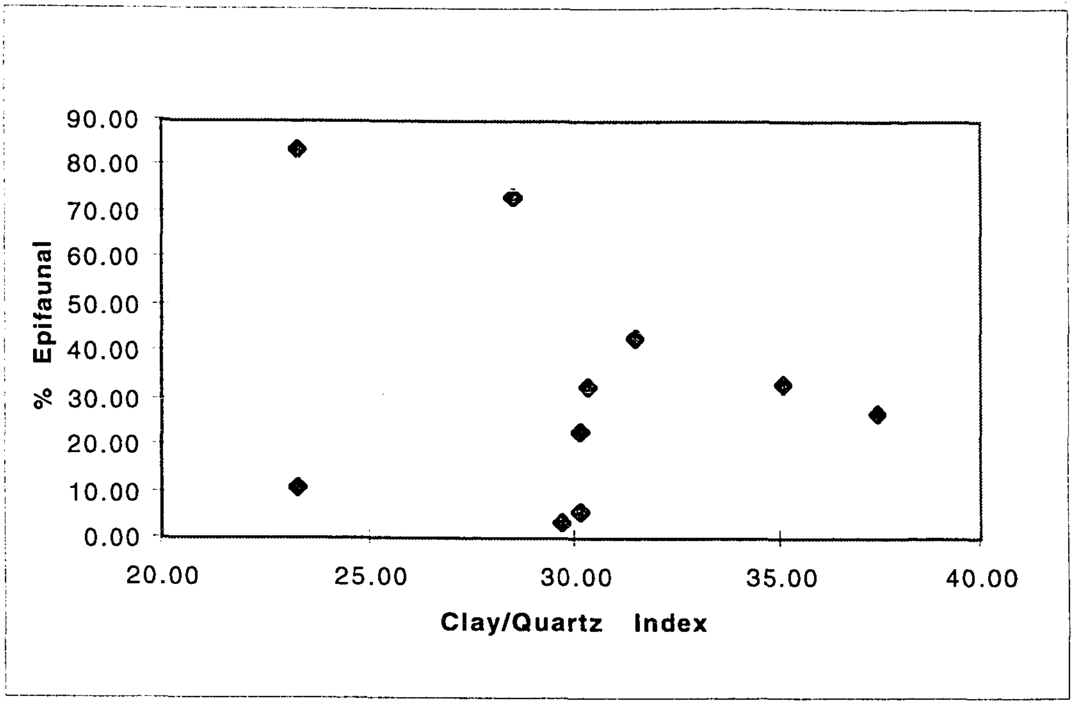

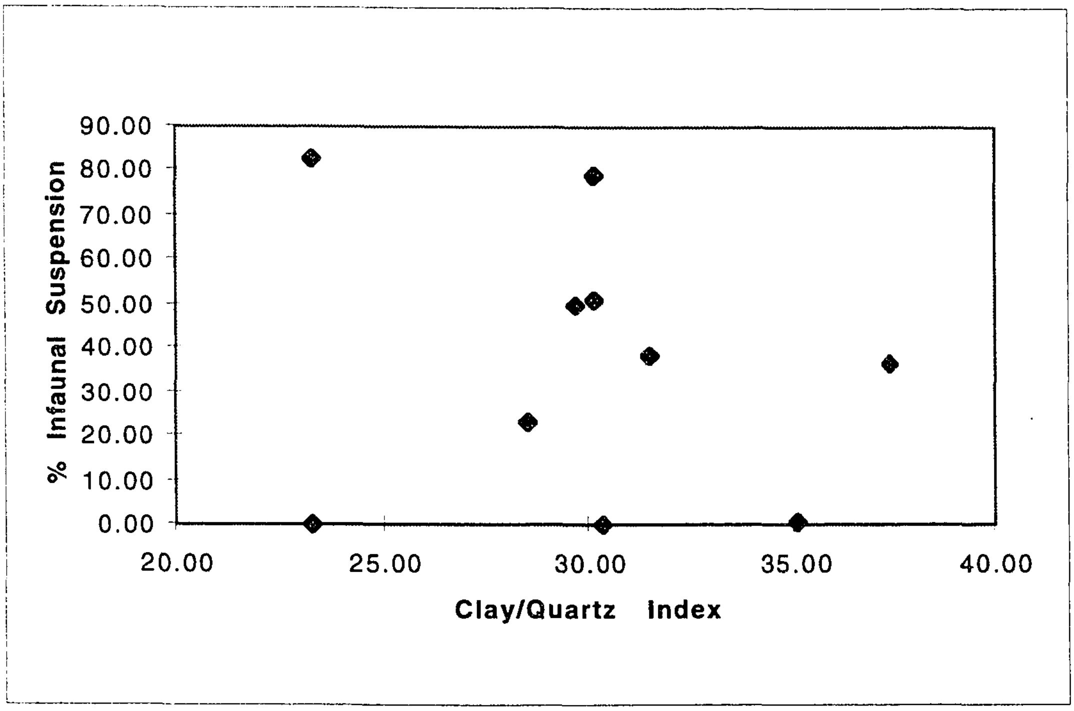

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Ichnofabric

Given the presence of a surprisingly robust and complex ichnofabric in Cincinnatian mudstones (Gaines et al., 1996), it is logical to seek a relationship between the ichnofabric and body fossil assemblage of sampled mudstones. In the Fairview Formation, Guiseffi (1982) observed that where body fossils are present, the mudstone lacked bedding planes. The obliteration of bedding surfaces was attributed to bioturbation. Barren mudstones, it was noted, contained distinct bedding planes, indicating a lack of bioturbation.

The results of this study do not further clarify this issue. While the majority of sampled mudstones were well bioturbated, a few (such as Russell Branch Middle) did not appear to contain distinct burrows which would indicate bioturbation. On the other hand, many relatively unfossiliferous mudstones have been observed that were well burrowed. No relationship was observed between the intensity of bioturbation and the density of body fossil occurrences, with the exception of the Dornbusch locality, which was sparsely fossiliferous and relatively unbioturbated. As lack of bedding structures can be indicative of either extensive bioturbation (I.I. 6) or undisturbed event bed deposition (I.I. 1), it is very difficult to correlate ichnofabric to body fossil assemblages without much more detailed study. Some examples of ichnofabrics documented in this study are shown in Figures 47 through 50.

Sequence stratigraphy

Several workers (Holland, 1993; Goldman, 1994; Dattilo, 1994; Holland and Patzkowsky, 1996; Holland et al., 1997) have begun the process of interpreting the Cincinnatian Series in a sequence stratigraphic framework. Dattilo (1994) identified three sequences from the Kope Formation through the Corryville Member. Figure 51 depicts Dattilo's interpretation of progradational (regressive) and retrogradational (transgressive) stacking patterns of parasequences in this interval. While detailed parasequence

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Figure 47 - Ichnofabric of sample from Kope Formation (Kentucky Rt. 17). Drawing at bottom is a sketch of burrows seen in the photographed sample.

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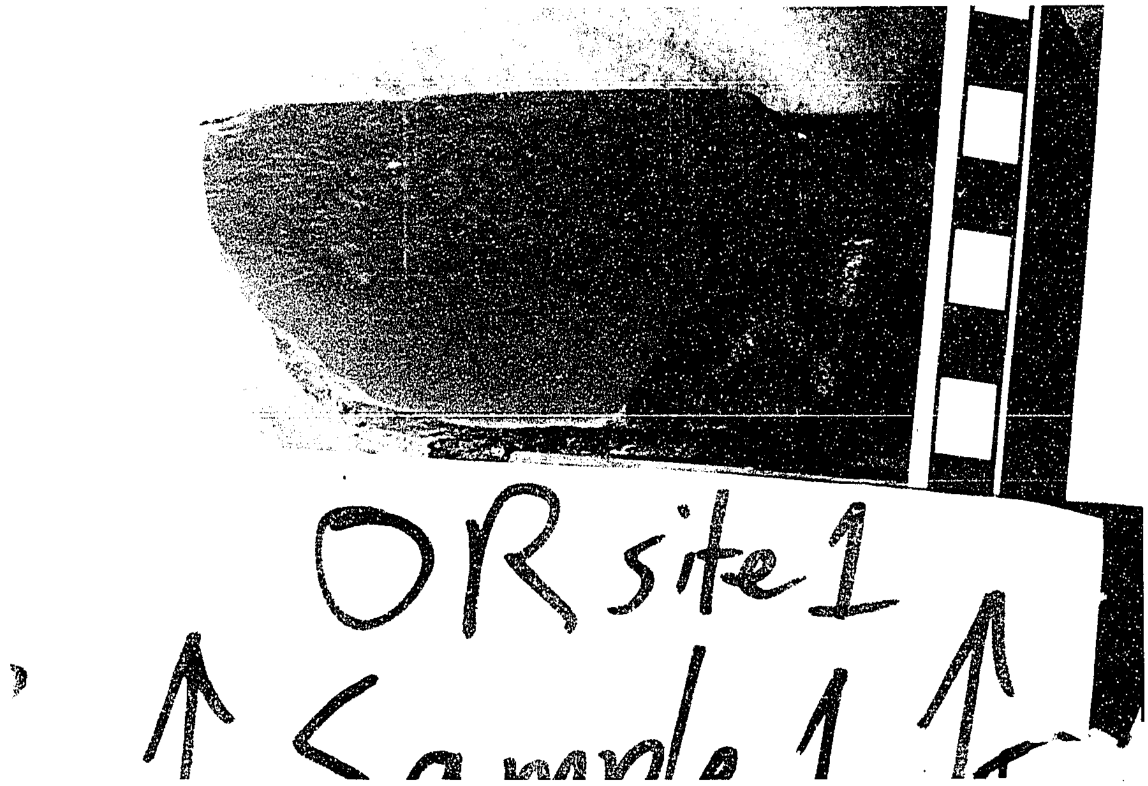

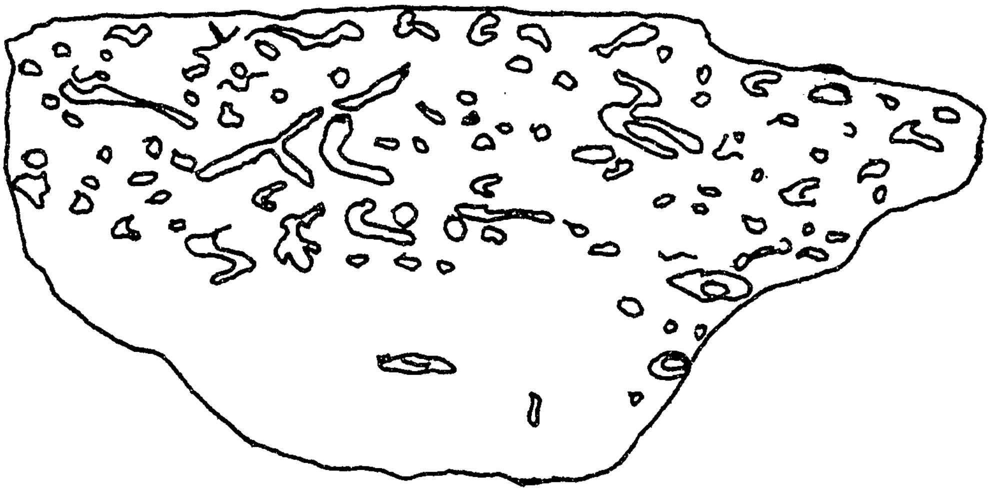

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Figure 48 - Ichnofabric of sample from Hannah Creek. Drawing at bottom is a sketch of burrows seen in the photographed sample.

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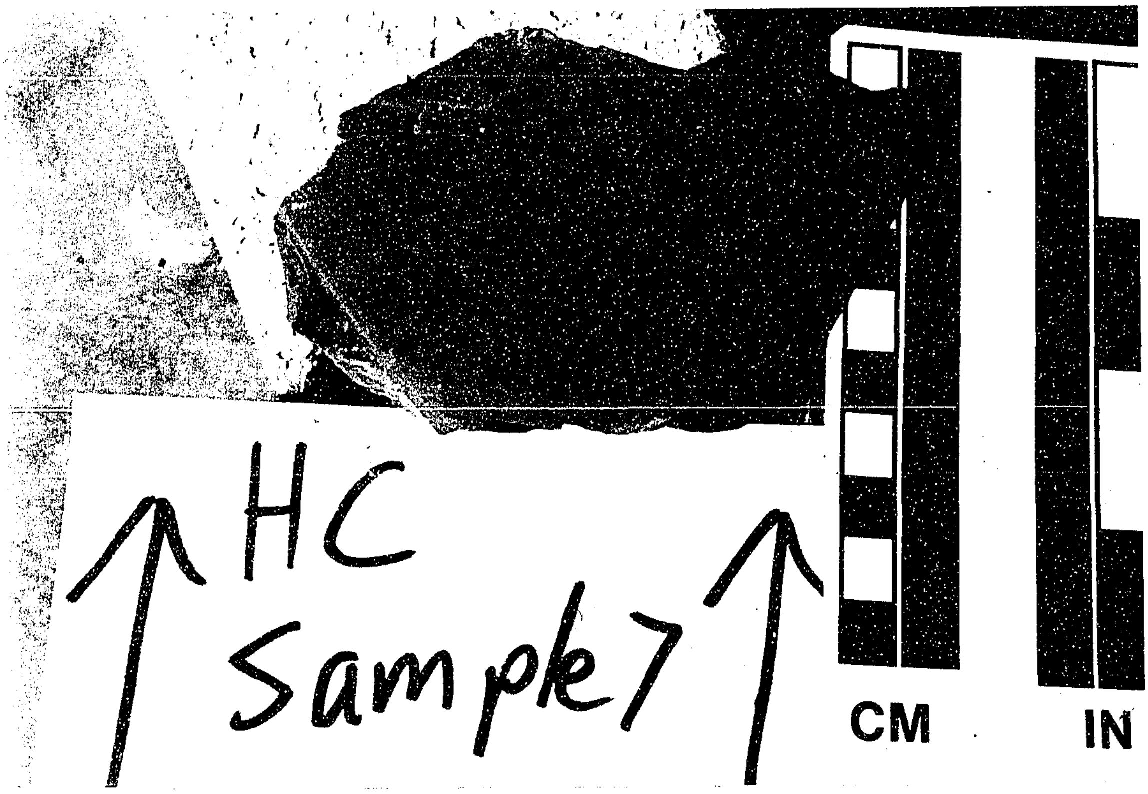

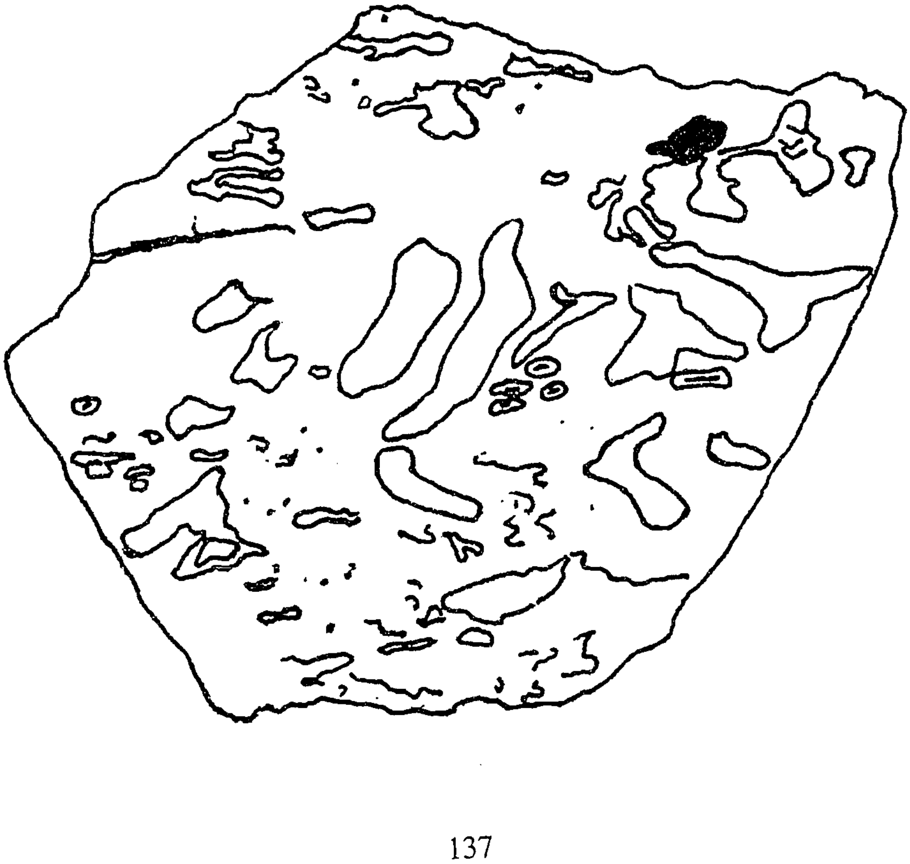

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Figure 49 - Ichnofabric of sample from Hannah Creek. Drawing at bottom is a sketch of burrows seen in the photographed sample.

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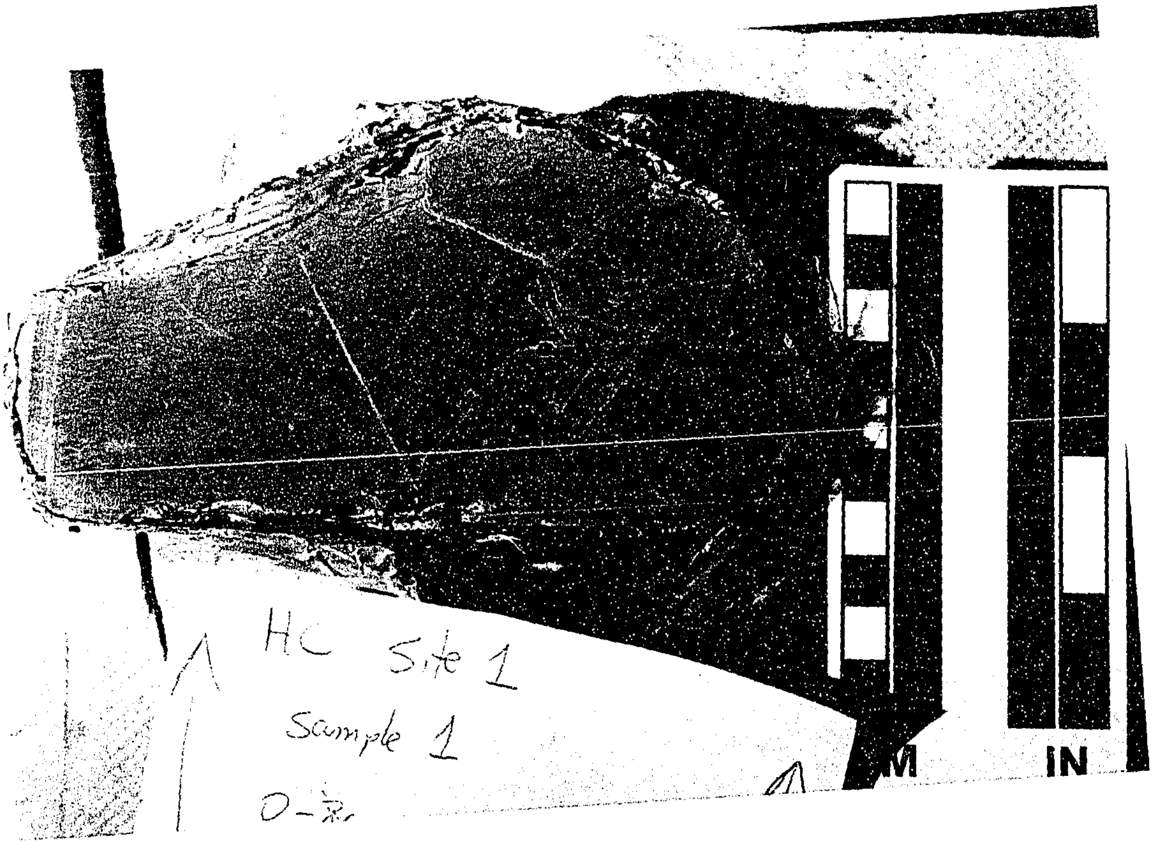

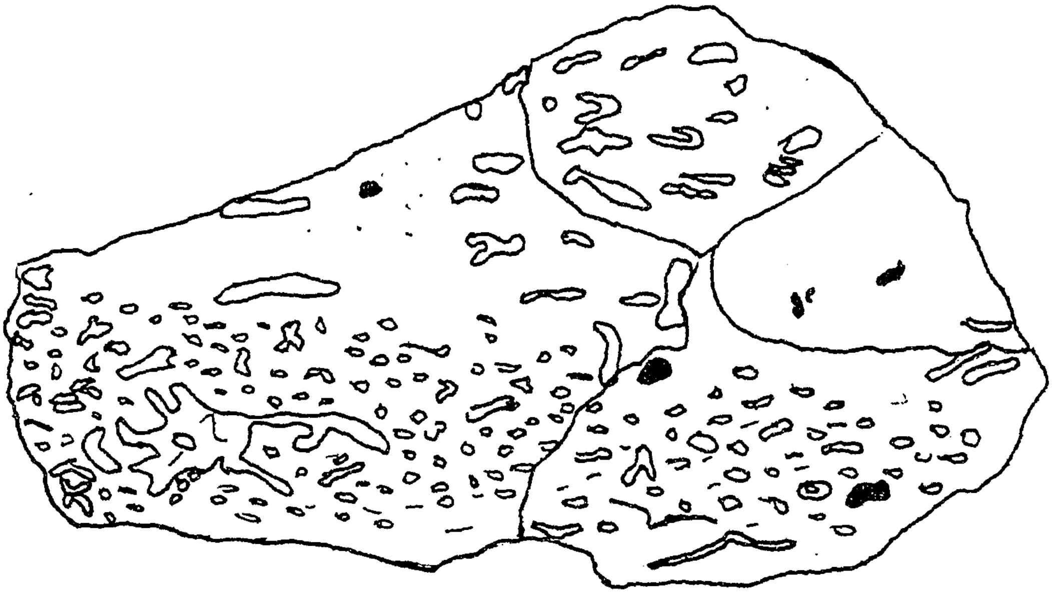

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Figure 50 - Ichnofabric of sample from Clear Fork. Drawing at bottom is a sketch of burrows seen in the photographed sample.

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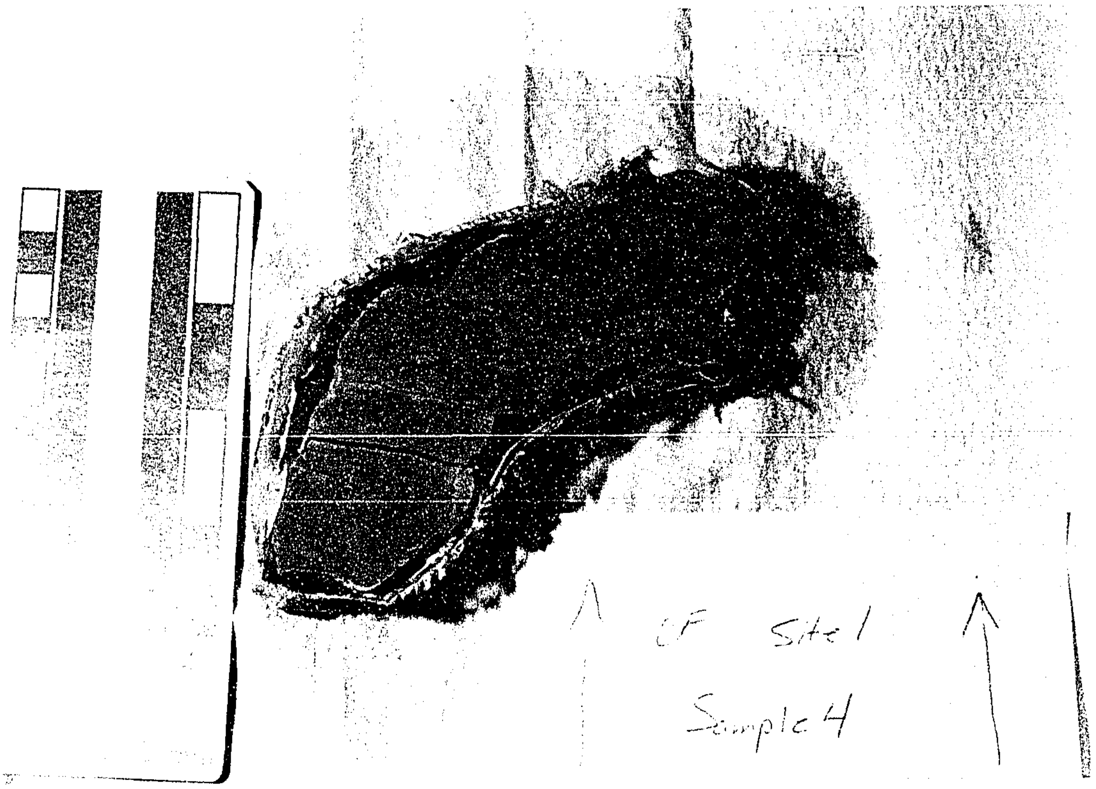

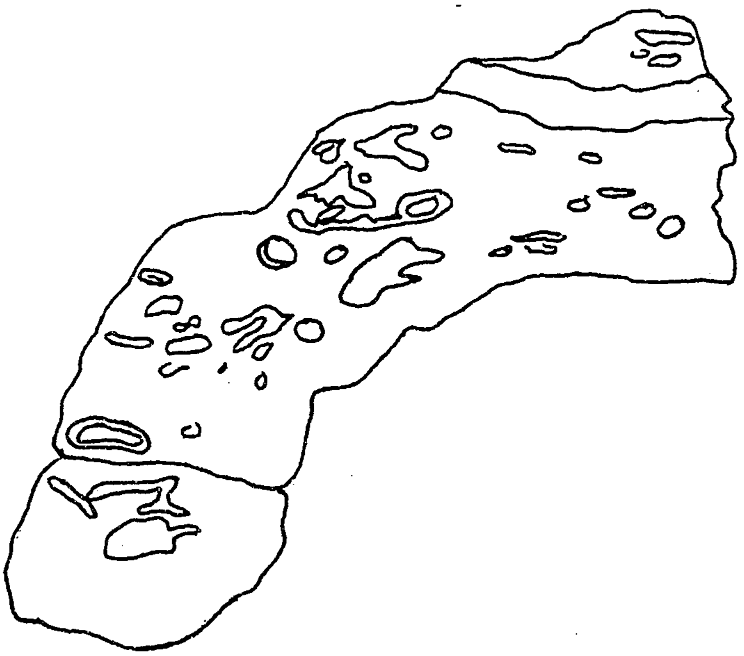

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information was unavailable for the Richmondian strata, sequences have been delineated. Holland and Patzkowsky (1996) identified six sequences in the Cincinnatian, including three in the Richmondian (see Figure 7). Figure 52 shows a sea level curve based on Holland (1993) but incorporating information from Holland and Patzkowsky (1996), Dattilo (1994), and Goldman (1994). Samples from this study have been plotted on this curve.

Of the six sequences denoted by Holland and Patzkowsky (1996), all but C6 contain at least one fossiliferous mudstone. The C4 sequence (consisting of a single formation, the Arnheim), is not represented in this study, but does contain the mudstone community described by Ferree (1993). The sequences representing the largest transgressions (C1, C2 and C5) all contain numerous mudstones and are represented by multiple samples, while the smaller transgressions (C3, C4) are represented by only a single fossiliferous mudstone horizon. Holland (1996a) classified facies as offshore, transitional, or shoreface. All of the fossiliferous mudstones documented here were found in the offshore and transitional facies.

Given the occurrence of fossiliferous mudstones within these two types of facies, a relationship of faunal assemblage to these implied sea level curves could be expected. Are there similar shifts in fauna as one samples from increasingly shallower environments in the Lower and Upper Cincinnatian? Although much more intensive and systematic sampling is required to resolve this question, multivariate analyses of the faunal samples (discussed in Chapter 7) indicate a lack of any obvious trends in faunal composition, mean body size, or life habit that could be attributed to sea level change. Given the well documented and easily observed shifts in the composition of articulate brachiopod/ bryozoan assemblages in limestones from the same sequences (Fox, 1968; Frey, 1978; Diekmeyer, 1990; Holland, 1996a), it is surprising that obvious trends were not observed in the mudstone faunas. As more mudstone horizons are sampled in detail, it is likely that the effect of sea level on these communities will become more apparent.

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Figure 51 - Delineation of sequences and parasequences in the Lower Cincinnatian. From Dattilo, 1994.

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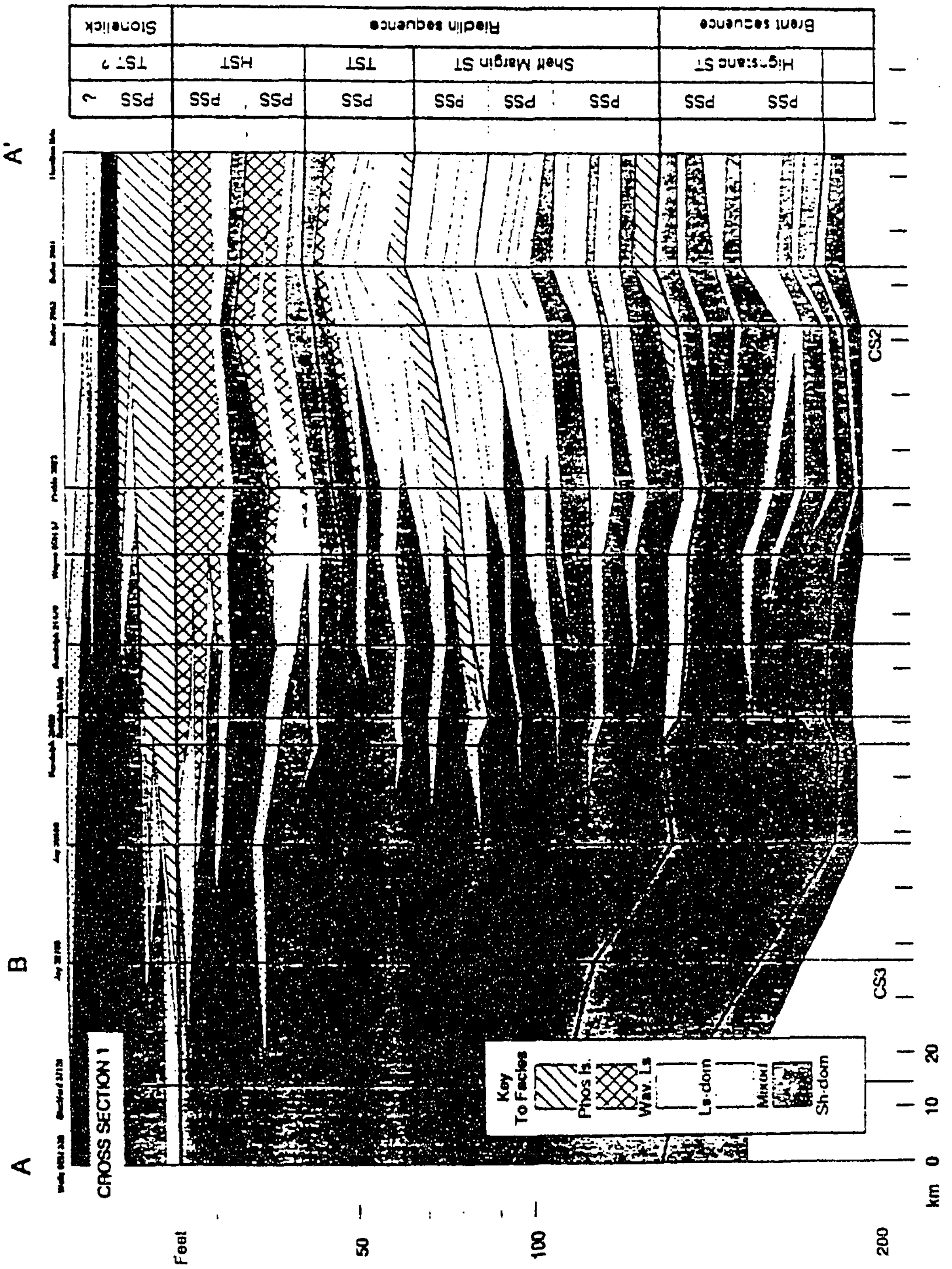

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Figure 52 - Stratigraphic distribution of samples relative to an approximate sea-level curve, based on Holland (1993), Dattilo (1994), Goldman (1994), and Holland and Patzkowsky (1996).

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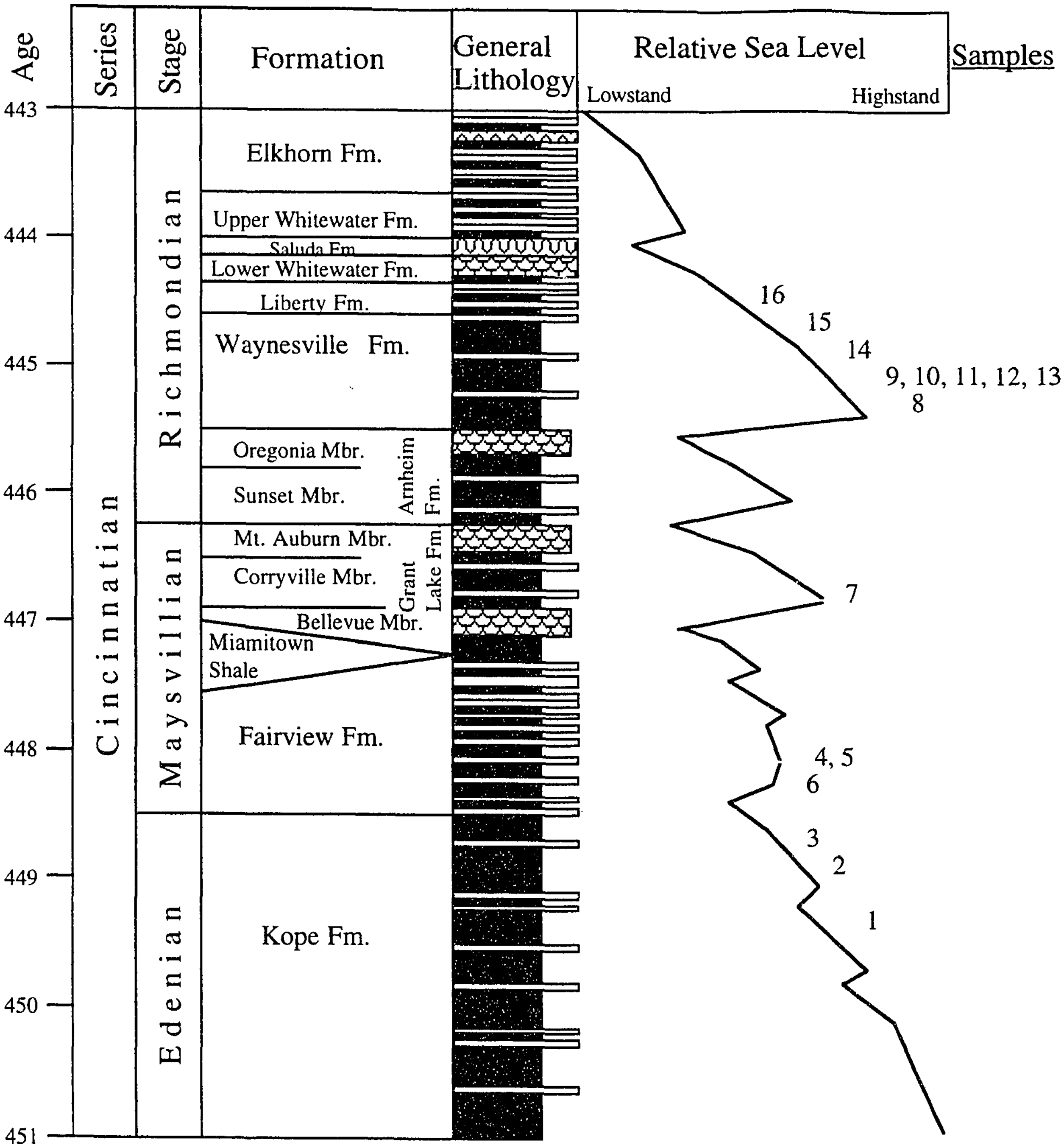

Key

1. Orphanage Road (Frey, 1987b)
2. Backbone Creek
3. Backbone Upper
4. Reading Road (Guiseffi, 1982)
5. Springdale (Guiseffi, 1982)
6. Harrison (Guiseffi, 1982)
7. Dornbusch
8. Russell Lower
9. East Fork Blue Creek
10. Russell Middle
11. Bon Well Hill (Guiseffi, 1982)
12. Harper's Run (Frey, 1987a)
13. US Rt. 42 (Frey, 1987a)
14. Russell Top
15. Hannah Creek
16. Clear Fork

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Summary

Comparison of fossiliferous to barren mudstones reveals that, other than the presence of fossils, no clear cut, consistent differences were observed. An intriguing pattern is the relatively argillaceous composition of more diverse mudstones, and, inversely, the relative lack of clay in unfossiliferous mudstones. Because the main goal of this study was to compare communities dispersed throughout the Cincinnatian Series, sampling of mudstones was sporadic as well. To fully assess the impact of sea level and other environmental factors on the composition of the mudstone communities would require detailed sampling of mudstone horizons within a single sequence, preferably at more than a single locality.

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Chapter 6: Coordinated Stasis

With the suggestion that "blocks of stable faunas and large-scale punctuational patterns will come to be seen throughout the fossil record" (Brett and Baird, 1995, p. 311), a challenge was set for all paleontologists. One of the primary objectives of this report is to test for patterns of coordinated stasis in the recurrent mudstone faunas of the Cincinnatian Series.

The coordinated stasis hypothesis predicts that there will be a minimum of changes in taxonomic and community structure within an E-E subunit (Ecological-Evolutionary subunit), and a high degree of turnover in the short periods between E-E subunits at the regional scale. Immigrant taxa will generally be limited to "incursion epiboles" (Brett and Baird, 1995) and will not become established in the fauna in successive intervals (possibly due to strong bonds between species within the community; Ivany, 1996). Little or no directional morphological changes would occur within individual lineages, although species names might change. Evolutionary branching events would be extremely rare, and rates of local extinction would be at a minimum within the interval.

One of the most convincing examples of coordinated stasis is the Middle Devonian Hamilton fauna described by Brett and Baird (1995). In this interval, 80% of species persisted from the bottom to the top of the interval, and the few observed instances of morphometric change were non-directional (Brett and Baird, 1995). In the most diverse biofacies, only five out of fifty lineages failed to persist from the bottom to the top of the sequence.

Brett et al. (1996) sharpened the definition of coordinated stasis by quantifying it. In an interval of coordinated stasis, "60% or more of species level lineages persist from oldest to youngest samples of appropriate biofacies" (Brett et al., 1996, p. 3). Between intervals, "fewer than 40% of lineages, and typically less than 20% [persist]" (Brett et al., 1996, p. 3). Any observed morphological changes within a lineage are "non-directional"

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(i.e. reversible) and "result in no net increase in diversity" (Brett et al., 1996, p. 3). Finally, a coordinated stasis interval is defined as "an interval of faunal stability persisting at least 10 times longer than the pulse of change that marks its boundary" (Brett et al., 1996, p. 4-5).

Although the type example of coordinated stasis (Brett et al., 1996) shows stasis at the species level, the authors note that, due to inconsistent taxonomic practices, there are many cases where "minor [morphological] variants within a lineage are split into distinct species" (Brett et al., 1996, p. 6). In this case, community stasis at the genus level can be relevant, as long as the criterion that morphological changes are non-directional is satisfied. In this chapter, both genus-level and species-level stasis and turnover are discussed.

In testing an interval for coordinated stasis, the authors (Brett et al. 1996) suggest bulk sampling of "large collections at numerous horizons" (Brett et al., 1996, p. 7) that represent all recurrences of the studied biofacies, especially from the top and bottom of the interval. Relevant information includes "(a) species composition, (b) species richness corrected for sample size, (c) dominance diversity (Shannon Weaver Index or others), (d) rank abundance of the more common genera and species, and, (e) trophic/substrate guild structure, (proportion of deposit feeders, suspension feeders, infauna versus epifauna, etc.)" (Brett et al., 1996, p. 7).

In sum, the hypothesis of coordinated stasis sets forth the following criteria for an interval to qualify as an E-E subunit:

1) Holdover of lineages from the previous interval less than 40%

2) Carryover of lineages into next interval less than 40%

3) Persistence within the interval greater than 60%

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4) Little evolutionary morphological change within the interval (not addressed in this study)

5) Conservation of rank abundances and guild structure within the interval

To test for coordinated stasis in an interval of the geological record, Brett et al. (1996) suggested several guidelines. Because the Silurian/Devonian E-E subunits ranged in timespan from 3 to 7 million years (Brett and Baird, 1995), a test interval must be approximately this long. Ideally, it should be possible to track facies laterally as they respond to sea level changes. Lacking this, it should at least be possible to sample a similar facies, representing a particular environment, several times as it recurs throughout the sequence. Third, to compare communities above and below to those within the sequence, samples must be taken above and below the test interval. It is necessary to collect abundance data rather than simply presence/absence, in order to test the consistency of faunal hierarchies and dominance patterns within communities. Finally, morphometric studies must be conducted to determine the extent of directional, evolutionary change that has occurred within individual lineages through the interval.

The Cincinnatian mudstone communities described previously fit most of the criteria for a coordinated stasis study. The Cincinnatian interval represents a timespan of approximately 6 million years (Holland and Patzkowsky, 1996), which is comparable to length of E-E subunits documented by Brett and Baird (1995). Within the Cincinnatian, there are six sequences (Holland and Patzkowsky, 1996), all but one of which contain the offshore/transitional mudstone biofacies that are the subject of this study.

The definition of persistence given by Brett and Baird (1995, p. 292) is "the proportion of species [or genera] that range (within the appropriate facies) from the lowest to the highest parts of the fauna." Unfortunately, in practice this definition can be interpreted in several ways. Examination of the data in this study reveals the presence of

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several taxa that range through the entire Cincinnatian but were not recorded in samples from both the Upper and Lower Cincinnatian. Should persistence include taxa which range through the interval but appear in the "appropriate facies" in question only in samples from a part of the interval? Should taxa that appear in only a single formation (such as *Plectorthis plicatella* in the Fairview) count against persistence, or do these belong to "incursion epiboles" (Brett and Baird, 1995) and therefore are not included? Finally, there is the issue of rare taxa. Any taxa represented in the database by only two or three individuals will almost certainly not appear in assemblages at the top and bottom of the interval. Whether their lack of persistence reflects actual turnover rather than a lack of sufficient sampling is unclear. Related to this is the issue of the rare taxa recorded by Frey (1987a) in the*Treptoceras duseri* shale (see discussion in Chapter 4), the result of a particularly comprehensive study of this horizon. Should these count as non-persistent taxa, or be ignored? In this case, it seemed clear that inclusion of these taxa would artifactually lower persistence rates because of unequal intensity of sampling, so they were not included.

To address these ambiguities, persistence was calculated using three methods. Brett and Baird's (1995) description of coordinated stasis implies that whole assemblages remain persistent while preserving abundance hierarchies throughout an E-E subunit. Ideally, this could be measured simply by comparing samples at the bottom and top of the interval. However, in this study the bottom and top samples (Orphanage Road and Clear Fork) were unusual and not representative of the interval. Instead, the stratigraphic interval investigated here was divided into Lower (Edenian and Maysvillian) and Upper (Richmondian) sections, with seven samples in the Lower and nine samples in the Upper. To be counted as persistent, a taxon had to be present in at least one sample from the Lower and one sample from the Upper sections. The proportion of these taxa is denoted as "Persistence" in the results below. This is considerably more lenient than the description of

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persistence in Brett and Baird (1995), which implies that persistent taxa should be present in *every* recurrence of the biofacies.

In conducting the above analysis, it was discovered that many of the taxa that did not appear in samples from both intervals of the Cincinnatian did in fact have ranges spanning the entire Cincinnatian, so that their absences from samples did not reflect actual extinctions or originations. To measure the magnitude of this effect, "Range Persistence" was calculated as well. This was simply the proportion of the mudstone taxa that range throughout the interval, or, in other words, the percentage of taxa that did not originate or become extinct within the Cincinnatian interval. Because the range data are global and therefore do not account for immigration or local extinction, Range Persistence can be regarded as an upper limit of persistence. As a conservative test of coordinated stasis, this statistic would only be relevant if it falls below 60%.

While the Cincinnatian is well suited for the study of community-level stability within the interval, calculating the other metrics of coordinated stasis, holdover and carryover, into bounding time intervals is problematic. Ideally, similar facies would be represented above and below the study interval, so that equivalent communities could be compared. The Cincinnatian Series is bounded above by a large unconformity followed by Silurian limestone (Cumings, 1922). Below, the Cincinnatian rocks are underlain by another unconformity and the poorly exposed Point Pleasant Limestone (Cumings, 1922). The Middle Ordovician Lexington Limestone, just to the south of Cincinnati, also lacks comparable mudstone facies. While other Middle Ordovician facies may be found in the Appalachian basin in the eastern United States, this was well beyond the field range of this study. Studies of Appalachian basin communities (Bretsky, 1969; Springer and Bambach, 1985; Titus, 1986) indicate that, although a similar suite of taxa was present in these faunas, the biofacies and associated environmental regimes were quite different.

Although sampling equivalent communities above and below the Cincinnatian Series was beyond the scope of this study, "Range Holdover" and "Range Carryover"

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could be calculated based on reported ranges of Cincinnatian mudstone genera. Range Holdover is the percentage of taxa appearing in the Lower Cincinnatian mudstones that originated earlier, regardless of location. Range Carryover is the percentage of Upper Cincinnatian (Richmondian) mudstone taxa that also appear in the Lower Silurian. As with the Range Persistence calculations, these metrics can be regarded as upper limits, and must be interpreted carefully. If Range Holdover and Carryover fall in the 0-40% range, then the predictions of coordinated stasis are confirmed. If these statistics are greater than 40%, then coordinated stasis cannot be disproven because the presence of taxa in another time interval does not necessarily imply that these genera appeared together in equivalent biofacies in the Cincinnati region. Coordinated stasis does not require extinction between intervals, merely that similar communities occurred within, and not across, interval boundaries.

Although the coordinated stasis model is posited to apply to rare and common taxa equally (Brett et al., 1996), it is possible with the limited sample sizes used here that rare taxa were simply not sampled in many sites (McKinney et al., 1996; Boucot, 1996), although they may have been present in small numbers. It is also possible that many rare taxa occurred in samples by chance rather than being fully integrated members of the community (McKinney et al., 1996). Finally, it is possible that small populations of rare taxa are more likely to experience turnover than common taxa (Boucot, 1990, 1996). To analyze these effects, weighted percentages were calculated for persistence, holdover, and carryover. To do this, the mean percent abundance of each taxon in all samples was calculated. Weighted persistence is the sum of mean percent abundances of all persistent taxa. Weighted holdover is the sum of mean percent abundances of holdover taxa, and weighted carryover is the sum of mean percent abundances of carryover taxa. Similarity of weighted and unweighted metrics would indicate similar patterns of persistence and turnover for rare and common taxa. Disparity between weighted and unweighted metrics, on the other hand, could demonstrate significantly higher rates of turnover for rare taxa.

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Species

Although species-level identifications of most fossils were not made by the author, previous workers (Frey, 1983 and 1987b; Guiseffi, 1982) did identify most taxa to the species level. All species-level statistics presented below are based on their species identifications, with the exception of several species identified only by the author. Range data were not available at the species level, so Range Persistence, Range Holdover and Range Carryover rates were calculated for genera only.

As noted in Chapter 3, identification of the lingulids was problematic. In the species-level analysis presented below, the lingulids are listed based on their identifications by Guiseffi (1982) and Frey (1987a, 1987b). In all other analyses, the lingulids were treated as a single taxon, resulting in an elevated persistence rate within the Cincinnatian. As with other decisions that have been made regarding calculation of the metrics of coordinated stasis within the study interval, an attempt has been made to construct a test that is conservative relative to the hypothesis that coordinated stasis was *not* present in the Cincinnatian.

Results

Results of the test for coordinated stasis in Cincinnatian mudstone faunas are shown in Tables 22-25. Persistence in the Cincinnatian (Table 24) contrasts sharply with the Upper Silurian/Devonian data of Brett and Baird (1995). Species persistence in the Cincinnatian was far below the predicted minimum of 60%, a discrepancy that cannot be attributed solely to misidentification of species. Nearly all the abundant mollusk genera were represented by different species in the Lower and Upper Cincinnatian, including *Sinuites*, *Ambonychia*, *Psiloconcha*, *Treptoceras*, *Cuneamya*, *Rhytimya*, and *Cymatonota* (Table 23).

Brett et al. (1996) noted that species level turnover within an E-E subunit does not necessarily preclude coordinated stasis if strong bimodality in turnover and stability can be

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Table 22 - Presence and absence data for mudstone fauna in sampled intervals and surrounding intervals. Middle Ordovician and Lower Silurian range data from Frey (1987b) and Robison and Teichert (1979).

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Genus	Mean Abundance	M. Ordovician	L. Cincinnatian (Eden., Maysvill.)	U. Cincinnatian (Richmondian)	L. Silurian
lingulids	20.1%	X	XX	XX	X
Sinuites	10.1%	X	XX	XX	
Zygospira	9.6%	X	XX	XX	
Ambonychia	6.6%	X	XX	XX	
Psiloconcha	6.5%		XX	XX	
Flexicalymene	6.1%	X	XX	XX	
Treptoceras	5.1%	X	XX	XX	
Cuneamya	4.1%	X	XX	XX	X
Trematis	3.6%	X	XX	XX	
Isotelus	3.5%	X	XX	XX	
Cleidophorus	3.0%	X	XX	XX	X
Corallidomus	2.5%			XX	
Rhytimya	1.7%		XX	XX	X
Modiolopsis	1.7%	X	XX	XX	X
Ancienta	1.6%			XX	
Pholadomorpha	1.5%			XX	
Caritodens	1.4%	X	XX	XX	?
Cymatonota	1.3%		XX	XX	
Hyolithes	1.1%	X	XX	XX	X
Deceptrix	1.1%	X	XX	XX	X
Rafinesquina	0.8%	X	XX	XX	
Ruedemania	0.7%	X	XX	-	X
Technophorus	0.6%	X	XX		
Orthodesma	0.5%	X	-	XX	
Conularia	0.5%	X	-	XX	X
Spatiopora	0.5%			XX	X
Lyrodesma	0.4%	X	XX	-	X
Whiteavesia	0.4%		XX	XX	
Platycorphe	0.4%	X	-	XX	
Lophospira	0.3%	X	XX	-	X
Stromotocerium	0.3%	X	-	XX	X
Liospira	0.2%	X	XX	XX	X
Cornulites	0.2%	X	XX	XX	X
Fusispira	0.2%	X	XX	-	X
Cincinnaticrinus	0.2%	X	-	XX	no data*
Trocholites	0.2%	X	XX		
Cyrtodontula	0.2%	X	XX		
Homotelus	0.2%		XX		
Platystrophia	0.2%	X	XX	XX	X
Eridonychia	0.2%	X	-	XX	
Hebertella	0.2%	X	-	XX	
Tetradium	0.1%	X	-	XX	
Plectorthis	0.1%		XX		
Cycloconcha	0.1%		-	XX	
Cyrtolites	0.1%	X	-	XX	X
Sphenospira	0.1%	X	-	XX	X
Loxoploxus	0.0%	X	XX	-	X
Amphilichas	0.0%	X	-	XX	
Obalina	0.0%	no data*		XX	no data*
Iocrinus	0.0%	X	-	XX	

*Not listed in Robison and Teichert, 1979

Key

XX Documented in quantitative samples

X Ranges into that interval

- Missing from quantitative samples within range

? Possible occurrence in that interval

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Table 23 - Species recorded in Lower and Upper Cincinnatian samples. Starred* species identified by the author, all other data from Guiseffi (1982) and Frey (1987a, 1987b).

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Genus	Species, Eden./Maysvill.	Species, Richmondian
Pseudolingula	*covingtonensis*	*covingtonensis*
Lingulops		*vanhornei*
Sinuites	*globularis*	
Sinuites	*cancellatus*	
Sinuites		*subcompressus*
Zygospira	*modesta*	*modesta*
Ambonychia	*radiata*	
Ambonychia		*casteri*
Ambonychia		*suberecta*
Psiloconcha	*inornata*	
Psiloconcha	*sinuata*	
Psiloconcha		*grandis*
Psiloconcha		*suberecta*
Flexicalymene	*meeki*	*meeki*
Treptoceras	*transversum*	
Treptoceras		*duseri*
Cuneamya	*neglecta*	
Cuneamya		*miamiensis*
Trematis	*millipunctata*	*millipunctata*
Trematis	*crassipunctata* *	
Isotelus	*maximus*	*maximus*
Cleidophorus	sp.*	*planulatus*
Corallidomus		*versaillesensis*
Rhytimya	*byrnesi*	*byrnesi*
Rhytimya	*mickleboroughi*	
Modiolopsis	*modiolaris*	*modiolaris*
Modiolopsis	*simulatrix*	
Ancienta		*ohioensis*
Pholadomorpha		*pholadiformis*
Caritodens	*demissa*	*demissa*
Cymatonota	*recta*	
Cymatonota		*semistriata*
Hyolithes	sp.	sp.

Genus	Species, Eden./Maysvill.	Species, Richmondian
Deceptrix	sp.	sp.
Rafinesquina	*alternata*	*alternata* *
Ruedemania	*lirata*	
Technophorus	*cincinnatiense*	
Orthodesma		sp.
Conularia	sp.	*formosa*
Spatiopora		*maculosa*
Lyrodesma	*postriatum*	
Whiteavesia	sp.*	sp.
Platycorphe		*christyi*
Lophospira	sp.	
Stromatocerium		*granulosum*
Liospira	*micula*	sp.
Cornulites	sp.	*flexuosus*
Fusispira	*sulcata*	
Cincinnaticrinus		sp.*
Trocholites	sp.	
Cyrtodontula	sp.	
Homotelus	sp.	
Platystrophia	*hopensis*	
Platystrophia		*clarksvillensis* *
Eridonychia		*crenata*
Hebertella		*occidentalis* *
Tetradium		*ontario*
Plectorthis	*plicatella*	
Cycloconcha		sp.
Cyrtolites		*ornatus* *
Sphenospira		sp.*
Loxoploxus	*bowdeni*	
Loxoploxus	*hammeli*	
Amphilichas		sp.*
Obalina		sp.
Iocrinus		*subcrassus*

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Table 24 - Persistence, Holdover, and Carryover in the Cincinnatian Sequence mudstones. Values consistent with coordinated stasis shown in **bold**.

Table 25 - Genus Persistence, Holdover, and Carryover statistics, based entirely on range data.

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	Unweighted	**Weighted**
Species persistence in the Cincinnatian	24.2%	NA
Genus persistence in the Cincinnatian	48.0%	**89.3%**

	Unweighted	**Weighted**
Range Persistence in Cincinnatian	**82.0%**	**92.7%**
Range Holdover from M. Ordovician	84.4%	89.2%
Range Carryover into Silurian	48.8%	**38.5%**
Range Persistence from M. Ordovician to Upper Cincinnatian*	**71.4%**	**82.9%**

*Extending a proposed Cincinnatian E-E subunit into the Middle Ordovician.

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demonstrated at the genus level. As long as the criteria of carryover, holdover, and persistence are met, the taxonomic level is not critical. Furthermore, the splitting of genera into morphospecies can be highly volatile, and since different criteria are necessarily used for different groups of organisms, these identifications may not reflect the true "similarity" of taxa. Genus-level identifications are less volatile and can be profitably applied to coordinated stasis problems. It must be emphasized, however, that use of genus-level data provides an extremely conservative test of coordinated stasis. While low rates of genus persistence would certainly contradict coordinated stasis, high genus persistence would not be a proof of coordinated stasis without extensive morphological data and evidence that genus level turnover at interval boundaries was equally high.

The rate of unweighted genus persistence in Cincinnatian mudstone communities was also well below 60% (Table 24). One could argue that the presence of unusual, outlier assemblages such as Orphanage Road (which contains six genera found nowhere else) depresses this statistic. If this unit were removed from the dataset, the total percentage of persistent genera would rise to 59%, very close to the cutoff point. However, the presence in the Orphanage Road assemblage of characteristic mudstone taxa (*Sinuites*, *Zygospira*, *Flexicalymene*, *Ambonychia*, *Cleidophorus*, and *Modiolopsis*), demonstrates that this unit should not be excluded from the dataset.

While unweighted persistence does not support coordinated stasis, weighted persistence (Table 24) and range persistence (Table 25) tell a different story. The large discrepancy between weighted and unweighted persistence is a reflection of the high degree of persistence of the most dominant taxa. Of the 20 most abundant genera in the dataset, 17 were persistent. Therefore, the most important faunal elements of these communities *did* persist.

There are several possible explanations for the large discrepancy between the unweighted and weighted genus persistence data. First, that rare genera simply weren't found in many places where they did in fact exist, and sampling was not comprehensive

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enough to thoroughly census rare genera. Anecdotal evidence from the thoroughly sampled *Treptoceras duseri* shale (Frey, 1983, 1987a) suggests that large collections are more likely to recover unique rare taxa than discover recurrences of rare taxa identified in other samples. Inclusion of the uncommon genera from Frey's (1987a) *Treptoceras duseri* samples in the database would significantly *decrease* (from 48% to 39%) rather than increase the overall proportion of persistent genera.

A second explanation for the apparent difference in persistence between abundant and rare taxa is that rare taxa fundamentally experience higher turnover rates (Boucot, 1990; McKinney, 1996; Boucot, 1996). While this could account for a few of the non-persistent taxa (e.g. *Trocholites*, *Cyrtodontula*), many others did in fact range through the Cincinnatian (e.g. *Ruedemannia*, *Platycorphe*, *Amphilichas*, *Loxoplocus*). For many of these genera, it appears that their occasional presence in the mudstone faunas resulted from blurring of biofacies boundaries. Many of the "rare" gastropods present in the Orphanage Road sample, for instance, are common in Cincinnatian calcisiltites. *Tetradium*, found at Harper's Run and US Rt. 42, is abundant in shallower limestone facies in higher strata. The crinoids *Iocrinus* and *Cincinnaticrinus* are also more common in other biofacies. The presence of these taxa was probably due to specialized environmental conditions or chance, and bears little ecological or evolutionary significance.

The relative lack of extinction and origination at the genus level within the Cincinnatian is further illustrated by the range persistence results (Table 25). Of the fifty genera documented here, at most five (*Technophorus*, *Homotelus*, *Plectorthis*, *Trocholites*(?), and *Cyrtodontula*(?)) became extinct within the interval, a rate of 10%. In addition, only four genera (*Corallidomus*, *Pholadomorpha*, *Ancienta,* and *Obalinas*(?)) originating in or immigrating into the Cincinnatian were documented in this database, although several immigrant cephalopods were recorded in the *Treptoceras duseri* shale (Frey, 1987a).

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In summary, analysis of persistence at the species level shows no evidence that the type Cincinnatian can be interpreted as an E-E subunit for mudstone communities. At the genus level, persistence was also well below the estimate of Brett et al. (1996), although the weighted persistence demonstrates that most of the dominant taxa *did* persist throughout the interval. Based on weighted persistence, it could be argued that some form of stasis did exist in these communities.

Coordinated stasis, however, also requires demonstration of turnover between E-E subunits. As explained earlier, only range data was available for calculation of turnover statistics, which leads to overestimates of carryover and holdover. Although coordinated stasis could not be disproven based on these figures, the results are striking nevertheless. Of the 45 genera whose ranges include the Lower Cincinnatian, 38 originated in the Middle Ordovician, a holdover rate of 84%. In fact, the range holdover from the Middle Ordovician is greater than the Range Persistence within the Cincinnatian! Even accounting for a certain degree of overestimation, it is extremely unlikely that the base of the Cincinnatian could be considered an E-E subunit boundary. Range Carryover into the Silurian was also somewhat higher than the predicted value of 40%. If regional data were available, however, it is probable that actual carryover would fall well below 40%. The Ordovician-Silurian boundary, which marks one of the greatest mass-extinction events in history, should easily qualify as an E-E subunit boundary!

The lack of a turnover event at the base of the Cincinnatian has consequences for the persistence statistics discussed above. Extension of the proposed interval of stability into the Middle Ordovician would reduce range persistence to approximately 70%, and this does not take into account any mudstone taxa present in the Middle Ordovician that went extinct prior to the Cincinnatian. If appropriate facies could be found, it would be extremely interesting to sample mudstone communities from the below the base of the Cincinnatian strata.

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Table 26 - Most common species of brachiopods and corals of the lowest and highest exposures of a Hamilton biofacies, illustrating the similarity in rank abundances between the lowest and highest beds. Species which have the same rank abundance in lower and upper collections are underlined (Derived from Brett and Baird, 1995, Table 9.7).

Table 27a - Five most common genera from Backbone Creek and Russell Middle samples, illustrating the lack of similarity in rank abundances. Genera which have the same rank abundance in lower and upper samples are underlined.

Table 27b - Five most common genera from Harrison and Harper's Run samples, illustrating the lack of similarity in rank abundances. Genera which have the same rank abundance in lower and upper samples are underlined.

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Lowest Brachiopods	**Highest Brachiopods**
1. *Mediospirifer audacalus**	1. *Mediospirifer audacalus**
2. *Athyris cora*	2. (tie) *Camarotoechia* spp. *Spinatrypa spinosa*
3. *Protodouvillina inequistriata**	3. *Protodouvilliana inequistriata**
4. *Pseudoatrypa devoniana**	4. *Pseudotrypa devoniana**
Lowest Corals	**Highest Corals**
1. *Aulocysis* sp.*	1. *Aulocyctis* sp.*
2. *Amplexiphyllum* sp.*	2. *Amplexiphyllum hamiltonae**
3. *Heterophrentis simplex**	3. *Cystiphylloides americanum*
	4. *Heterophrentis simplex**

*Ranked in other locality

Backbone Creek	**Russell Middle**
1. *Sinuites*	1. Lingulids
2. *Zygospira*	2. *Ambonychia*
3. *Deceptrix*	3. *Psiloconcha**
4. *Psiloconcha**	4. *Corallidomus*
5. *Isotelus*	5. *Flexicalymene*

*Among top five in other locality

Harrison	**Harper's Run**
1. *Sinuites**	1. *Treptoceras*
2. *Psiloconcha*	2. *Flexicalymene*
3. *Isotelus*	3. *Sinuites**
4. *Ambonychia*	4. *Cuneamya**
5. *Cuneamya**	5. *Pholadomorpha*

*Among top five in other locality

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While it could be argued based on range data that individual lineages do remain stable, it is clear from the low persistence of genera in actual samples (Table 24) that the degree of stability documented in Silurian/Devonian E-E subunits (Brett and Baird, 1995) was not present in the Cincinnatian, even at the genus level. In spite of the general persistence of most common genera, the Cincinnatian communities show a wide variety of membership and rank abundance. Comparison of rank abundances of taxa in Hamilton (Brett and Baird, 1995) and Cincinnatian mudstone communities (Tables 26-27) demonstrate that while species rank abundances were remarkably similar in the two Hamilton communities, no such pattern can be found for Cincinnatian genera.

Summary

The tests of coordinated stasis in Cincinnatian mudstone communities yield the following results:

1) Species-level persistence in Cincinnatian mudstones was significantly lower than in the Silurian/Devonian E-E subunits documented by Brett and Baird (1995).

2) Based on actual occurrence in samples, genera did not persist in Cincinnatian mudstones at rates comparable to the Silurian/Devonian E-E subunits documented by Brett and Baird (1995).

3) Weighted persistence shows that common genera did persist at rates within the range predicted by coordinated stasis, indicating that these genera appeared more consistently than rare genera and did not experience a high rate of turnover (at this taxonomic level) during the study interval.

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4) Within a background of low genus turnover, actual community assemblages varied widely, with differences apparent both in rank abundances of common taxa and in composition of the less abundant fraction. This is in strong contrast to patterns of stability observed in Silurian/Devonian E-E subunits (Brett and Baird, 1995).

5) While an E-E subunit boundary could potentially be placed at the base of the Silurian, the lack of a turnover event at the base of the Cincinnatian, as shown by genus range data, indicates that the lower boundary of a proposed E-E subunit must be placed deeper within the Middle Ordovician.

Related studies

The above analysis of Cincinnatian communities describes a somewhat muddled picture. Although unweighted metrics generally do not fall in the ranges predicted by coordinated stasis, the high rate of persistence among the more common genera, as shown by weighted persistence, does indicate that the basic structure of the communities remained similar throughout the interval.

It could be argued that, even if the Cincinnatian mudstone faunas *did not* show a pattern of coordinated stasis, this may not be representative of the Cincinnatian fauna as a whole. Coordinated stasis does not require an equal degree of stability in every community within an E-E subunit. In the Upper Clinton/Lockport Fauna (Brett and Baird, 1995) for example, only 42% of the corals persisted from the bottom to the top of the interval. However, when combined with data from other biofacies, the overall persistence rate for the E-E subunit rises to 66%. By the same token, while community stability might be relatively low in Cincinnatian mudstones, this could be overshadowed by an overall pattern of stability of brachiopod/bryozoan communities found in limestones. Two studies of Middle and Upper Ordovician marine benthic communities in Eastern North America (Titus, 1986; Patzkowsky and Holland, 1996) allow for this issue to be addressed.

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Although compiled before the advent of the coordinated stasis concept, an exhaustive database from the Trenton Group of New York (Titus, 1986) is ideal for a test of this theory. Titus (1986) documented faunal abundances in three communities (designated *Liospira*, *Encrinurus*, and *Trematis*) that could all be identified in the Lower, Middle, and Upper Trenton Group, a period spanning approximately 6 million years of the Middle and Upper Ordovician (Sweet and Bergstrom, 1971, Patzkowsky and Holland, 1997). As with the Cincinnatian mudstone data, unweighted persistence was well below the predicted minimum of 60% for both species and genera in all three communities (Table 28). Also like the Cincinnatian communities, weighted persistence rates were much higher than unweighted persistence, especially for genera. Weighted persistence of genera was above 80% for all three communities, and species weighted persistence increased above the critical 60% for two out of three communities (Table 28). Given the completeness of this database (over 750 samples were collected), it is unlikely that this discrepancy is an artifact of incomplete collecting. Rather, an evolutionary (i.e. increased volatility of small populations) or stochastic (i.e. unusual environmental conditions, biofacies mixing via post-mortem transport, or chance) explanation is more probable.

Titus (1986) noted that while there was turnover at the species-level, trophic structure of these communities remained quite stable:

> While the similarities are striking, changes did occur and it is those changes that are of the greatest interest. The community was not fixed during Trentonian time; it evolved. This community evolution, however, was within limits that allowed the maintenance of certain community integrity (p.813).

As in the Cincinnatian mudstones, the Trenton data could be interpreted as consistent with coordinated stasis only by considering weighted persistence. Unfortunately, holdover and carryover data were not available. A study that does incorporate this information in an explicit test of coordinated stasis was conducted by Patzkowsky and Holland (1997), who documented articulate brachiopods in the Middle

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Table 28 - Test of coordinated stasis for Trenton Group communities, based on data from Titus (1986). Values consistent with coordinated stasis shown in **bold**.

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	Unweighted Persistence*	**Weighted Persistence***
Liospira Community Genera	37%	**88%**
Liospira Community Species	31%	37%-51%†
Encrinurus Community Genera	39%	**85%**
Encrinurus Community Species	31%	**60%-82%††**
Trematis Community Genera	39%	**82%**
Trematis Community Species	27%	**60%**

*Persistent taxa were present in the Lower and Upper occurrences of each biofacies. Weighted persistence was calculated by summing the average abundances of persistent taxa.

†Titus (1986) questionably identified *Sowerbyella sericea* in the upper *Liospira* community, so it is unclear whether this abundant brachiopod is persistent, thus accounting for the discrepancy.

††Titus (1986) questionably identified the abundant brachiopods *Sowerbyella serices* in the upper *Encrinurus* community and *Sowerbyella subovalis* in the lower *Encrinurus* community, so it is unclear whether these abundant species are persistent.

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and Upper Ordovician of the Cincinnati Arch, Nashville Dome and Valley and Ridge of Tennessee, West Virginia, and Virginia.

Based on peaks of extinction and origination, three potential E-E subunits were defined and dubbed EE 4.1, 4.2, and 4.3 (Figure 53). As was discovered in this study, the base of the Cincinnatian did not correspond to a major turnover event that could be interpreted as an E-E subunit boundary. Instead, the base of the proposed interval of stasis extending into the Cincinnatian was placed at the boundary between the Rocklandian and Kirkfieldian stages of the Middle Ordovician. The boundary between EE 4.2 and EE 4.3 was placed at the base of the Richmondian, corresponding to the boundary between the Lower and Upper Cincinnatian used in this study, and bisecting the proposed interval of stasis tested above. The fact that the Cincinnatian Series could be viewed as a period of stasis by one researcher and as an E-E subunit boundary by another is an indication that the model of coordinated stasis does not apply well to this period.

Patzkowsky and Holland (1997) calculated carryover, turnover, and persistence rates at both the species and genus levels (Table 29). While species-level holdover and carryover rates were in agreement with coordinated stasis, species persistence within the proposed intervals of stasis was extremely low, far below the predicted 60%. At the level of genus, persistence rates were also low, while holdover and carryover rates were generally above 40%. In fact, at both the species and genus level, persistence levels within proposed E-E subunits were consistently lower than holdover and carryover rates between them. The strongly bimodal pattern of stasis and turnover predicted by coordinated stasis (Brett et al., 1996) clearly does not apply to these brachiopod communities.

Given this interpretation of E-E subunit boundaries, does the coordinated stasis model better fit the mudstone communities if the Cincinnatian Series is divided into two E-E subunits? As Table 30 shows, this interpretation is no more supportive of coordinated stasis. At both species and genus levels, rates of holdover and carryover exceed the allowable 40% across the Maysvillian/Richmondian boundary. Most tellingly, in this

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Figure 53 - Proposed ecological-evolutionary subunits for brachiopods in the Middle and Upper Ordovician of the eastern United States. From Patzkowsky and Holland, 1997.

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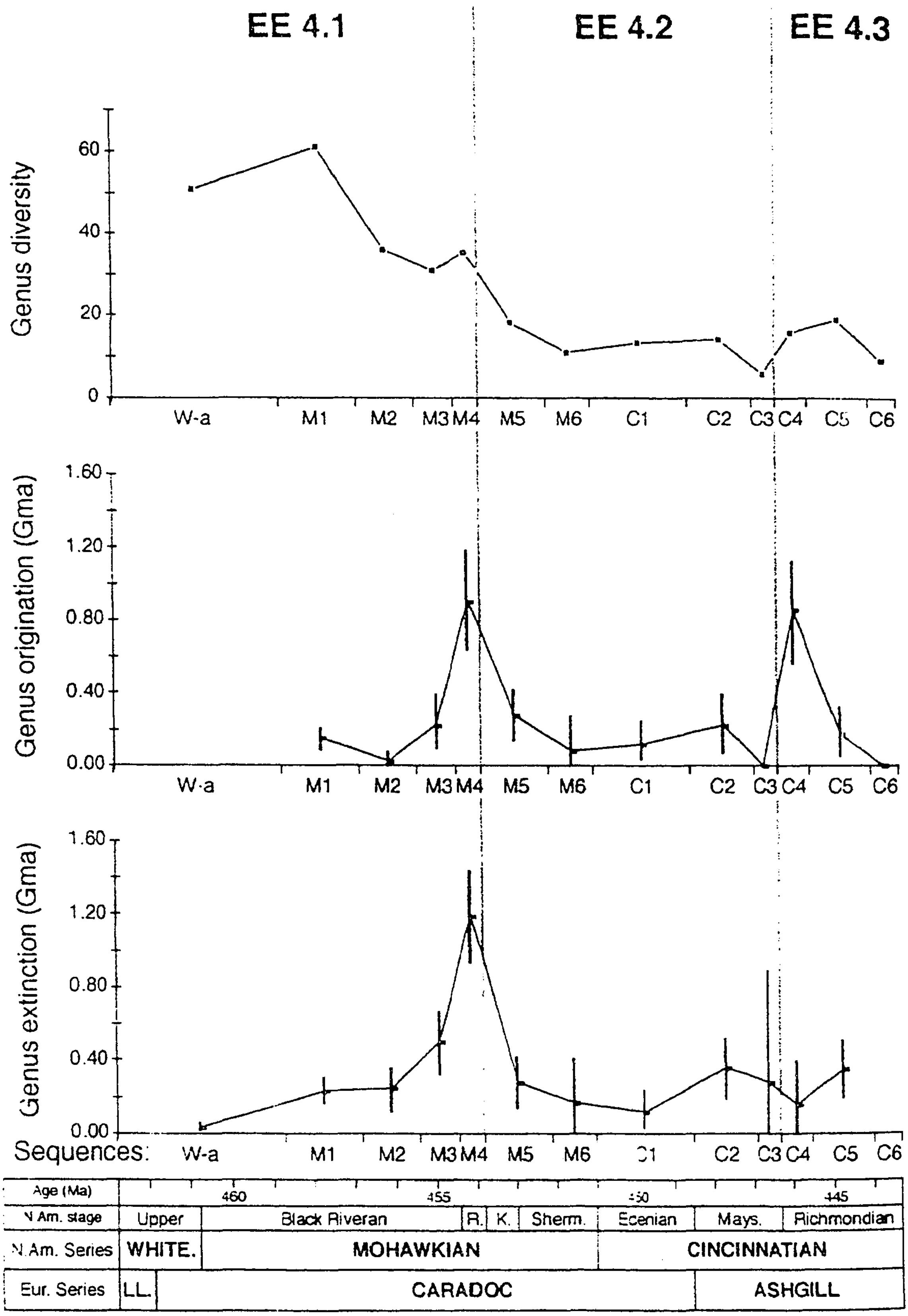

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Table 29 - Test of coordinated stasis for Upper Ordovician articulate brachiopods. Data from Patzkowsky and Holland (1997). Values consistent with coordinated stasis shown in **bold**.

Table 30 - Test of coordinated stasis in Cincinnatian mudstones, treating the Maysvillian/Richmondian as an EESU boundary. Values consistent with coordinated stasis shown in **bold**.

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	E-E 4.1	E-E 4.2	E-E 4.3
% Species Holdover		**4.8%**	**12.8%**
% Species Carryover	**1.3%**	**7.2%**	
% Species Persistence	0.3%	1.2%	10.6%
% Genus Holdover		57.7%	57.1%
% Genus Carryover	**19.5%**	46.2%	
% Genus Persistence	27.3%	19.2%	33.3%

	Unweighted	Weighted
Species Carryover	41.0%	NA
Species Holdover	**37.2%**	NA
Genus Carryover*	72.2%	96.8%
Genus Holdover*	65.0%	92.0%
Genus Range Persistence† (M. Ord.-L. Cin.)§	**84.4%**	**89.7%**

*Genus Range Carryover and Range Holdover are significantly higher.

†Percentage of Lower Cincinnatian genera that range into the Middle Ordovician. An overestimate because ignores any fauna present in earlier communities but absent in the Cincinnatian.

§There is also no data for persistence within the Upper Cincinnatian interval because this dataset is derived from only one sequence (C5 of Holland and Patzkowsky, 1996). No quantitative data was recovered from the C4 sequence, so it is therefore unreasonable to determine the extent of persistence in the Richmondian (EE 4.3 of Patzkowsky and Holland, 1997).

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model there is no evidence of bimodality between persistence and turnover. As with the brachiopod data (Patzkowsky and Holland, 1996), persistence rates (84.4%, 89.7% weighted) are similar to carryover (69.4%, 73.2%) and holdover (62.5%, 71.3%). Coordinated stasis would require a much greater difference in these values (Brett et al., 1996).

Brett and Baird (1995) stated that boundaries between E-E subunits are marked by “major collapse and restructuring events” (p. 287), and that “major changes occur in a suite of common species within particular successive faunas” (p. 291). Although abundance data was not available in Patzkowsky and Holland (1997), these authors did compile a list of the most abundant genera in each interval. Table 31 lists the most common brachiopod genera of EE 4.2 (corresponding to the Lower Cincinnatian) and EE 4.3 (Upper Cincinnatian). Note that *all* of the abundant brachiopod genera in EE 4.2 remained dominant in EE 4.3, and 77% (10 of 13) of EE 4.3 genera were also abundant in EE 4.2. Table 32 lists the ten most common mudstone taxa in the Lower and Upper Cincinnatian intervals. Again, around 70% of the dominant forms remained abundant across the boundary. In the mudstone and brachiopod communities, therefore, there is no evidence of a “major collapse and restructuring event” at the base of the Richmondian.

If there is no E-E subunit boundary either in the middle or at the base of the Cincinnatian Series, the only other possibility is to interpret the entire 11 ma period from the base of EE 4.2 to the top of EE 4.3 at the Silurian boundary as a single E-E subunit. Given the variability in mudstone faunas already demonstrated, it is unlikely that recurrence will improve with the addition of older samples. Final resolution of this question, of course, must await sampling of appropriate facies in the Middle Ordovician.

In general, the patterns shown by the Cincinnatian mudstones are amplified rather than overshadowed by studies of other Upper Ordovician faunas. Persistence rates in each case were much lower for species *and* genera than the persistence rates for species in Brett and Baird’s (1995) E-E subunits. Although stability was observed in common genera, no

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Table 31 - Most common brachiopod genera from EE 4.2 and EE 4.3, listed alphabetically. Taxa shared in both tables shown in **bold**. From Patzkowsky and Holland, 1997, Table 2.

Table 32 - Ten most common genera of Lower and Upper Cincinnatian mudstones, organized in order of relative abundance. Taxa in **bold** are found on both lists. Taxa underlined are among the 15 most common genera of the other interval.

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EE 4.2	EE 4.3
Hebertella	***Hebertella***
Leptaena*	*Hiscobeccus*
Onniella	***Leptaena***
Orthorynchula	***Onniella***
Platystrophia	***Orthorynchula***
Rafinesquina	*Plaesiomys*
Rynchotrema	***Platystrophia***
Sowerbyella	***Rafinesquina***
Strophomena	*Retrosirostra*
Zygospira	***Rhynchotrema***
	Sowerbyella
	Strophomena
	Zygospira

**Leptaena* was added to the E-E 4.2 list based on observations by the author of abundant *Leptaena* in Kope and Fairview beds.

Lower Cincinnatian	Upper Cincinnatian
Sinuites	**Lingulids**
Lingulids	***Zygospira***
Zygospira	***Flexicalymene***
Ambonychia	***Psiloconcha***
Trematis	*Treptoceras*
Psiloconcha	***Ambonychia***
Isotelus	*Corallidomus*
Flexicalymene	***Cuneamya***
Cuneamya	***Sinuites***
Modiolopsis	*Cleidophorus*

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bimodality existed between persistence and turnover at this taxonomic level. Rather than coordinated stasis, the paradigm that best describes these communities is a loose stability of community structure based on persistence of common genera, turnover at the species level, fluctuations in abundances of common genera as biofacies recur through time, and a large suite of less common taxa that appeared sporadically when circumstances allowed.

As more intervals of the fossil record are tested for patterns of coordinated stasis, two scenarios come to mind. If most other sections are found to be incompatible with this model, it could indicate that coordinated stasis is a unique feature of the Silurian/Devonian faunas rather than a universal phenomenon. Inversely, if the majority of studies from other time periods support coordinated stasis, then the question of why these Middle and Upper Ordovician faunas do not follow this pattern must be investigated.

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Chapter 7: Multivariate Statistical Analysis

Just as controversial as the pattern of coordinated stasis have been the processes proposed to account for it, especially the theory of "ecological locking" (Morris et al., 1995). In this chapter, the Cincinnatian mudstone faunal data will be examined more closely in light of these theories, and the broad patterns of faunal transition and stability denoted in the previous chapter will be analyzed in detail using the techniques of multivariate analysis.

Ivany (1996) divided proposed explanations for coordinated stasis into three classes--artifact (false stasis), extrinsic (physical environment) and intrinsic (ecological) causes. Three artifactual biases have been discussed in the literature. Stratigraphic bias (Holland, 1996b), the false appearance of sudden turnover caused by missing time in a stratigraphic sequence, is only relevant to intervals of stasis found within a single depositional sequence and sampled at a single outcrop. Taphonomic bias, dubbed "the devil's own model" by Miller (1993), has been effectively dismissed by Bennington and Bambach (1996) and Ivany (1996). Related to taphonomic bias is the assertion of McKinney et al. (1996) that "biased preservation and sampling of abundant species in the fossil record presents a false perception of faunal stability at many temporal and spatial scales" (p. 192). An increased rate of turnover among very rare fauna, however, cannot explain why the taxa accounting for 90% or more of individuals in a fauna do show bimodal patterns of stasis and change (McKinney et al., 1996). Baumiller (1996) provided a convincing refutation of all artifactual explanations of coordinated stasis by demonstrating that models incorporating continuous (time-homogeneous) turnover could not produce a pattern consistent with coordinated stasis, *regardless* of sampling intensity and degradation of the rock record. Baumiller (1996) concluded that an evolutionary or ecological mechanism is required to produce the bimodal patterns of stability and turnover present in Brett and Baird's (1995) Silurian/Devonian E-E subunits.

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Proposed extrinsic causes for coordinated stasis generally focus on stabilizing selection operating in unchanging environments. Several researchers (Brett and Baird, 1995; Bennington and Bambach, 1996) suggest that lineages reach their adaptive peaks relatively quickly, then remain stable for long periods of time until severe environmental changes alter adaptive landscapes and initiate a new period of rapid optimization. In A. Miller's (1997) "coincident relative stability" model, patterns of ecological stasis and change are reflections of long-term environmental stability. Sudden faunal changes coincide with environmental shifts, as represented by major lithological changes in the rock record. A. Miller (1997) argues that the coincident relative stability model could be disproven by documentation of E-E subunit boundaries that do not correspond to major lithological changes, a test which could be applied to most of the extrinsic explanations of coordinated stasis.

Based mostly on evidence from "incursion epiboles"--examples of immigrant taxa that flourish briefly then disappear, several workers (Morris et al., 1995; Brett and Baird, 1995; Ivany, 1996) have suggested that not only were ancient communities stable, but they appear to have been "resistant" to the permanent establishment of new taxa, and that the more passive extrinsic factors listed above are not able to account for this phenomenon. As a result, various theories based on intrinsic ecological factors have been proposed (Plotnick et al., 1994; W. Miller, 1996).

The most commonly cited intrinsic theory is "ecological locking" (Morris et al., 1995), which incorporates two ideas from modern ecological theory. The first is that subjection to frequent, low-intensity perturbations can, in a sense, buffer a community against high intensity, low-frequency perturbations and allow for overall community stability on geologic time scales (Morris et al., 1995). At the same time, strong levels of interaction between taxa act to resist the establishment of new immigrants, reduce the fitness of extreme variants, and even prevent the formation and persistence of isolates (see

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Morris et al., 1995). Stabilizing selection, in this case, is enforced by biological interactions rather than the stability in the physical environment.

While distinguishing patterns produced by intrinsic and extrinsic causes is extremely difficult even in the best examples of coordinated stasis, it is even more problematic in situations where coordinated stasis is not apparent at all. Nevertheless, a closer analysis of the dataset could demonstrate recurrent faunal associations, assess the impact of immigration and extinction on community membership, reveal gradual transitions along environmental or temporal gradients, and elucidate other patterns relevant to intrinsic and extrinsic factors controlling community composition.

The most effective way to analyze a dataset for patterns of similarity, turnover, and correlation is the use of multivariate techniques. In this study, two multivariate techniques, cluster analysis and factor analysis, were applied to the data. The following questions will be addressed in the discussion of these analyses:

1) What is the degree of variation in assemblages at the outcrop and horizon scale relative to the degree of interhorizon variability?

2) Which horizons are most and least similar throughout the interval? Is there a pattern of gradual change from the lowest to uppermost horizons? Are there examples of widely spaced horizons that are very similar?

3) Are there any recurring associations (or dissociation) between taxa that could indicate strong ecological relationships (e.g. ecological locking)?

4) Which faunal elements are contributing most strongly to the variations exhibited in the mudstone communities? Do these taxa represent immigrants, extinctions, lineages that

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Table 33 - Samples used in cluster and factor analysis. Letters (e.g., Backbone Creek B) indicate closely-spaced beds within a single mudstone outcrop. Numbers (e.g., Harrison 12-13) indicate samples on the same horizon.

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Series	Formation	Sample Name	Number
Edenian	Kope	Orphanage Road	1
Edenian	Kope	Backbone Creek B	2
Edenian	Kope	Backbone Creek A	3
Edenian	Kope	Backbone Upper	4
Maysvillian	Fairview	Reading Road A	5
Maysvillian	Fairview	Reading Road B	6
Maysvillian	Fairview	Springdale A	7
Maysvillian	Fairview	Springdale B	8
Maysvillian	Fairview	Harrison 12-13	9
Maysvillian	Fairview	Harrison 14-16	10
Maysvillian	Corryville	Dornbusch 1	11
Maysvillian	Corryville	Dornbusch 2	12
Richmondian	Waynesville	Russell Lower	13
Richmondian	Waynesville	East Fork A	14
Richmondian	Waynesville	East Fork B	15
Richmondian	Waynesville	Russell Middle A	16
Richmondian	Waynesville	Russell Middle B	17
Richmondian	Waynesville	Russell Middle C	18
Richmondian	Waynesville	Bon Well Hill A	19
Richmondian	Waynesville	Bon Well Hill B	20
Richmondian	Waynesville	Bon Well Hill C	21
Richmondian	Waynesville	Harper's Run	22
Richmondian	Waynesville	US Rt. 42	23
Richmondian	Waynesville	Russell Upper B	24
Richmondian	Waynesville	Russell Upper A	25
Richmondian	Waynesville	Hannah Creek B	26
Richmondian	Waynesville	Hannah Creek A	27
Richmondian	Waynesville	Hannah Creek 3-7	28
Richmondian	Liberty	Clear Fork A	29
Richmondian	Liberty	Clear Fork B	30

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undergo evolutionary change, or are they persistent taxa responding to environmental differences?

The database

To examine the degree of patchiness in the communities and compare intrahorizon to interhorizon similarity, samples within the database were divided into subsamples that reflect either separate locations along the same horizon in an outcrop or different levels within the total thickness of the sampled unit (Table 33). As in previous analyses, lingulids were lumped together as a single taxon, and genus-level data was used for all other taxa.

Cluster analysis

In cluster analysis, samples or variables are grouped into a dendrogram based on similarity. The relationship of cluster components to stratigraphic positions and constituent fauna can shed light on the questions listed above and thus help to distinguish between the models of ecological-locking, coincident relative stability, and lack of pattern altogether. Also, the outcrop-scale patchiness in communities can be resolved relative to interhorizon variation by the degree to which samples from within each outcrop cluster together.

Patterns of clustering can illustrate the degree of coordinated stasis present in a collection of samples. Figure 54 illustrates three possible results of cluster analysis in an idealized study of four formations. In a “strong coordinated stasis” scenario (Figure 54, column 1), one might expect several clusters representing recurrent community types within the data set, each of which contains samples from the lower, middle, and upper stages of the interval. A lack of stratigraphic mixing within clusters, on the other hand, could indicate either a total lack of stasis within the interval or an E-E subunit boundary within the study interval. In the complete lack of stasis example (Figure 54, column 2), some stratigraphic mixing occurs between adjacent horizons, but the overall pattern indicates a gradual, multiple-step transition from the oldest to youngest samples. In the

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Figure 54 - Idealized Q-mode cluster analysis dendrograms illustrating patterns confirming or contradicting coordinated stasis. In this scenario, each formation (A, B, C, D) contains four samples (1, 2, 3, 4). Formation "A" is oldest, formation "D" is youngest.

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<u>Coordinated Stasis</u>	<u>No Coordinated Stasis</u>	<u>Possible Coordinated Stasis</u>
Each cluster contains samples from bottom, middle, and top of sequence.	No cluster contains samples from all formations, gradual trend indicated from bottom to top of sequence.	An E-E subunit boundary between formations B and C. Two clusters, each containing mixed samples.

```
          |----A1
     |----|----B2
|----|
|    |  |------C4      I
|    |--|  |---D2
|       |--|
|          |---A3
|
|
|         |----A2
|    |----|----C3
|    |                II
|----|  |--|---B1
|    |--|  |---D3
|       |
|       |------C1
|
|       |------D4
|    |--|  |---D1    III
|----|  |--|---C2
     |
     |--|  |---A4
        |--| |-B4
           |-|-B3
```

```
          |----D1
     |----|----D2
|----|
|    |  |------C2      I
|    |--|  |---D4
|       |--|
|          |---D3
|
|
|       |------C4
|    |--|--|---C3
|----|     |---C1     II
|    |
|    |-----|---B3
|          |---B1
|
|
|       |------B4
|    |--|------B2
|----|               III
     |      |--A1
     |--| |-|--A2
        |-|
          |  |-A4
          |--|-A3
```

```
          |----C1
     |----|----D1
     |
     |  |------C4      I
     |--|  |---C2
     |  |--| |-D4
|----|     |-|-D3
|    |
|    |    |----D2
|    |----|----C3
|
|
|       |--|---A1
|    |--|  |---A2     II
|    |  |
|    |  |------B1
|----|
     |  |------A3
     |--|
     |  |------B2
     |
     |--|  |---A4
        |--| |-B4
           |-|-B3
```

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two E-E subunit case (Figure 54, column 3), one might expect two groups of clusters representing samples above and below the boundary. A limited numbers of samples could make it difficult to distinguish these two scenarios in all but the most clear cut of circumstances.

A lack of recurrence in communities, as indicated by a lack of stratigraphic mixing within clusters, could indicate that not enough samples were taken. It is very possible that recurrent communities were out there, but were simply not sampled. A related explanation is that, among the samples used, environments were not sufficiently repeating to allow similar communities to develop. Although it is clear from the limestone brachiopod biofacies that conditions were at least roughly similar in the lower and upper stages of the Cincinnatian, it is also quite possible that major environmental differences such as temperature, food supply, oxygenation and substrate stability are not expressed in the lithology. Based on study of Ordovician depositional environments across North America, Patzkowsky and Holland (1997) noted that the base of the Richmondian marks a return to the paleoceanographic conditions not present since the Middle Ordovician. In this case, lack of recurrence, while unfavorable to an interpretation of ecological locking, does not contradict the environmentally driven extrinsic mechanisms of coordinated stasis.

Finally, lack of stratigraphic mixing within clusters in Figure 54 could be caused by turnover driven by extinction of once dominant forms and establishment of newly evolved and immigrant taxa. In this case, an interpretation of coordinated stasis is dependent on the sharpness and magnitude of this faunal transition.

Morris (1996) cites several examples of repeated faunal associations in the Hamilton fauna as characteristic of coordinated stasis. Exploring these relationships can be done with cluster analysis of R-mode data, which groups variables (e.g. genera) rather than samples. This is especially relevant to the ecological-locking hypothesis. If ecological locking is taking place, one would expect repeated associations of taxa with similar abundance patterns. In an R-mode analysis, this would be expressed as clusters of taxa

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that appear together throughout the interval. If clusters consist of genera that appear together in only one horizon, then there is no evidence of ecological locking.

To complete the cluster analysis, the statistical algorithm used in this study was the Unweighted Pair-Group Method with Arithmetic Averaging (UPGMA), described in Sneath and Sokal (1973). Data was subjected to a percent transformation, and for the R-mode analysis a range transformation was applied as well. The range transformation was conducted to allow taxa with similar distributions in samples to cluster together regardless of their absolute abundances. To measure similarity, the Quantified Dice coefficient, a common metric in ecological studies (Sepkoski, 1974), was used.

Cluster analysis results

The dendrogram for Q-mode cluster analysis (Figure 55) shows seven distinct clusters and two outliers (Table 34). Within these clusters, the lack of stratigraphic mixing is striking. Although six clusters contain samples from different horizons, only one cluster (VI) contains samples from the Lower (Edenian/Maysvillian) and Upper (Richmondian) Cincinnatian. The two older samples in this cluster contain an extremely low diversity, low abundance fauna consisting of lingulids (approximately 80%), *Flexicalymene*, and *Caritodens*. Other samples in this cluster (Hannah Creek, Russell Upper) are also dominated by lingulids but contain a diverse mollusk fauna as well. The inclusion of the older samples, then, is based primarily on the lingulids. No clusters contain moderate to high diversity samples from both the Lower and Upper Cincinnatian.

Of the three patterns in Figure 54, the dendrogram in Figure 55 most closely resembles the second and third. Like the second scenario (no evidence of coordinated stasis), most mixing in clusters is of horizons within the same formation or between adjacent formations (as in clusters II, IV, and V). However, the third model (E-E subunit boundary in the interval, probably at the base of the Richmondian) cannot be dismissed, because the one cluster that mixes samples across this boundary (cluster VI) only does so

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Figure 55 - Results of Q-mode cluster analysis, % transformed data, Quantified Dice coefficient. Cophenetic correlation coefficient: 0.8304.

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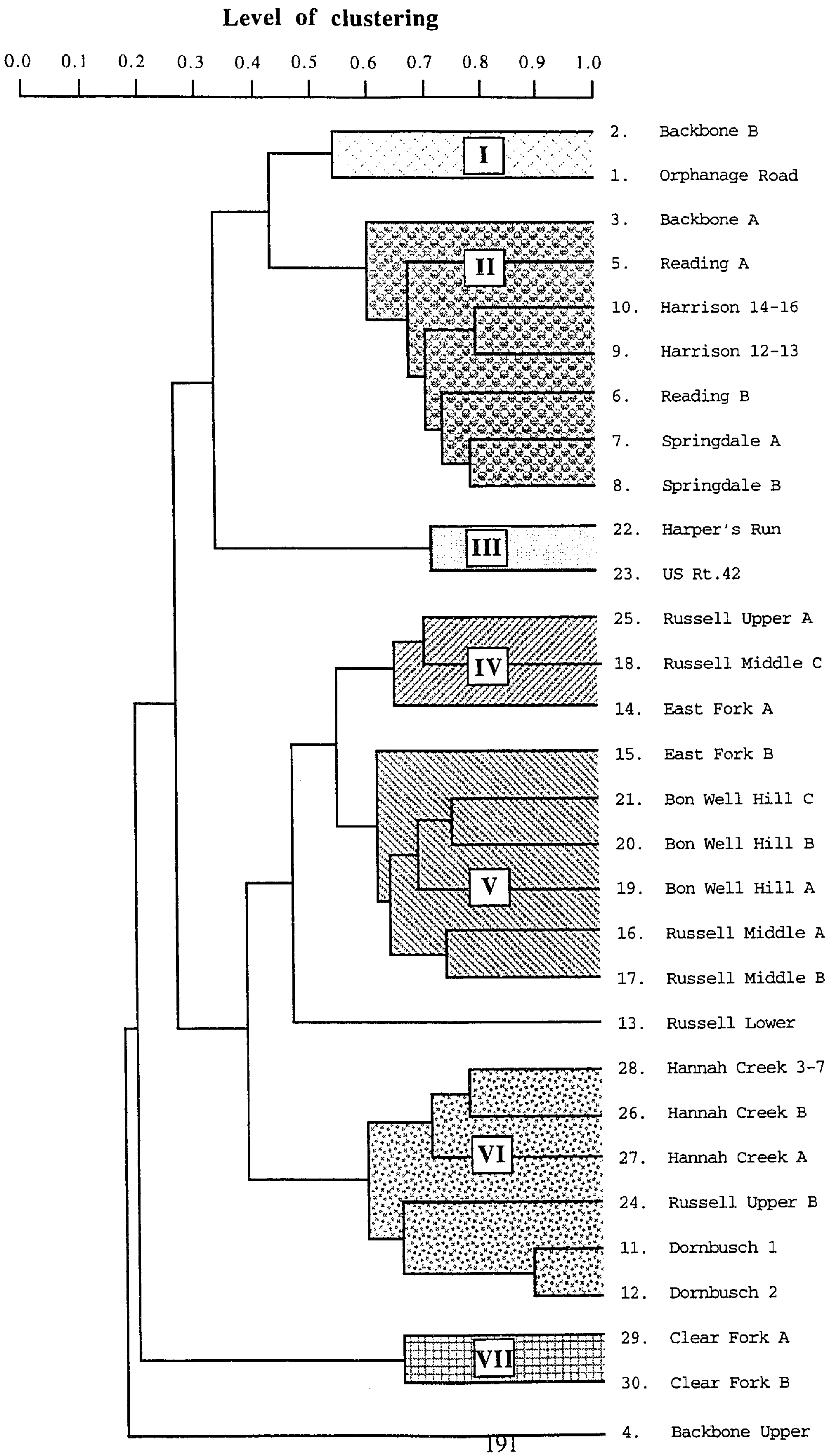

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Table 34 - Description of Q-mode clusters.

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No.	Description
I	Contains Kope samples that are rich in *Sinuites* and *Zygospira*. Aside from these elements, the fauna of these two units is quite dissimilar. Orphanage contains a diverse gastropod fauna that is not found in any other samples throughout the Cincinnatian.
II	Contains all the Mt. Hope samples of Guiseffi (1982), along with a single Kope sample that also contains a fauna dominated by *Sinuites* but also containing a diverse group of pelecypods including *Psiloconcha*, *Cuneamya*, *Cleidophorus*, *Rhytimya*, *Deceptrix*, *Ambonychia*, and *Modiolopsis*.
III	Contains the two samples from the *Treptoceras duseri* shale explored by Frey (1987a,b). Characteristic fauna includes the cephalopod *Treptoceras duseri*, as well as *Flexicalymene*, *Sinuites*, *Cuneamya* and the Richmondian newcomer *Pholodomorpha*.
IV	Contains several Waynesville samples that contain an elevated percentage of infaunal pelecypods such as *Psiloconcha*, *Rhytimya*, and *Cuneamya* as well as high abundances of lingulids.
V	Waynesville samples, most belonging to the "trilobite shale" described by Frey (1983). Similar to cluster IV in composition but distinguished by high abundances of epifaunal bivalves *Ambonychia* and *Corallidomus*.
VI	Lingulid-rich samples from three horizons in the Waynesville and Corryville formations. Only cluster that mixes samples from the Richmondian Stage with samples from the Maysvillian stage. However, similarity of Corryville to Waynesville samples is due simply to the high relative abundances of lingulids and possibly *Flexicalymene*, rather than to a recurrent assemblage.
VII	Consists of two samples from a single, unusual horizon in the Liberty formation. Unique assemblage of *Zygospira*, *Cincinnaticrinus*, lingulids and tiny *Flexicalymene* that give this horizon its local appellation, the "pea-size flexi bed."

*Two outliers did not fit into any cluster. The Russell Lower sample contained a unique assemblage of *Cleidophorus*, *Spatiopora*-encrusted *Treptoceras*, lots of scattered *Onniella* and small bryozoans, and the rare trilobite *Platycorphe*. Backbone Upper is a small sample from the Kope that contains an assemblage of *Trematis*, *Ambonychia*, and *Modiolopsis* along with a few scattered *Zygospira*.

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for very low diversity samples. What *is* clear is that this data does not support the existence of a single E-E subunit in the Cincinnatian, because there is no evidence of a single paleocommunity that recurs with similar structure in the bottom, middle, and upper portions of the interval. Given the evidence against the two E-E subunit model presented in the previous chapter, it appears that this analysis most consistently supports the "lack of any coordinated stasis" scenario for the Cincinnatian mudstones.

The lack of coordination and "ecological locking" is further demonstrated by the R-mode analysis (Figure 56). Although there are other valid interpretations, nine clusters have been delineated (Table 35), along with several outliers. Six of the nine clusters contain genera that appear together in only a single horizon. Clusters IV and V contain most of the more abundant genera in the mudstones, and also contain genera that occur together in samples from the Lower and Upper Cincinnatian. The association of the lingulids with the Richmondian *Ancienta* is a reflection of the increasing abundance of lingulids in Richmondian communities, especially at Russell Upper and Hannah Creek. Cluster IV contains a broad suite of mollusks and other taxa found, in varying abundances, at Backbone Creek, Reading Road, Springdale, Harrison, East Fork Blue Creek, Russell Middle, Bon Well Hill, Harper's Run and US Rt. 42. Within this cluster, possible associations of *Hyolithes* and *Lyrodesma*, *Ambonychia* and *Psiloconcha*, *Sinuites* and *Rhytimya*, and *Cuneamya* and *Isotelus* can be seen. The potential ecological significance of these associations, however, is undermined by their inconsistency. *Hyolithes* and *Lyrodesma* occur together in the Fairview samples, for instance, but *Lyrodesma* is missing at Bon Well Hill. While *Ambonychia* and *Psiloconcha* have similar abundances in many samples, their association breaks down when examined closely, as at Russell Middle (see Figure 23).

The lack of consistency in faunal associations reflects a general characteristic of these data: although communities of basically similar faunal elements occur in both the Edenian/Maysvillian and the Richmondian, the relative abundances of individual taxa are

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Figure 56 - Results of R-mode cluster analysis, % transformation, range transformation, Quantified Dice coefficient. Cophenetic correlation coefficient: 0.8697.

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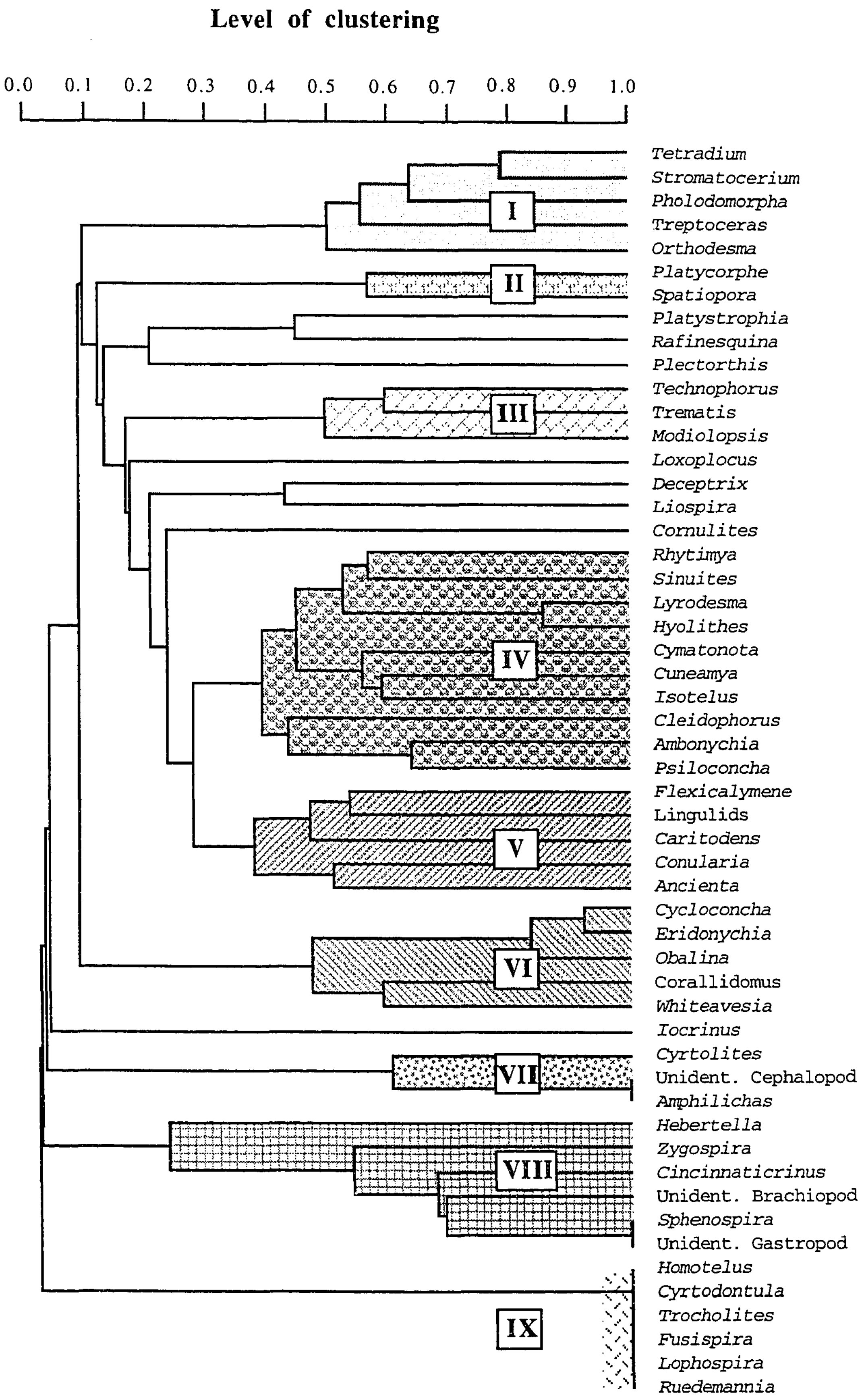

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Table 35 - Description of R-mode clusters and outliers.

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No.	Description
I	Five genera associated with the *Treptoceras duseri*mudstone sampled at Harper's Run and US Rt. 42 (Frey, 1987a)
II	Two genera which occur together at Russell Lower and Russell Middle. Because *Spatiopora* was found encrusting the cephalopod *Treptocerasi*, it should be grouped in cluster I. However, it was listed as <1% on Frey's lists at Harper's Run and US Rt. 42, so it was left off these samples (see Ch. 4).
III	Genera occurring together at Backbone Upper.
IV	Broad group containing most of the common mollusks and other genera that appear in both Lower and Upper Cincinnatian samples, especially Guiseffi's Fairview samples (Reading Road, Springdale, and Harrison) and samples from the "trilobite shale"/*Treptoceras duseri* shale (Russell Middle, Bon Well Hill, Harper's Run, and US Rt. 42).
V	Contains three taxa ubiquitous throughout the section (lingulids, *Flexicalymene*, *Caritodens*), and two genera associated with Richmondian samples (*Ancienta*, *Conularia*). Corresponds to cluster VI in the Q-mode analysis (see Figure 55, Table 34).
VI	Three genera reported only at Bon Well Hill (Guiseffi, 1982), and two genera (*Corallidomus*, *Whiteavesia*) found in many Richmondian horizons but particularly abundant at Bon Well Hill.
VII	Genera recorded only at the Hannah Creek locality.
VIII	Genera recorded only at the Clear Fork locality.
IX	Genera recorded only at the Orphanage Road locality.

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highly variable and seem to vary independently. This agrees with the observation of Patzkowsky and Holland (1997) that "species respond largely independently of other taxa" (p. 433). Both Q-mode and R-mode analyses of the mudstone faunas show no evidence of ecological bonds strong enough to enforce stasis in these communities.

Factor analysis

While clustering is extremely useful in grouping samples and variables together, other aspects of the data cannot be assessed well using this technique. A dendrogram can show relationships between samples within a cluster, but cannot illustrate the relative similarity of individual samples found in different clusters. Any gradual changes that appear on a gradient (temporal or environmental) would not show up well on a dendrogram. Cluster analysis cannot demonstrate which taxa contribute most strongly to variations among samples. Are major differences between samples caused by taxa that immigrate and become established, by taxa that have gone extinct, or by taxa that are relatively stable throughout the interval and are responding to environmental changes? Many of these issues can be addressed with the technique of factor analysis.

Factor analysis is a method analogous to linear regression but applied to a multivariate data set (Davis, 1986). Instead of projecting a line through a two dimensional scatter of data, a "best fit hyperellipsoid" is constructed in the multi-dimensional data space (where each axis corresponds to a variable). The orthogonal axes of this hyperellipsoid correspond to the principal vectors upon which data points (samples) are projected. Graphs on which each sample is plotted by its coordinates on pairs of factors can then be produced. Similar samples will tend to plot closely together, and dissimilar samples will tend to plot farther apart.

Factor analysis adds two major pieces of information to the cluster analysis. First, it provides a multidimensional picture of data, so that absolute similarities between samples and groups of samples can be seen in space. Secondly, factor analysis shows which

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variables are causing most of the variation among samples. Principal Factor Loading values indicate how strongly each factor is correlated to a particular sample (Davis, 1986). Very high *or* low loadings indicate that a particular sample has been highly influential in determining that factor. The Principal Factor Score has a similar meaning to the factor loading but for variables instead of samples. Again, high or low scores indicate that a variable is highly correlated to a particular factor.

Although there is no foolproof way to determine the number of factors to use, in this study only the first three factors will be discussed, accounting for 47.9%, 20.7%, and 9.5% respectively of the total variance in the samples (cumulative variance = 78.1%). Lower ranking factors mainly distinguished highly unusual samples such as Clear Fork and Backbone Upper, which have already been identified as deviant from perusal of the raw data.

The final decision to make in factor analysis is whether or not to rotate factors. In some cases, rotating factors can lead to a greater spread of data and therefore increase the total variation explained by each factor (Davis, 1986). In this analysis, both rotated and unrotated factor analyses were performed, and very similar patterns were found. Only the unrotated analysis is discussed below (rotated results are listed in Appendix 8).

Evidence for coordinated stasis and ecological locking could be corroborated in factor analysis by several patterns. As in cluster analysis, groups of samples should contain a mixture of horizons. Factors should be correlated to groups of persistent taxa that recur throughout the interval, rather than to individual, non-persistent taxa. No major factor should divide older and younger samples.

A gradual transition in community structure through time, on the other hand, would be indicated clearly on a factor analysis plot. In this case, there would be a continuous sweep from oldest to youngest samples, with the samples ordinated roughly by age. Significant changes in the composition of samples through time would be indicated by the

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correlation of factors, as shown by the factor scores, to non-persistent taxa or taxa that show temporal changes in abundance.

In the case of an E-E subunit boundary in the middle of the interval, the pattern shown by factor analysis ought to be very close to the hypothesized pattern of cluster analysis. All factors should clearly differentiate samples from below and above the boundary, and most factors should be correlated to non-persistent taxa. To distinguish from the gradual transition case, samples within each E-E subunit should plot in a mixed, non-ordered way.

Factor analysis results

In plots of factor analysis data (Figures 57-59), groups of samples previously delineated by cluster analysis generally plot together, with some overlap, suggesting that most clusters are well defined. An interesting pattern that is not apparent on the cluster analysis dendrogram is the closeness of Cluster II (containing *Sinuites*-rich Kope and Fairview samples) to the mostly Richmondian Clusters IV, V, and VI on Factors 1 and 3 (Figure 57).

Factor 1 distinguishes sites containing the most common taxa, from sites containing more unusual assemblages, such as Orphanage, Clear Fork, and Harper's Run (Figures 57, 58). Scores on Factor 1 are highly correlated to mean abundance of taxa (Figure 60). The group of taxa with high scores on Factor 1 (Table 36) corresponds to the broad collection of common fauna found in Clusters IV and V of the R-mode cluster analysis (Figure 56).

The most useful factor for showing transitions from the Lower to Upper Cincinnatian samples is Factor 2 (Figures 57 and 59), which distinguishes lingulid-dominated samples of the Upper Cincinnatian from the *Sinuites*-dominated samples of the Lower Cincinnatian (Table 36). Samples 1 through 10 (except for sample 4) are rich in *Sinuites*, while samples 11 through 30 contain abundant lingulids and relatively few

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Figure 57 - Factor analysis results, Factors 1 and 2. For key to numbers, see Table 33.

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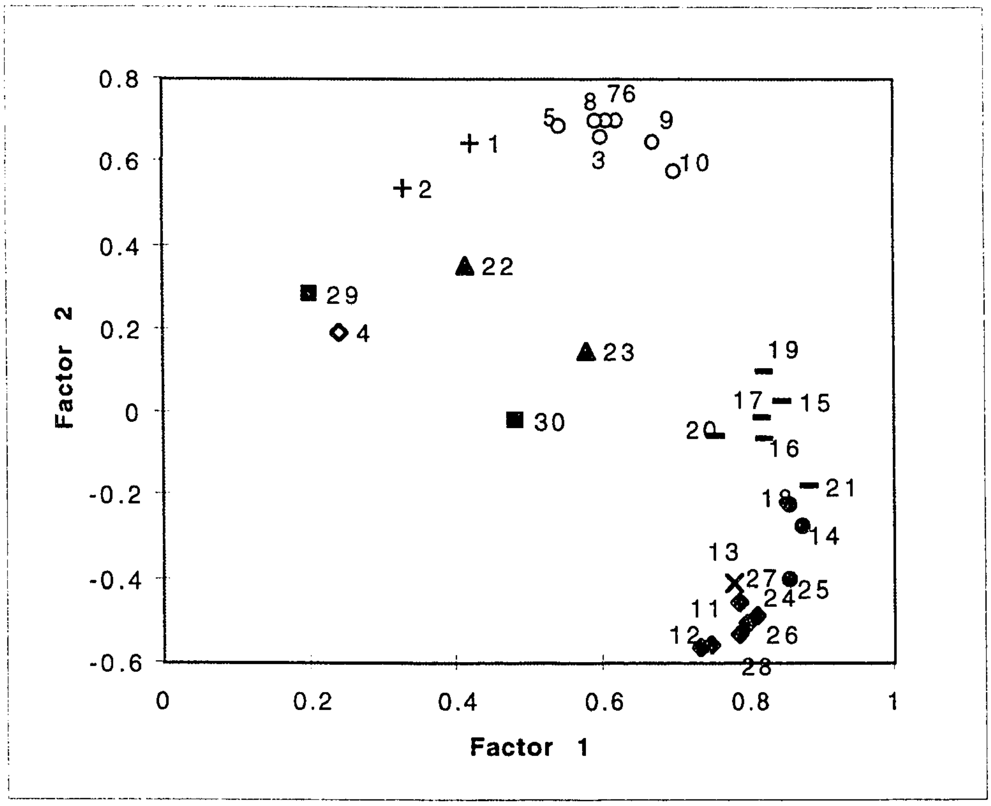

Legend

Cluster I	+	Cluster VI	◆
Cluster II	○	Cluster VI	■
Cluster III	▲	Backbone Upper	◇
Cluster IV	●	Russell Lower	×
Cluster V	▬		

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Figure 58 - Factor analysis results, Factors 1 and 3. For key to numbers, see Table 33.

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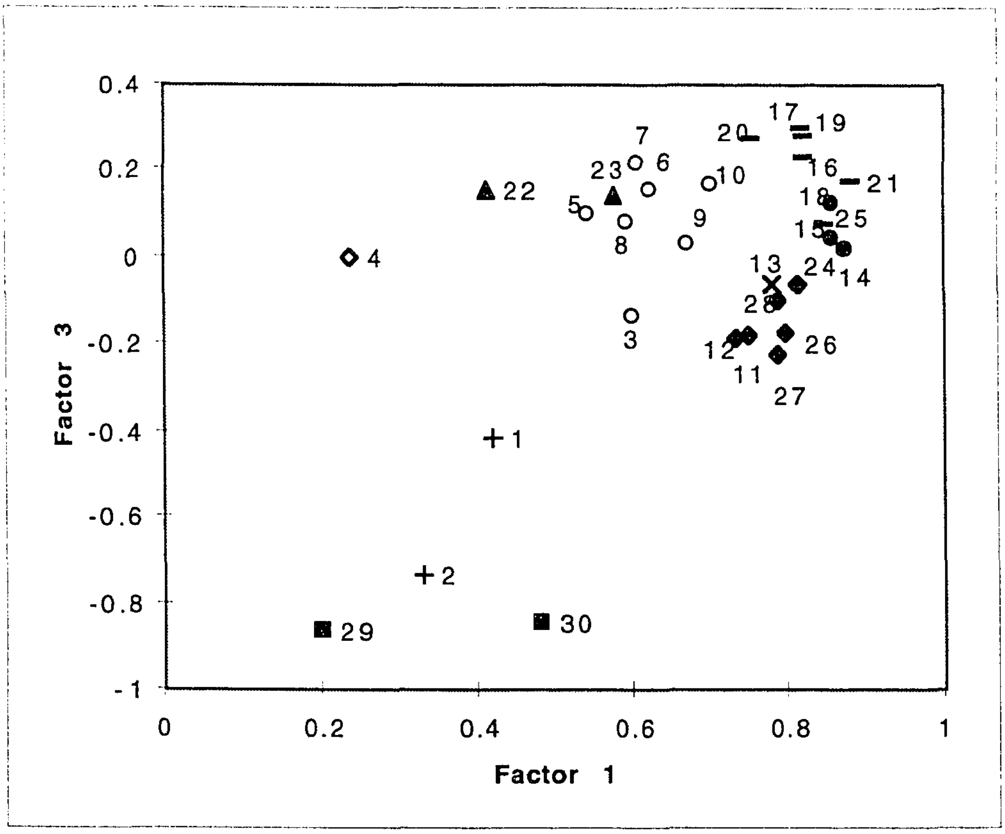

Legend

Cluster I	+	Cluster VI	◆
Cluster II	○	Cluster VI	■
Cluster III	▲	Backbone Upper	◇
Cluster IV	●	Russell Lower	×
Cluster V	▬		

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Figure 59 - Factor analysis results, Factors 2 and 3. For key to numbers, see Table 33.

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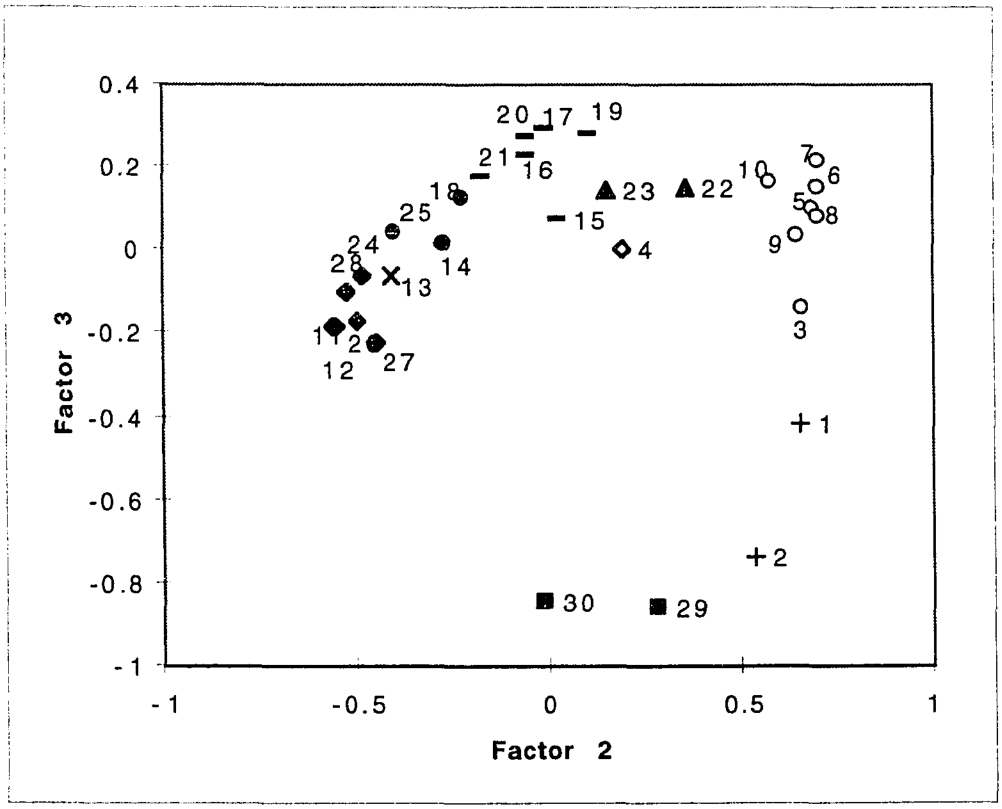

Legend

Cluster I	+	Cluster VI	◆
Cluster II	○	Cluster VI	■
Cluster III	▲	Backbone Upper	◇
Cluster IV	●	Russell Lower	×
Cluster V	▬		

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Figure 60 - Mean abundance vs. Factor 1 principal factor scores, with regression line ($R^2 = 0.94$)

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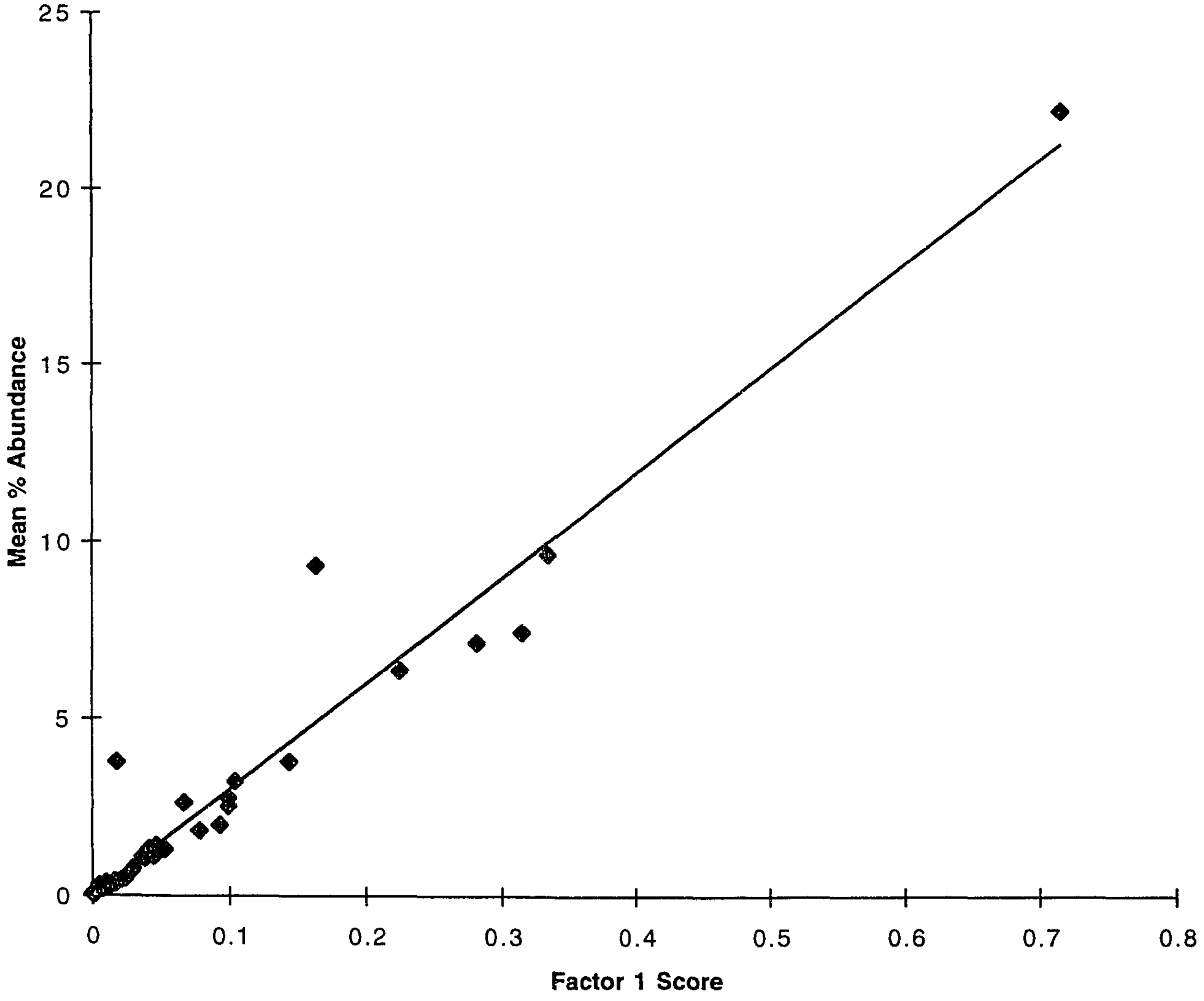

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Table 36 - List of faunal elements most correlated to Factors 1, 2, and 3.

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Factor 1			
Highest Factor Scores	**Factor Score**	**Lowest Factor Scores**	**Factor Score**
Lingulids	0.716	*Iocrinus*	0.001
Sinuites	0.335	*Amphilichas*	0.001
Psiloconcha	0.315	*Sphenospira*	0.001
Ambonychia	0.282	*Loxoplocus*	0.001
Flexicalymene	0.225	*Homotelus*	0.002
Factor 2			
Highest Factor Scores	**Factor Score**	**Lowest Factor Scores**	**Factor Score**
Sinuites	0.673	Lingulids	-0.579
Zygospira	0.271	*Ancienta*	-0.049
Cuneamya	0.181	*Corallidomus*	-0.041
Ambonychia	0.147	*Conularia*	-0.014
Isotelus	0.134	*Spatiopora*	-0.012
Factor 3			
Highest Factor Scores	**Factor Score**	**Lowest Factor Scores**	**Factor Score**
Ambonychia	0.233	*Zygospira*	-0.884
Corallidomus	0.214	Lingulids	-0.148
Psiloconcha	0.214	*Ruedemannia*	-0.048
Cuneamya	0.127	*Deceptrix*	-0.046
Sinuites	0.095	*Lophospira*	-0.022

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Sinuites, with the exception of the two *Treptoceras duseri* samples. Besides lingulids, and at a much lower level, several of the new Richmondian genera are also correlated negatively with Factor 2, including *Ancienta* and *Corallidomus*. The shift from *Sinuites* to lingulids as the most dominant taxon, along with the integration of the new Richmondian taxa, are the two primary differences between older and younger mudstone communities.

The third factor is correlated most highly with the third most abundant genus in this database, *Zygospira*, and the common bivalves *Ambonychia*, *Psiloconcha*, and *Corallidomus*. The significance of this axis is not clear, especially because *Zygospira* was observed but not included in Guiseffi's samples, but it does reinforce the status of the Clear Fork sample as an interesting outlier.

How do these observations affect arguments for or against coordinated stasis and proposed controlling causes? Most temporal changes in community composition are summed by Factor 2, which is correlated to both persistent taxa (*Sinuites*, lingulids) and non-persistent taxa (*Ancienta*, *Corallidomus*). The grouping of the Dornbusch samples with the lingulid-rich Richmondian samples may indicate that the transition from characteristic Lower to Upper Cincinnatian communities occurred in two steps--the first being an environmental change favorable to lingulids and unfavorable to *Sinuites*, the second a faunal turnover at the base of the Richmondian corresponding to the proliferation of several new taxa (Holland, 1996a). The latter proliferation does not follow the pattern of an epibole, because most of the new taxa were common elements in multiple horizons of the Richmondian.

The presence of significant differences between older and younger samples, along with the preponderance of assemblages that do not recur (i.e. Clear Fork, Harper's Run/U.S. Rt. 42, Russell Lower, Backbone Upper, and Orphanage Rd.), argues against any interpretation of coordinated stasis in Cincinnatian mudstones. Extensive qualitative observation of Cincinnatian mudstones has convinced the author that further sampling of mudstone faunas is likely to increase rather than decrease the proportion of unique

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assemblages found in the interval. For instance, Ferree (1994) documented a mudstone in the Sunset Member of the Arnheim Formation (Richmondian) with an unusual association of graptolites and lingulids; Dattilo (1994) has observed lingulid and deposit-feeding pelecypod assemblages in the Miamitown Shale; and the author has observed a unique assemblage of bryozoan-encrusted gastropods in the Kope and crinoid-rich mudstones in the Kope and Liberty Formations. Inclusion of these horizons in this study would have increased the number of outliers and added to the number of non persistent taxa in this study.

From the variety and lack of repetition of faunal associations within the Cincinnatian mudstone assemblages, it is evident that strong ecological bonds could not have controlled the faunal composition of these communities. Instead, it appears that the taxa inhabiting these mudstones reacted independently to a complex set of mostly environmental variables.

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Conclusions

1) A variety of assemblages are present in the Cincinnatian mudstones. At one extreme are high diversity, mollusk-rich mudstones displaying excellent preservation. At the other extreme are relatively barren mudstones that are either unfossiliferous or contain thin, interbedded shell hash layers. Intermediate to these are mudstones which contain a low density, low diversity (but well preserved) fauna consisting primarily of lingulids and trilobites. The fossiliferous mudstone communities appear in at least 18 observed horizons in the Cincinnatian Series.

2) In general, assemblages along a horizon were similar on an outcrop scale and in many cases at scales of a kilometer and even tens of kilometers. This indicates that patterns of faunal composition are real and not an artifact of random "patchiness" of colonization or local taphonomic effects.

3) Mudstones containing a diverse fossil assemblage appear to be slightly richer in clay than more barren mudstones. There is circumstantial evidence that these mudstones are more intensely bioturbated as well, but ichnofabric data is surprisingly inconsistent. More detailed sampling must be done to confirm these trends and more fully assess the impact of sea level and other environmental variables on community composition.

4) Mudstone communities from the Edenian and Maysvillian could be distinguished from Richmondian communities by the following characteristics:

A) Generally smaller body size in all taxa in the Edenian/Maysvillian communities

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B) Prevalence of *Sinuites* as the dominant taxon in Edenian/Maysvillian communities

C) Prevalence of lingulids as the dominant taxa in Richmondian communities

D) Presence of *Corallidomus*, *Ancienta*, and *Pholadomorpha* as common elements of the Richmondian communities

Samples from the top of the Maysvillian appeared to be more similar to Richmondian samples than to other Maysvillian samples.

5) The results of this investigation suggest that Cincinnatian mudstone communities do not conform well to the model of community level stability and sudden turnover proposed by the theory of coordinated stasis. Species and genus level persistence were well below the critical 60% level, although the most common faunal elements did persist through the interval. These patterns were consistent with studies of other faunas in the same time period, suggesting that the coordinated stasis model does not apply well to the entire Middle and Upper Ordovician of North America.

6) Within the Cincinnatian mudstone communities, there was a lack of recurrent faunal associations that could indicate strong ecological bonds. A significant proportion of sampled communities contained unique faunal assemblages not found elsewhere, and rank abundances of more common taxa were highly variable even among the most similar communities. Rather than moving in "lockstep", individual faunal elements appeared to react individually to a variety of environmental parameters.

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Future Research

In this study, general trends in community structure in Cincinnatian mudstones have been elucidated. One problem with the sporadic sampling methods of study was that it was nearly impossible to observe changes on an environmental gradient, in order to compare these changes to temporal differences. Guiseffi (1982) partially addressed this issue by collecting from three sites on an east west transect. Unfortunately, these samples were not on the same horizon, and multivariate analysis indicates these communities were similar in structure and do not clearly demonstrate the effects of environmental gradient on faunal composition.

The Kope formation has been interpreted by several authors (Holland, 1993; Jennette and Pryor, 1993) as a generally shallowing upward sequence. Recent authors (Dattilo, 1994; Holland et al., 1997) have further refined the cycles of transgression and regression present in the Kope. Diekmeyer (1990) demonstrated that the limestone faunas strongly reflected the shallowing upward trend, and that this evidence could be used to fine tune interpretations of depth and cyclicity. It would be extremely interesting to sample the mudstones of the Kope Formation, layer by layer, to see if a similar pattern could be observed in the constituent faunas. By collecting faunal, taphonomic, and ichnologic data within a well-documented stratigraphic framework, the responses of these mudstone communities to certain environmental parameters could be much more clearly ascertained.

In addition, this study and others indicate that similar mudstone communities may be found in other regions from strata below the base of the Cincinnatian Series. If possible, sampling of equivalent mudstone communities in the Middle Ordovician and Lower Silurian would allow for more accurate assessment of patterns of turnover and carryover at the base of the Cincinnatian interval.

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Appendix 1

Locality Listing

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Appendix 1

Locality Register

Localities of mudstones sampled by the author:

Backbone Creek

Streamcuts located along creek approximately 0.6 upstream of rte. 132 bridge just north of highway 32 north of Batavia, Ohio. Pristine exposures of Kope strata along length of stream. Sampled mudstone located near top of Kope formation, approximately 5 meters below Kope/Fairview contact, corresponding to the lower half of cycle 39 of Holland, et. al. (1997) (Backbone Creek sample) and cycle 40 (Backbone Upper sample). Batavia Township, Claremont County, Ohio (39°05'20"N, 84°10'10"W; Batavia, Ohio 7.5 minute quadrangle).

Dornbusch

Exposures of Corryville Member strata on unnamed stream south of I-275 and west of Colerain Avenue. Sampled horizon located on stream 150 m north of terminus of Yellowstone Drive. Colerain Township, Hamilton County, Ohio (39°14'52"N, 84°36'30"W; Cincinnati West, Ohio 7.5 minute quadrangle).

Russell Branch Lower

Streamcut located on west side of an unnamed bridge, 0.6 km south of junction with St. Marys Road, 0.5 km northeast of St. Marys, Indiana. 0.6 m of Waynesville mudstone exposed, Fort Ancient member. Butler Township, Franklin County, Indiana. (39°20'58" N, 85°06'08"W; Spades, Indiana 7.5 minute quadrangle).

Russell Branch Middle

Streamcuts located on stream that runs parallel to driveway. Sampled outcrop corresponds to the Trilobite Shale (Frey, 1983, 1987a; Brandt, 1980), and is located exactly 0.9 km NE of St Marys, Indiana. The top of the sampled outcrop marks the upper boundary of the Ft. Ancient member of the Waynesville formation. Butler Township, Franklin County, Indiana. (39°21'05" N, 85°06'00"W; Spades, Indiana 7.5 minute quadrangle).

Russell Branch Top

Thin exposure of mudstone located approximately 0.25 km upstream of Russell Branch Middle outcrop. Clarksville member of Waynesville formation. Butler Township, Franklin County, Indiana. (39°21'11" N, 85°05'54"W; Spades, Indiana 7.5 minute quadrangle).

East Fork Blue Creek

Isolated streamcut exposure of Waynesville mudstones. Outcrop located just west of Blue Creek Road, 9.4 km south of Rte. 52 junction, 2.3 km north of St. Peter Road junction. Horizon in Waynesville formation, but further stratigraphic control difficult to obtain due to isolated nature of outcrop and lack of identifiable beds above or below outcrop. Highland Township, Franklin County, Indiana (39°20'21"N, 85°01'54"W; Spades, Indiana 7.5 minute quadrangle).

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Hannah Creek

Streamcuts located east of Rte. 101, 0.7 km south of Roseburg, Indiana. Section exposes approximateley 10m of the upper Waynesville formation. The mudstone marks the top of the *Onniella meeki* zone and is within the *Catazyga headi* zone (Frey, 1976), although no *Catazyga headi* were found here. Liberty Township, Union County, Indiana (39°35'00"N, 84°56'43"W; New Fairfield, Indiana 7.5 minute quadrangle).

Clear Fork

Streamcuts located 1 km north of Tony Road, 1.6 km east of junction with Rte. 229 NE of Oldenberg, Indiana. Section exposes approximately 1.6 m of mudstone and limestone layers which correspond to the *Loxoplocus bowdeni* zone (Frey, 1976) and is known to local collectors as the "pea size flexi zone". Unfortunately, the distinctive *Thaerodonta* zone (Frey, 1976) is not exposed here, so it is difficult to determine the exact stratigraphic level of these layers. Butler Township, Franklin County, Indiana (39°21'15"N, 85°10'9"W; Batesville, Indiana 7.5 minute quadrangle).

Additional localities sampled by the author for ichnofabric and mineralogic data:

Backbone Creek

Streamcuts located along creek approximately 0.6 upstream of rte. 132 bridge just north of highway 32 north of Batavia, Ohio. Sampled mudstone strata from throughout the Fairview Formation, beginning just above the Kope/Fairview contact. Batavia Township, Claremont County, Ohio (39°05'20"N, 84°10'10"W; Batavia, Ohio 7.5 minute quadrangle).

Second Creek

"Streamcuts along Second Creek below and west of Cozzandale Road Bridge (Osgood, 1970). The uppermost portion of the Corryville and the Corryville-Mt. Auburn contact are present at a small waterfall close to the bridge. An excellent Mt. Auburn exposure occurs northeast of the bridge just around the first stream meander. Harlan Township, Warren County, Ohio (39°19'25"N; 84°05'31"W; Pleasant Plain, Ohio 7.5 minute quadrangle)." (Goldman, 1993)

Monroe

Construction site that has since been covered over, exact location uncertain. Corryville shales excavated by Dan Cooper, part of collection stored in the collections of the Cincinnati Museum of Natural History.

Salt Creek

Streamcuts along the south bank of Salt Creek exposing Waynesville strata, exact position undetermined. Located 1.6 km east of 1260 West Road bridge, 1.8 km north of Hamburg Road junction, approximately 4 km northwest of Oldenberg, Ohio. Ray Township, Franklin County, Indiana (39°21'50"N; 85°14'32"; Batesville, Indiana 7.5 minute quadrangle).

Harvey Branch

Streamcuts along both sides of Harvey Branch which runs parallel to 1000 West Road, 2.2 km north of Oldenberg, Indiana. Collecting fossils is now prohibited, contact the owner to get permission to explore this exceptional exposure of a highly fossiliferous, Upper Waynesville exposure, the source of the large *Isotelus maximus* that graces the cover of Cincinnati Fossils (Davis, 1992). Mudstone samples used in this study were borrowed from the collections of the Cincinnati Museum of Natural History. Ray

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Township, Franklin County, Indiana (39°21'35"N; 85°12'28"W; Batesville, Indiana 7.5 minute quadrangle).

Localities sampled by other authors for analysis of faunal composition:

Orphanage Road

"1.5-m-thick claystone unit exposed 18 m above road level. Kope Formation (Edenian), roadcut on the north side of Orphanage Road, just west of junction with Kentucky Rt. 17 and north of I-275 E, Kenton County, Kentucky. Covington, Kentucky 7.5' Quadrangle, Longitude: 84° 33' W, Latitude: 39° 31' 30" N." (Frey, 1987b)

Harrison

Claystone bed on roadcut on north side of I-74 just east of Ohio-Indiana border. Sampled horizon located 4.5 meters above the base of the Mt. Hope Member of the Fairview Formation. Located in the S1/2 of the NE1/4 of the NW1/4 of Sec. 18, R. 1E, T. 2N, on the Harrison, Ohio-Indiana 7.5 minute quadrangle. (Guiseffi, 1982)

Springdale

Claystone bed on roadcut on eastern side of I-275, just north of junction with I-74. Sampled horizon located 9 meters above the base of the Mt. Hope Member of the Fairview Formation. Located in the NE1/4 of the NE1/4 of the SW1/4 of Sec. 31, R. 1, T. 2, on the Addyston, Ohio 7.5 minute quadrangle. (Guiseffi, 1982)

Reading Road

Claystone bed on roadcut on northeast of junction of Reading Road (U.S. 42) and Galbraith Rd. Sampled horizons located 4.5 meters and 5 meters above the base of the Mt. Hope Member of the Fairview Formation. Located in the E1/2 of the SE1/4 of Sec. 32, R. 1, T. 4, on the Cincinnati East, Ohio 7.5 minute quadrangle. (Guiseffi, 1982)

Mt. Orab

Quarry located on Sicily Road, 0.8 km north of Rte. 32 near Sardinia, Ohio. Exposure of mudstone from the Sunset Member of the Arnheim Formation. Highland County, Ohio; Sardinia, Ohio 7.5-minute quadrangle. (Ferree, 1994)

Bon Well Hill

"Shelly claystone bed, 60 cm below the top of the Trilobite shale unit, Waynesville Formation (early Richmondian), Bon Well Hill roadcut on Rt. 101, north side of the road, 2 km northeast of Brookville, Franklin County, Indiana." (Frey, 1987b)

Harper's Run

"Streambank exposures along the north and south forks of Harpers Run, south of Strout Road at Camp Whip-Poor-Will, G.S.A. outdoor center, Warren County, Ohio (Oregonia, Ohio 7.5' quadrangle, Long. 84°05' W, Lat. 39°23' N)." (Frey, 1987a)

US Rt. 42

"Roadcut along U.S. Rt. 42, west side of the road, 3 km northeast of Waynesville, Warren County, Ohio (Waynesville, Ohio 7.5' quadrangle, NE1/4, SE1/4 sec 26, R4, T4)." (Frey, 1987a)

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Appendix 2

Description of Sampled Outcrops

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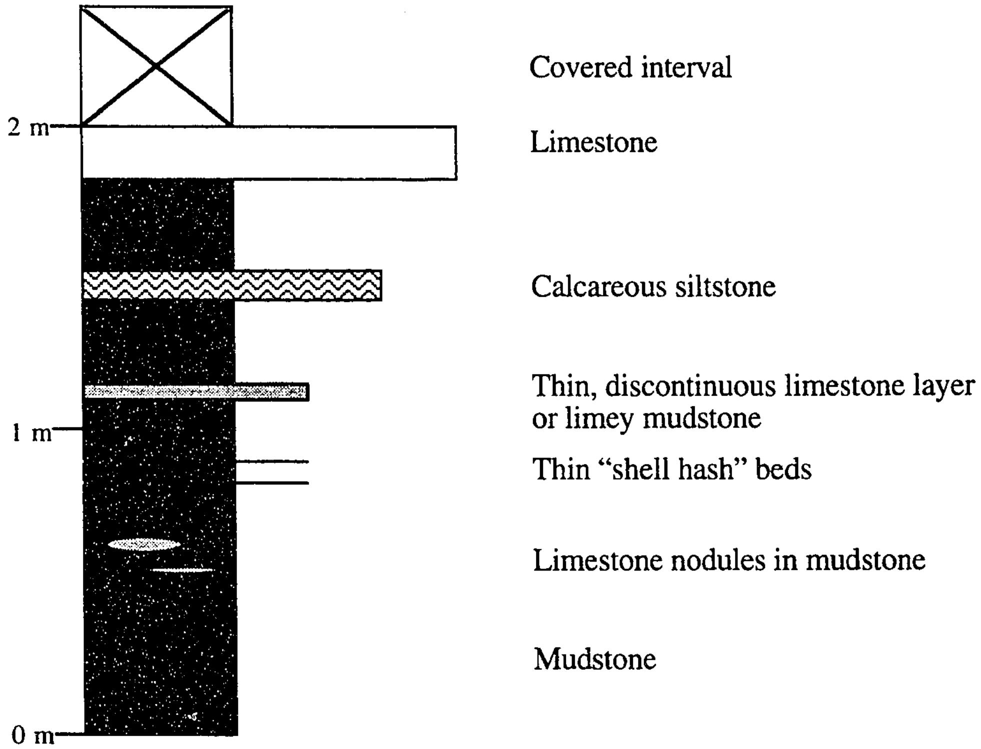
Key to Stratigraphic Columns



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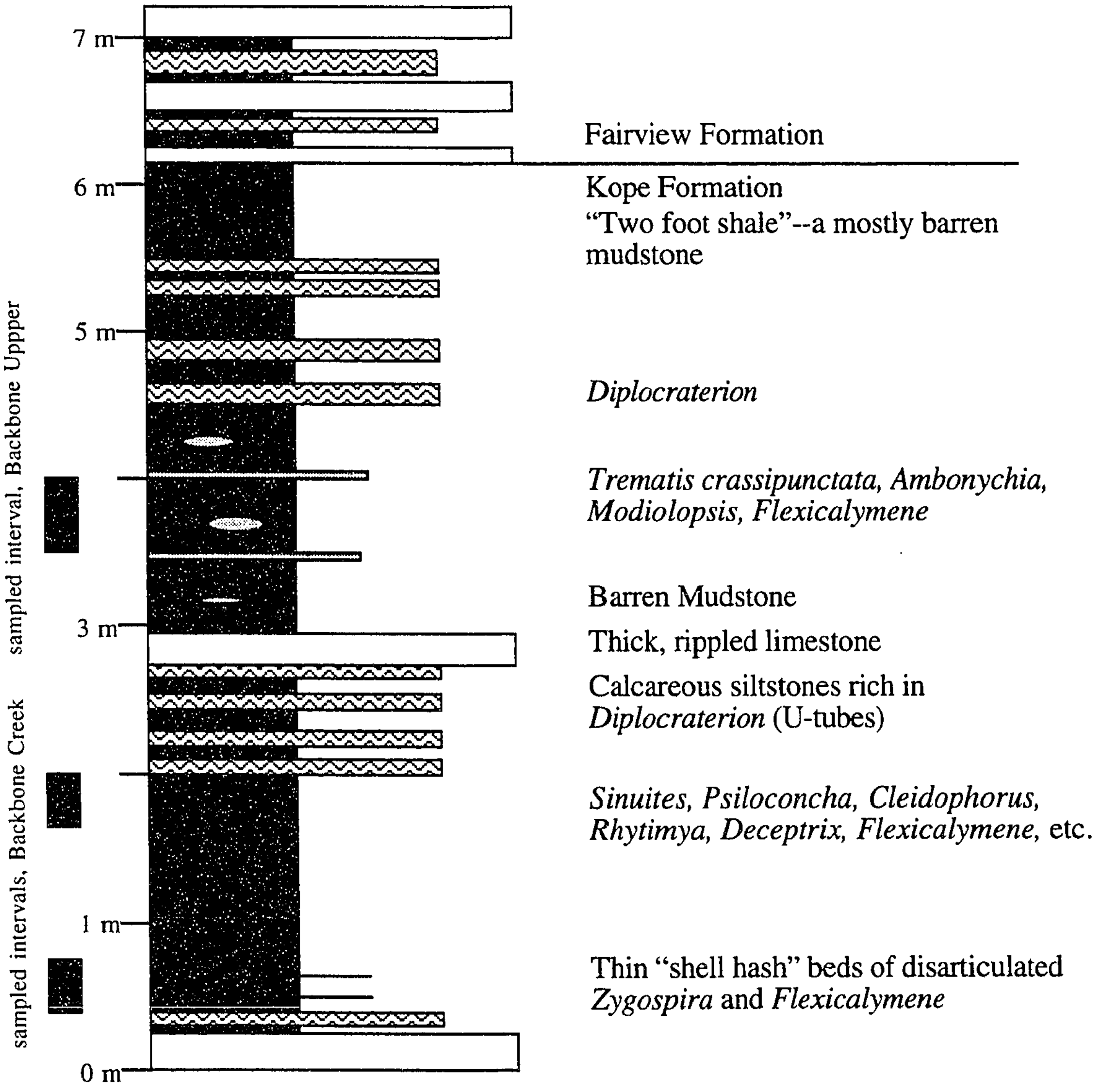
Backbone Creek, Backbone Upper



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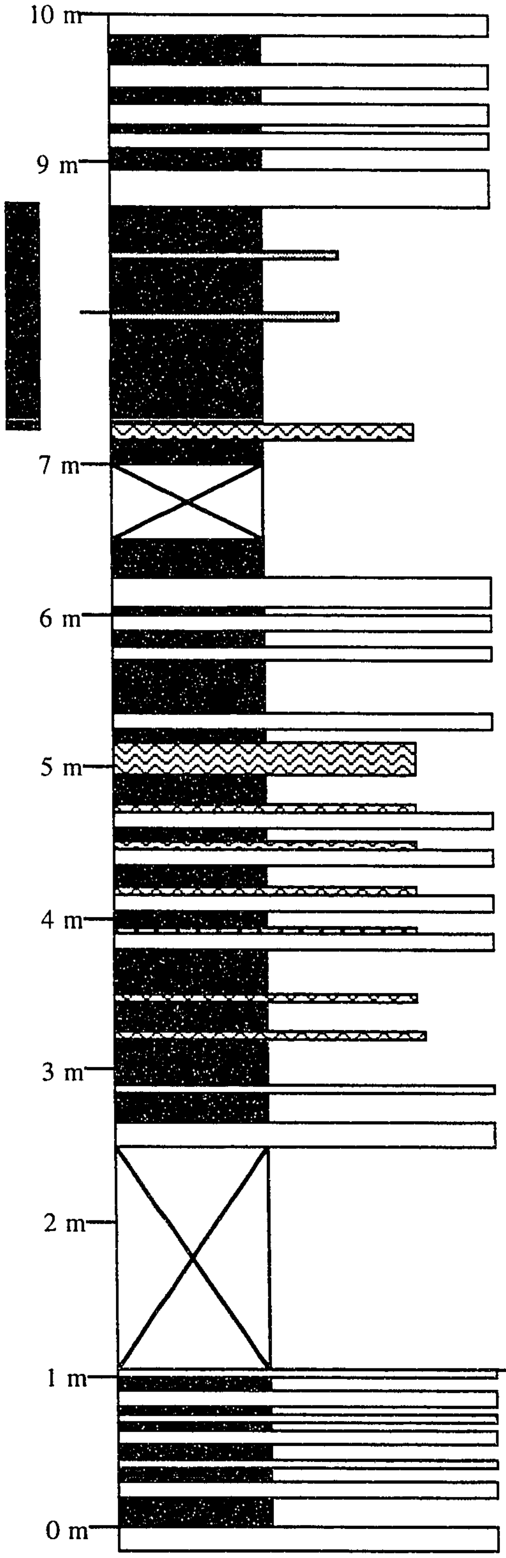
Dornbusch



Thick limestones with highly fragmented bryozoan pieces with *Iocrinus* columnals

Rippled limestone with crinoid columnals, *Rafinesquina*

Thin limestone beds capped by thin "glazes" of calcareous siltstone. *Chondrites, Diplocraterion*

Rafinesquina nasuta, Parvohallopora, Ambonychia, Modiolopsis, Cyclonema, and cephalopods

Rafinesquina nasuta on loose slabs

Corryville Member

Bellevue Formation

Thinly bedded limestones and mudstones, with *Platystrophia, Onniella, Zygospira, Rafinesquina, Ectenocrinus, Parvohallopora, Batostomella*

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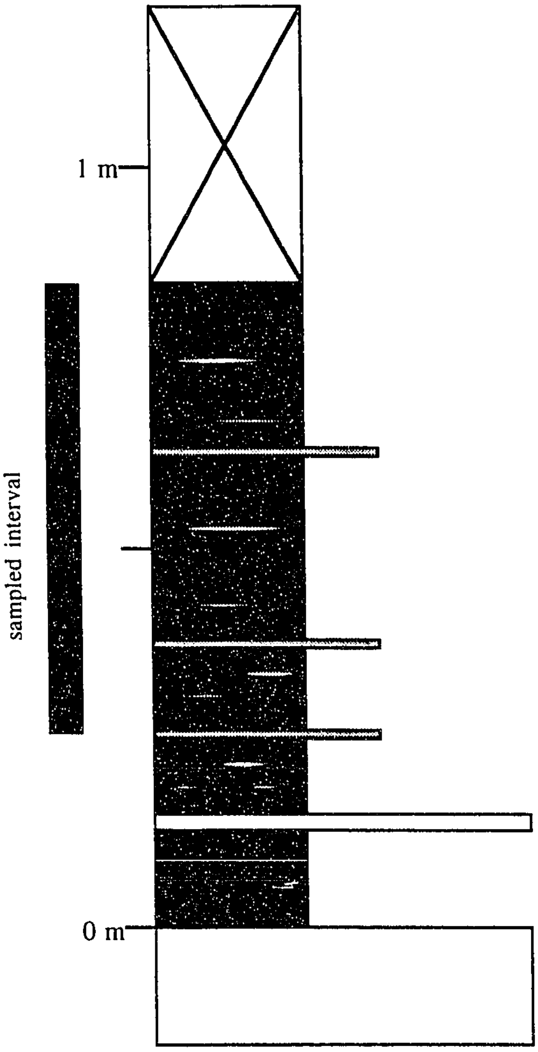
Russell Branch Lower



Mudstone interlayered with thin, *Onniella* shell beds

Thin limestone contains *Onniella*, *Iocrinus*, and thin, branching bryozoans

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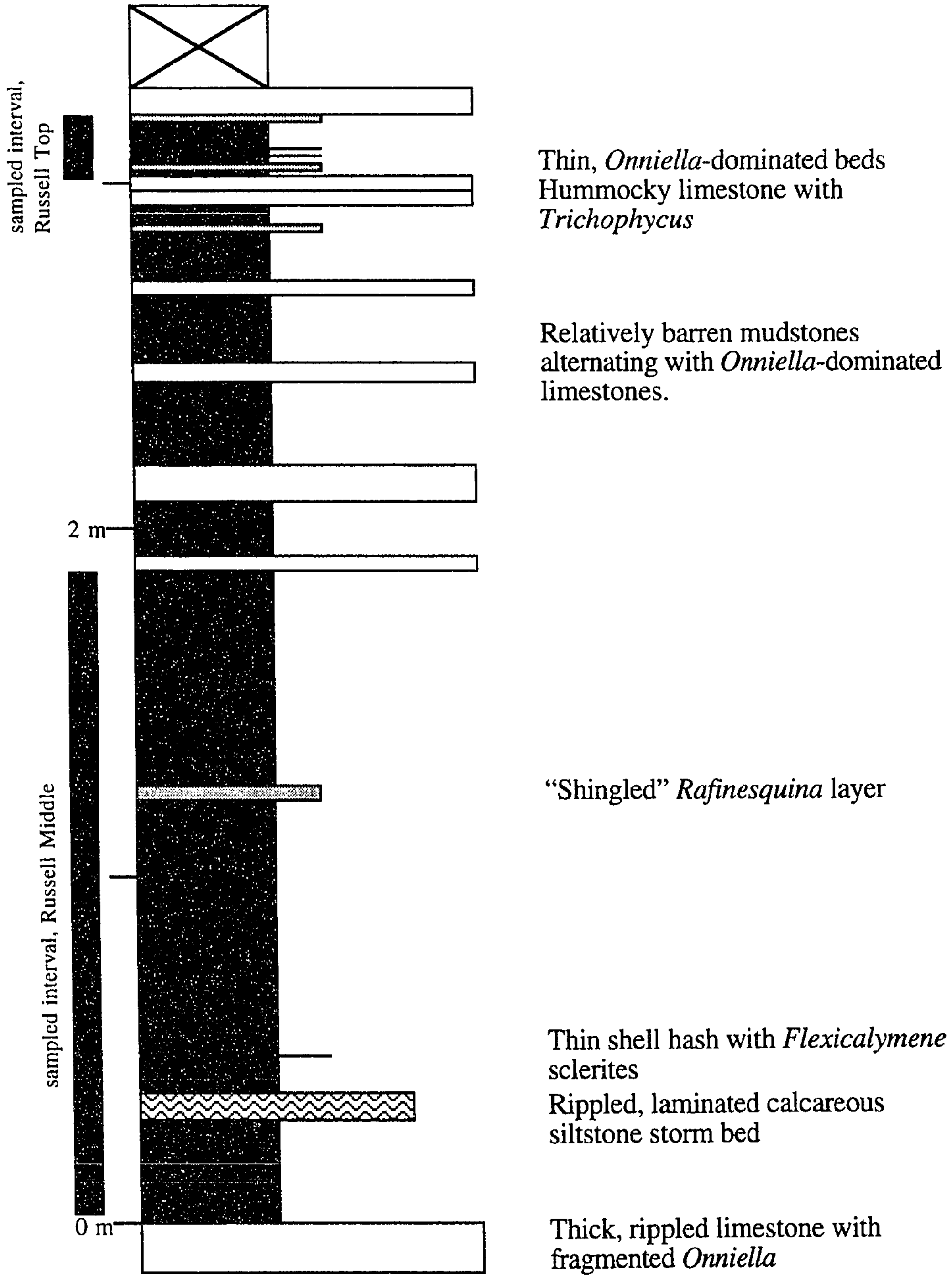
Russell Middle, Russell Upper



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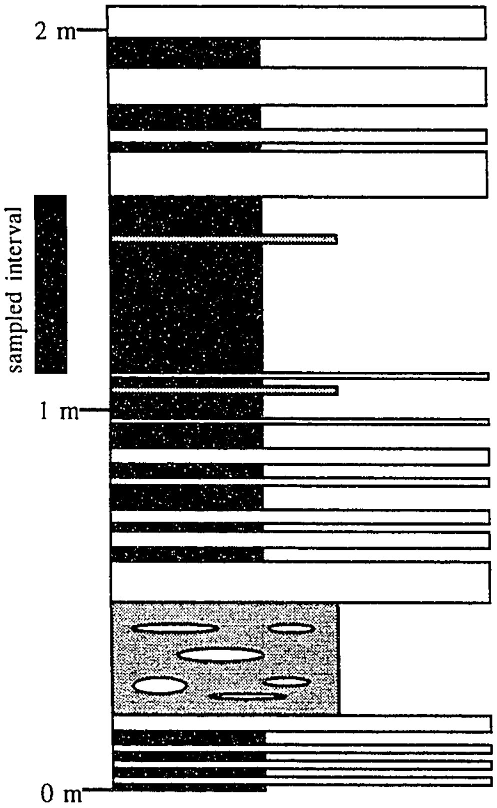
Hannah Creek



Platystrophia, Rafinesquina, Batostoma

Massive, ledge-forming limestone. Fragmented *Onniella, Platystrophia*

Rafinesquina, Platystrophia, Onniella, Leptaena, Parvohallopora

Limey, densely fossiliferous mudstone with *Rafinesquina*

Batostoma, Rafinesquina

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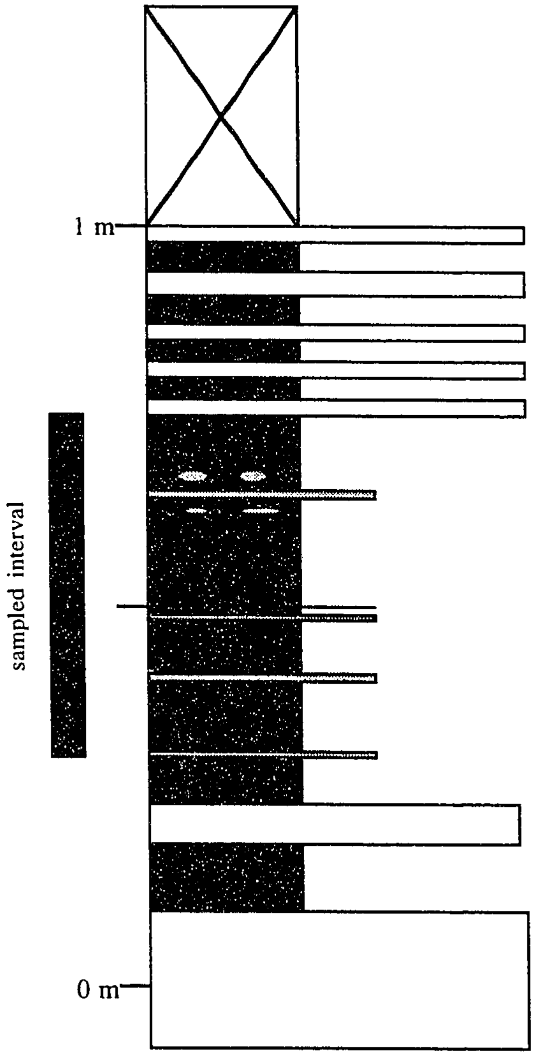
Clear Fork



Limestones rich in *Strophomena, Hebertalla* with occasional fragment of *Flexicalymene, Isotelus*

Limestones contain *Hebertella, Strophomena, Zygospira, Platystrophia*

Thick, rippled limestone with fragmented brachiopods

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Appendix 3

Raw Abundance Data

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Appendix 3

Faunal Abundance Data for Sites Excavated in this Study

		Site:	Backbone Creek	Backbone Creek	Backbone Upper	Dornbusch	Dornbusch	Dornbusch	Dornbusch	Russell Lower	E. Fk. Blue Creek
		Sample:	1a	1b	1	1a	1b	2a	2b	1	1a
		Position:	135-150 cm	0-30 cm		20-30 cm	0-20 cm	20-40 cm	0-20 cm	0-40 cm	
Phylum	**Class**	**Genus**									
Annelida	Problematica	*Ancienta*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	3.00
Annelida	Problematica	*Cornulites*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Trilobita	*Amphilichas*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Trilobita	*Flexicalymene*	5.50	0.20	0.20	3.20	2.50	1.40	0.00	2.80	5.90
Arthropoda	Trilobita	*Isotelus*	6.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	3.00
Arthropoda	Trilobita	*Platycorphe*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
Brachiopoda	Articulata	*Hebertella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Onniella* (xx = pres.)	0.00	xx	xx	0.00	0.00	0.00	0.00	xx	xx
Brachiopoda	Articulata	*Platystrophia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Rafinesquina*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Brachiopoda	Articulata	? brachiopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Zygospira*	7.50	12.00	1.00	2.00	0.00	2.00	0.00	0.50	1.00
Brachiopoda	Inarticulata	Lingulids	1.50	0.00	0.00	29.00	16.00	35.00	10.50	25.50	9.50
Brachiopoda	Inarticulata	*Trematis*	0.00	0.00	5.50	0.00	0.00	2.00	0.50	0.50	1.50
Bryozoa	Trepostomata	*Spatiopora*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
Bryozoa	Trepostomata	? (xx = present)	0.00	xx	0.00	0.00	0.00	0.00	xx	xx	xx
Coelenterata	Conulata	*Conularia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Echinodermat	Crinoidea	*Cincinnaticrinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Echinodermat	Crinoidea	*Iocrinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermat	Crinoidea	? crinoid	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Cephalopoda	*Treptoceras*	4.00	0.00	1.00	0.00	0.00	0.00	0.00	8.00	0.00
Mollusca	Cephalopoda	? cephalopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	*Liospira*	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	*Sphenospira*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	? gastropod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Monoplacopho	*Cyrtolites*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Monoplacopho	*Sinuites*	15.00	5.00	xx	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Ambonychia*	1.00	1.50	2.50	0.00	0.00	0.00	0.00	0.00	3.00
Mollusca	Pelecypoda	*Caritodens*	0.50	0.00	0.00	2.00	1.00	1.50	0.50	0.00	0.50
Mollusca	Pelecypoda	*Cleidophorus*	3.00	1.50	0.00	0.00	0.00	0.00	0.00	11.50	0.00
Mollusca	Pelecypoda	*Corallidomus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00
Mollusca	Pelecypoda	*Cuneamya*	0.50	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00
Mollusca	Pelecypoda	*Cymatonota*	1.50	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.50
Mollusca	Pelecypoda	*Deceptrix*	6.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Modiolopsis*	1.50	0.00	1.50	0.50	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Pholadomorpha*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Psiloconcha*	7.50	0.00	0.00	0.00	0.00	0.00	0.00	7.00	3.00
Mollusca	Pelecypoda	*Rhytimya*	4.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	1.50
Mollusca	Pelecypoda	*Whiteavesia*	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Mollusca	Rostroconcha	*Technophorus*	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00

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Appendix 3

Faunal Abundance Data for Sites Excavated in this Study

		Site:	E. Fk. Blue Creel	Russell Middle	Russell Middle	Russell Middle	Russell Middle	Russell Middle	Russell Middle	Russell Middle	Russell Middle
		Sample:	1b	1a	1b	1c	1d	1e	1f	1g	1h
		Position:		160-180 cm	140-160 cm	115-140 cm	100-112 cm	80-100 cm	70-80 cm	50-70 cm	30-50 cm
Phylum	**Class**	**Genus**									
Annelida	Problematica	*Ancienta*	2.00	7.00	3.00	6.00	3.00	6.00	2.00	2.00	3.00
Annelida	Problematica	*Cornulites*	0.00	0.00	0.00	0.00	1.00	2.00	0.00	1.00	0.00
Arthropoda	Trilobita	*Amphilichas*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Trilobita	*Flexicalymene*	1.40	3.40	5.20	11.00	11.80	2.80	4.10	2.70	2.80
Arthropoda	Trilobita	*Isotelus*	0.00	1.00	2.00	10.00	2.00	6.00	2.00	0.00	1.00
Arthropoda	Trilobita	*Platycorphe*	0.00	1.00	0.00	0.00	0.00	1.00	2.00	0.00	0.00
Brachiopoda	Articulata	*Hebertella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Onniella* (xx = pres.)	xx*	0.00	0.00	0.00	xx	0.00	xx	xx	xx
Brachiopoda	Articulata	*Platystrophia*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Rafinesquina*	0.00	0.00	0.00	xx	xx	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	? Brachiopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Zygospira*	2.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Inarticulata	Linguilds	5.00	5.50	18.50	23.00	11.50	7.50	10.50	15.00	10.50
Brachiopoda	Inarticulata	*Trematis*	0.50	0.00	0.00	1.50	1.00	1.00	0.00	1.00	0.00
Bryozoa	Trepostomata	*Spatiopora*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bryozoa	Trepostomata	? (xx = present)	xx	xx	xx	xx	xx	0.00	0.00	0.00	xx
Coelenterata	Conulata	*Conularia*	0.00	0.00	0.00	5.00	3.00	0.00	2.00	1.00	0.00
Echinodermat	Crinoidea	*Cincinnaticrinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermat	Crinoidea	*Iocrinus*	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
Echinodermat	Crinoidea	? Crinoid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Cephalopoda	*Treptoceras*	1.00	0.00	2.00	0.00	4.00	8.00	4.00	0.00	2.00
Mollusca	Cephalopoda	? Cephalopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	*Liospira*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	*Sphenospira*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Gastropoda	? Gastropod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Monoplacopho	*Cyrtolites*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Monoplacopho	*Sinuites*	1.00	2.00	1.00	17.00	5.00	4.00	0.00	0.00	2.00
Mollusca	Pelecypoda	*Ambonychia*	3.50	7.50	12.00	34.00	25.00	3.00	9.50	6.00	3.00
Mollusca	Pelecypoda	*Caritodens*	0.50	0.00	0.00	1.50	1.50	5.50	2.00	0.50	0.50
Mollusca	Pelecypoda	*Cleidophorus*	1.50	1.00	0.00	0.00	1.00	1.00	0.50	0.00	0.00
Mollusca	Pelecypoda	*Corallidomus*	3.00	0.50	6.50	37.00	18.00	9.50	3.00	2.50	0.50
Mollusca	Pelecypoda	*Cuneamya*	1.50	1.00	1.00	0.00	0.50	1.50	2.00	0.00	0.00
Mollusca	Pelecypoda	*Cymatonota*	0.50	0.00	0.50	5.00	1.00	0.00	3.50	2.50	2.00
Mollusca	Pelecypoda	*Deceptrix*	1.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Modiolopsis*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Pholadomorpha*	0.00	0.50	0.00	0.00	0.00	1.00	0.00	0.00	0.50
Mollusca	Pelecypoda	*Psiloconcha*	6.00	0.00	6.50	7.00	8.00	8.50	13.50	9.50	11.00
Mollusca	Pelecypoda	*Rhytimya*	3.50	0.00	1.50	1.00	2.50	1.50	1.00	0.50	0.50
Mollusca	Pelecypoda	*Whiteavesia*	0.50	0.00	0.00	1.00	0.00	0.50	0.00	0.00	0.00
Mollusca	Rostroconcha	*Technophorus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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Appendix 3

Faunal Abundance Data for Sites Excavated in this Study

		Site:	Russell Middle	Russell Top	Russell Top	Hannah Creek	Hannah Creek	Hannah Creek	Hannah Creek	Hannah Creek	Clear Fork	Clear Fork
		Sample:	1i	1a	1b	1a	1b	2a	2b	3 to 7	1a	1b
		Position:	0-20 cm	10-13 cm	0-10 cm	30-50 cm	0-30 cm	30-50 cm	0-30 cm	0-50 cm	50-60 cm	0-50 cm
Phylum	**Class**	**Genus**										
Annelida	Problematica	*Ancienta*	2.00	6.00	6.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00
Annelida	Problematica	*Cornulites*	8.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Arthropoda	Trilobita	*Amphilichas*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Arthropoda	Trilobita	*Flexicalymene*	6.50	5.00	0.50	4.40	16.00	2.70	6.60	14.60	2.30	1.50
Arthropoda	Trilobita	*Isotelus*	0.00	0.00	1.00	0.00	7.00	1.00	0.00	0.00	0.00	0.00
Arthropoda	Trilobita	*Platycorphe*	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Hebertella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00
Brachiopoda	Articulata	*Onniella* (xx = pres.)	xx	xx	xx	xx	xx	xx	xx	xx	0.00	0.00
Brachiopoda	Articulata	*Platystrophia*	0.00	0.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00
Brachiopoda	Articulata	*Rafinesquina*	0.00	1.00	0.00	1.00	2.50	0.00	15.00	0.00	0.00	0.00
Brachiopoda	Articulata	? Brachiopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00
Brachiopoda	Articulata	*Zygospira*	0.00	0.00	0.00	1.00	7.00	1.00	3.00	0.00	48.00	80.00
Brachiopoda	Inarticulata	Lingulids	18.00	14.50	106.00	9.50	31.00	11.50	36.50	40.50	0.00	40.50
Brachiopoda	Inarticulata	*Trematis*	2.00	0.00	0.00	0.00	3.50	0.00	1.00	1.00	0.00	0.00
Bryozoa	Trepostomata	*Spatiopora*	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bryozoa	Trepostomata	? (xx = present)	0.00	0.00	0.00	xx	xx	xx	xx	xx	xx	xx
Coelenterata	Conulata	*Conularia*	0.00	2.00	0.00	0.00	0.00	2.00	3.00	1.00	0.00	0.00
Echinodermat	Crinoidea	*Cincinnaticrinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.48	1.00
Echinodermat	Crinoidea	*Iocrinus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinodermat	Crinoidea	? Crinoid	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Cephalopoda	*Treptoceras*	1.00	1.00	3.00	0.00	1.00	0.00	0.00	2.00	0.00	0.00
Mollusca	Cephalopoda	? Cephalopod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00
Mollusca	Gastropoda	*Liospira*	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Mollusca	Gastropoda	*Sphenospira*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
Mollusca	Gastropoda	? Gastropod	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00
Mollusca	Monoplacopho	*Cyrtolites*	0.00	0.00	1.00	0.00	0.00	0.00	2.00	1.00	0.00	0.00
Mollusca	Monoplacopho	*Sinuites*	3.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Ambonychia*	3.00	3.50	5.50	0.50	0.50	0.50	1.00	3.50	1.00	0.50
Mollusca	Pelecypoda	*Caritodens*	2.50	0.00	0.50	0.50	0.50	0.00	1.00	1.00	1.00	3.50
Mollusca	Pelecypoda	*Cleidophorus*	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Corallidomus*	1.50	1.00	0.00	2.00	0.00	0.00	1.00	3.00	0.00	0.00
Mollusca	Pelecypoda	*Cuneamya*	1.00	0.50	8.50	0.50	1.50	0.00	3.50	0.00	0.00	0.00
Mollusca	Pelecypoda	*Cymatonota*	3.00	0.50	0.50	0.50	2.50	0.00	1.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Deceptrix*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00
Mollusca	Pelecypoda	*Modiolopsis*	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Pholadomorpha*	0.00	0.00	0.00	0.00	2.00	2.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Psiloconcha*	19.50	6.00	27.50	0.00	0.50	0.00	0.00	0.00	3.00	1.50
Mollusca	Pelecypoda	*Rhytimya*	2.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Pelecypoda	*Whiteavesia*	0.00	0.00	0.50	0.00	0.50	0.00	0.00	0.00	0.00	0.00
Mollusca	Rostroconcha	*Technophorus*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Appendix 4

Size Data

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Appendix 4

Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
Backbone	Ambonychia	0.50	6.00
Backbone	Ambonychia	0.50	6.40
Backbone	Caritodens	0.50	4.50
Backbone	Cleidophorus	0.50	7.00
Backbone	Cleidophorus	0.50	9.80
Backbone	Cleidophorus	0.50	12.00
Backbone	Cleidophorus	0.50	5.00
Backbone	Cleidophorus	0.50	7.00
Backbone	Cleidophorus	0.50	7.50
Backbone	Cleidophorus	0.50	8.00
Backbone	Cleidophorus	0.50	12.00
Backbone	Cleidophorus	0.50	13.00
Backbone	Cymatonota	1.00	28.00
Backbone	Deceptrix	0.50	3.50
Backbone	Deceptrix	0.50	4.00
Backbone	Deceptrix	0.50	8.50
Backbone	Deceptrix	0.50	2.00
Backbone	Deceptrix	0.50	3.50
Backbone	Deceptrix	1.00	4.80
Backbone	Deceptrix	0.50	6.00
Backbone	Deceptrix	1.00	6.00
Backbone	Deceptrix	0.50	8.00
Backbone	Deceptrix	0.50	8.50
Backbone	Deceptrix	0.50	10.00
Backbone	Liospira	1.00	7.00
Backbone	Liospira	1.00	14.00
Backbone	Modiolopsis	1.00	40.00
Backbone	Psiloconcha	0.50	19.00
Backbone	Psiloconcha	0.50	6.30
Backbone	Psiloconcha	0.50	11.00
Backbone	Psiloconcha	1.00	12.00
Backbone	Psiloconcha	0.50	17.00
Backbone	Psiloconcha	1.00	17.00
Backbone	Psiloconcha	0.50	19.00
Backbone	Psiloconcha	1.00	19.50
Backbone	Psiloconcha	0.50	22.00
Backbone	Psiloconcha	0.50	24.00
Backbone	Psiloconcha	1.00	25.00
Backbone	Psiloconcha	1.00	
Backbone	Rhytimya	1.00	19.00
Backbone	Rhytimya	1.00	11.50
Backbone	Rhytimya	1.00	19.00
Backbone	Rhytimya	1.00	21.00
Backbone	Sinuites	1.00	8.50
Backbone	Sinuites	1.00	14.00
Backbone	Sinuites	1.00	17.00
Backbone	Sinuites	1.00	18.00
Backbone	Sinuites	1.00	22.25
Backbone	Sinuites	1.00	7.00
Backbone	Sinuites	1.00	8.00
Backbone	Sinuites	1.00	8.00
Backbone	Sinuites	1.00	10.00
Backbone	Sinuites	1.00	10.00
Backbone	Sinuites	1.00	11.00
Backbone	Sinuites	1.00	13.00
Backbone	Sinuites	1.00	14.00
Backbone	Sinuites	1.00	15.00
Backbone	Sinuites	1.00	15.00

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
Backbone	1.20	1.60
Backbone	4.00	
Backbone		5.00
Backbone		6.00
Backbone	5.00	
Backbone		4.30
Backbone	3.80	3.30
Backbone	4.50	
Backbone	3.50	
Backbone	1.50	
Backbone		4.00
Backbone	5.00	
Backbone	3.50	
Backbone		5.00
Backbone		4.00
Backbone		3.50
Backbone		4.00
Backbone		4.00
Backbone	1.50	
Backbone	3.00	
Backbone	3.00	
Backbone	3.00	
Backbone		3.50
Backbone		6.00
Backbone	2.00	
Backbone		1.00
Backbone	3.00	
Backbone	2.00	
Backbone	3.00	
Backbone	4.00	
Backbone Upper		4.90
Backbone Uppe	5.00	
Backbone Uppe	4.00	
Dornbusch	3.35	4.11
Dornbusch	3.68	2.90
Dornbusch	2.60	2.00
Dornbusch		6.68
Dornbusch		6.81
Russell Lower		4.36
Russell Lower	4.00	
Russell Lower	1.50	
Russell Lower		1.50
Russell Lower		2.50
Russell Lower	3.00	
Russell Lower	5.00	
Russell Lower	5.00	
Russell Lower		5.00
Russell Lower		2.50
E. Fk. Bl. Ck.	3.67	3.88
E. Fk. Bl. Ck.		2.31
E. Fk. Bl. Ck.		2.48
E. Fk. Bl. Ck.	1.93	
E. Fk. Bl. Ck.	1.76	
E. Fk. Bl. Ck.		3.60

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Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
Backbone	Sinuites	1.00	16.00
Backbone	Sinuites	1.00	17.00
Backbone	Sinuites	1.00	18.00
Backbone	Sinuites	1.00	12.00
Backbone	Sinuites	1.00	14.00
Backbone	Whiteavesia	0.50	17.00
Back. Upper	Ambonychia	1.00	25.00
Back. Upper	Ambonychia	0.50	43.25
Back. Upper	Isotelus	1.00	29.00
Back. Upper	Modiolopsis	0.50	35.00
Back. Upper	Modiolopsis	1.00	37.00
Back. Upper	Technophorus	1.00	7.50
Back. Upper	Trematis	0.50	9.50
Back. Upper	Trematis	0.50	10.00
Back. Upper	Trematis	0.50	12.50
Back. Upper	Trematis	0.50	13.00
Back. Upper	Trematis	0.50	15.00
Back. Upper	Trematis	0.50	16.10
Back. Upper	Trematis	0.50	16.80
Back. Upper	Trematis	0.50	19.50
Back. Upper	Trematis	0.50	22.00
Back. Upper	Treptoceras	1.00	20.00
Dornbusch	Caritodens	0.50	3.30
Dornbusch	Caritodens	0.50	8.00
Dornbusch	Caritodens	0.50	8.00
Dornbusch	Caritodens	0.50	9.30
Dornbusch	Caritodens	0.50	9.60
Dornbusch	Caritodens	0.50	3.35
Dornbusch	Caritodens	0.50	7.00
Dornbusch	Caritodens	0.50	7.50
Dornbusch	Modiolopsis	0.50	76.00
Dornbusch	Psiloconcha	1.00	26.00
Russell Lower	Cleidophorus	0.50	3.40
Russell Lower	Cleidophorus	0.50	4.30
Russell Lower	Cleidophorus	0.50	5.50
Russell Lower	Cleidophorus	0.50	5.50
Russell Lower	Cleidophorus	0.50	8.00
Russell Lower	Cleidophorus	0.50	8.50
Russell Lower	Cleidophorus	0.50	9.00
Russell Lower	Cleidophorus	0.50	9.00
Russell Lower	Cleidophorus	0.50	9.50
Russell Lower	Cleidophorus	0.50	12.50
Russell Lower	Cleidophorus	0.50	13.50
Russell Lower	Cuneamya	1.00	29.00
Russell Lower	Psiloconcha	0.50	10.00
Russell Lower	Psiloconcha	0.50	11.30
Russell Lower	Psiloconcha	0.50	17.00
Russell Lower	Psiloconcha	0.50	17.00
Russell Lower	Psiloconcha	0.50	21.00
Russell Lower	Psiloconcha	0.50	21.00
Russell Lower	Rhytimya	1.00	22.50
E. Fk. Bl. Cr.	Ambonychia	0.50	15.00
E. Fk. Bl. Cr.	Ambonychia	0.50	28.00
E. Fk. Bl. Cr.	Ambonychia	0.50	30.00
E. Fk. Bl. Cr.	Caritodens	0.50	12.10
E. Fk. Bl. Cr.	Caritodens	0.50	14.00
E. Fk. Bl. Cr.	Cleidophorus	0.50	12.00

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
E. Fk. Bl. Ck.	2.50	
E. Fk. Bl. Ck.	2.50	
E. Fk. Bl. Ck.		6.00
E. Fk. Bl. Ck.		9.00
E. Fk. Bl. Ck.		6.00
E. Fk. Bl. Ck.		6.00
E. Fk. Bl. Ck.	5.00	
E. Fk. Bl. Ck.	7.00	
E. Fk. Bl. Ck.	4.00	
E. Fk. Bl. Ck.	4.00	
E. Fk. Bl. Ck.		7.00
E. Fk. Bl. Ck.		3.00
E. Fk. Bl. Ck.		7.00
E. Fk. Bl. Ck.		10.00
E. Fk. Bl. Ck.	6.00	
E. Fk. Bl. Ck.	2.50	
E. Fk. Bl. Ck.	3.00	
E. Fk. Bl. Ck.	3.00	
E. Fk. Bl. Ck.	6.00	
E. Fk. Bl. Ck.	6.00	
E. Fk. Bl. Ck.		5.00
E. Fk. Bl. Ck.		3.50
E. Fk. Bl. Ck.		11.00
E. Fk. Bl. Ck.		2.00
E. Fk. Bl. Ck.		4.00
E. Fk. Bl. Ck.		3.00
E. Fk. Bl. Ck.		9.00
E. Fk. Bl. Ck.		8.00
E. Fk. Bl. Ck.		8.00
E. Fk. Bl. Ck.		4.00
E. Fk. Bl. Ck.	9.62	10.21
E. Fk. Bl. Ck.		10.84
Russell Middle		5.46
Russell Middle		5.99
Russell Middle	5.01	
Russell Middle	4.57	4.69
Russell Middle	7.50	
Russell Middle	5.84	
Russell Middle	5.71	6.84
Russell Middle	7.44	
Russell Middle	7.60	
Russell Middle		3.86
Russell Middle	3.83	4.08
Russell Middle	6.92	7.13
Russell Middle	7.03	6.73
Russell Middle	8.45	
Russell Middle	7.68	7.64
Russell Middle	4.14	
Russell Middle	3.58	
Russell Middle	5.86	5.86
Russell Middle	5.90	5.33
Russell Middle	7.75	
Russell Middle		4.24
Russell Middle		4.20
Russell Middle	7.92	8.89
Russell Middle	7.88	
Russell Middle	5.90	7.40
Russell Middle		4.44
Russell Middle	4.77	4.85
Russell Middle	8.73	

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Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
E. Fk. Bl. Cr.	Cleidophorus	0.50	19.00
E. Fk. Bl. Cr.	Corallidomus	0.50	17.00
E. Fk. Bl. Cr.	Corallidomus	1.00	45.60
E. Fk. Bl. Cr.	Corallidomus	1.00	47.00
E. Fk. Bl. Cr.	Corallidomus	0.50	48.50
E. Fk. Bl. Cr.	Cuneamya	0.50	13.00
E. Fk. Bl. Cr.	Cuneamya	0.50	24.50
E. Fk. Bl. Cr.	Cuneamya	0.50	26.00
E. Fk. Bl. Cr.	Cymatonota	0.50	40.00
E. Fk. Bl. Cr.	Deceptrix	0.50	7.50
E. Fk. Bl. Cr.	Flexicalymene	0.50	3.60
E. Fk. Bl. Cr.	Psiloconcha	0.50	4.75
E. Fk. Bl. Cr.	Psiloconcha	0.50	8.50
E. Fk. Bl. Cr.	Psiloconcha	0.50	18.00
E. Fk. Bl. Cr.	Psiloconcha	0.50	23.00
E. Fk. Bl. Cr.	Psiloconcha	0.50	23.00
E. Fk. Bl. Cr.	Rhytimya	1.00	27.00
E. Fk. Bl. Cr.	Sinuites	1.00	21.50
Russell Middle	Ambonychia	0.50	60.00
Russell Middle	Ambonychia	0.50	42.00
Russell Middle	Ambonychia	0.50	54.00
Russell Middle	Ambonychia	1.00	31.00
Russell Middle	Ambonychia	1.00	49.00
Russell Middle	Ambonychia	1.00	45.00
Russell Middle	Ambonychia	1.00	23.00
Russell Middle	Ambonychia	1.00	46.00
Russell Middle	Ambonychia	0.50	37.00
Russell Middle	Ambonychia	0.50	61.00
Russell Middle	Ambonychia	0.50	27.00
Russell Middle	Ambonychia	1.00	60.00
Russell Middle	Ambonychia	0.50	45.00
Russell Middle	Ambonychia	1.00	35.30
Russell Middle	Ambonychia	1.00	55.00
Russell Middle	Ambonychia	0.50	55.00
Russell Middle	Ambonychia	1.00	39.30
Russell Middle	Ambonychia	1.00	5.25
Russell Middle	Ambonychia	0.50	32.00
Russell Middle	Ambonychia	0.50	17.00
Russell Middle	Ambonychia	0.50	24.50
Russell Middle	Ambonychia	0.50	40.00
Russell Middle	Ambonychia	0.50	34.00
Russell Middle	Ambonychia	0.50	23.50
Russell Middle	Ambonychia	0.50	32.50
Russell Middle	Ambonychia	0.50	28.00
Russell Middle	Ambonychia	0.50	32.00
Russell Middle	Ambonychia	0.50	30.00
Russell Middle	Ambonychia	0.50	30.00
Russell Middle	Ambonychia	0.50	40.00
Russell Middle	Ambonychia	1.00	29.00
Russell Middle	Ambonychia	1.00	43.00
Russell Middle	Ambonychia	1.00	52.00
Russell Middle	Ambonychia	1.00	46.00
Russell Middle	Caritodens	0.50	8.50
Russell Middle	Caritodens	0.50	15.75
Russell Middle	Caritodens	0.50	12.00
Russell Middle	Caritodens	0.50	15.00
Russell Middle	Caritodens	0.50	17.00
Russell Middle	Caritodens	0.50	17.70
Russell Middle	Cleidophorus	0.50	13.50
Russell Middle	Cleidophorus	0.50	12.60

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
Russell Middle		4.77
Russell Middle		4.69
Russell Middle	6.01	7.63
Russell Middle	5.56	7.56
Russell Middle		7.55
Russell Middle	5.58	7.42
Russell Middle	6.01	6.92
Russell Middle		9.32
Russell Middle		10.43
Russell Middle	6.48	8.18
Russell Middle	6.22	7.89
Russell Middle		6.07
Russell Middle		6.60
Russell Middle	3.47	
Russell Middle	3.81	
Russell Middle	8.25	
Russell Middle	4.11	4.21
Russell Middle		3.75
Russell Middle		5.74
Russell Middle		6.29
Russell Middle	3.53	3.04
Russell Middle		3.78
Russell Middle		4.87
Russell Middle		5.00
Russell Middle		3.42
Russell Middle		3.78
Russell Middle	4.63	4.39
Russell Middle	4.59	5.74
Russell Middle		9.65
Russell Middle		9.49
Russell Middle	6.45	6.83
Russell Middle		7.03
Russell Middle		6.68
Russell Middle		6.40
Russell Middle	5.90	6.42
Russell Middle	5.56	6.15
Russell Middle		6.78
Russell Middle		6.52
Russell Middle		10.41
Russell Middle		10.76
Russell Middle		9.16
Russell Middle		9.09
Russell Middle		9.34
Russell Middle		9.52
Russell Middle		7.69
Russell Middle		6.57
Russell Middle		7.04
Russell Middle		7.87
Russell Middle		7.62
Russell Middle		7.67
Russell Middle		7.56
Russell Middle		
Russell Middle	2.20	3.60
Russell Middle	3.64	3.18
Russell Middle	6.85	
Russell Middle	6.95	
Russell Middle		6.90
Russell Middle		8.97
Russell Middle		
Russell Middle		
Russell Middle	6.62	8.59

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Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
Russell Middle	Cleidophorus	0.50	11.00
Russell Middle	Cleidophorus	0.50	6.00
Russell Middle	Cleidophorus	0.50	14.80
Russell Middle	Cleidophorus	0.50	11.00
Russell Middle	Corallidomus	1.00	35.00
Russell Middle	Corallidomus	1.00	41.00
Russell Middle	Corallidomus	1.00	52.30
Russell Middle	Corallidomus	1.00	46.00
Russell Middle	Corallidomus	1.00	50.50
Russell Middle	Corallidomus	1.00	56.80
Russell Middle	Corallidomus	1.00	45.00
Russell Middle	Corallidomus	0.50	17.50
Russell Middle	Corallidomus	1.00	45.00
Russell Middle	Corallidomus	1.00	56.00
Russell Middle	Corallidomus	1.00	48.00
Russell Middle	Corallidomus	1.00	48.50
Russell Middle	Corallidomus	1.00	47.50
Russell Middle	Corallidomus	0.50	28.00
Russell Middle	Corallidomus	0.50	44.50
Russell Middle	Corallidomus	1.00	51.00
Russell Middle	Corallidomus	1.00	46.00
Russell Middle	Corallidomus	1.00	27.50
Russell Middle	Corallidomus	1.00	55.00
Russell Middle	Corallidomus	1.00	38.00
Russell Middle	Corallidomus	1.00	50.50
Russell Middle	Corallidomus	0.50	37.00
Russell Middle	Corallidomus	1.00	32.00
Russell Middle	Corallidomus	0.50	22.00
Russell Middle	Corallidomus	0.50	27.00
Russell Middle	Corallidomus	0.50	27.50
Russell Middle	Corallidomus	0.50	37.50
Russell Middle	Corallidomus	1.00	37.00
Russell Middle	Corallidomus	1.00	37.00
Russell Middle	Cuneamya	1.00	32.75
Russell Middle	Cuneamya	0.50	16.25
Russell Middle	Cuneamya	0.50	26.50
Russell Middle	Cuneamya	0.50	33.25
Russell Middle	Cuneamya	0.50	19.00
Russell Middle	Cuneamya	1.00	23.00
Russell Middle	Cuneamya	0.50	21.25
Russell Middle	Cuneamya	0.50	41.00
Russell Middle	Cymatonota	0.50	32.00
Russell Middle	Cymatonota	0.50	28.50
Russell Middle	Cymatonota	1.00	35.00
Russell Middle	Cymatonota	1.00	31.00
Russell Middle	Deceptrix	0.50	5.00
Russell Middle	Deceptrix	1.00	6.80
Russell Middle	Modiolopsis	0.50	25.00
Russell Middle	Pholadomorpha	0.50	60.00
Russell Middle	Pholadomorpha	1.00	59.00
Russell Middle	Pholadomorpha	1.00	56.00
Russell Middle	Pholadomorpha	1.00	74.00
Russell Middle	Psilconcha	1.00	29.00
Russell Middle	Psiloconcha	0.50	7.00
Russell Middle	Psiloconcha	1.00	23.50
Russell Middle	Psiloconcha	1.00	21.00
Russell Middle	Psiloconcha	0.50	25.00
Russell Middle	Psiloconcha	0.50	17.50
Russell Middle	Psiloconcha	0.50	20.00
Russell Middle	Psiloconcha	1.00	20.00
Russell Middle	Psiloconcha	0.50	24.00

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
Russell Middle	6.89	8.53
Russell Middle	8.94	9.29
Russell Middle	5.00	
Russell Middle	3.00	
Russell Middle	7.00	
Russell Middle	4.00	
Russell Middle	6.00	
Russell Middle	7.00	
Russell Middle	7.00	
Russell Middle	6.00	
Russell Middle	7.00	
Russell Middle	7.00	
Russell Middle		9.00
Russell Middle		10.00
Russell Middle		7.00
Russell Middle		9.00
Russell Middle		9.00
Russell Middle		9.00
Russell Middle	5.00	
Russell Middle	8.00	
Russell Middle	7.00	
Russell Middle	4.00	
Russell Middle	8.00	
Russell Middle		9.00
Russell Middle		8.00
Russell Middle		11.00
Russell Middle		8.00
Russell Middle	7.00	
Russell Middle	3.00	
Russell Middle	3.00	
Russell Middle	5.00	
Russell Middle	5.00	
Russell Middle	5.00	
Russell Middle	9.00	
Russell Middle		6.00
Russell Middle		6.00
Russell Middle		5.00
Russell Middle		7.00
Russell Middle		6.00
Russell Middle		9.00
Russell Middle	3.00	
Russell Middle	6.00	
Russell Middle	6.00	
Russell Middle	8.00	
Russell Middle	4.00	
Russell Middle	8.00	
Russell Middle	4.00	
Russell Middle	4.00	
Russell Middle		6.00
Russell Middle		5.00
Russell Middle		7.00
Russell Middle	6.81	6.90
Russell Middle	7.01	6.48
Russell Middle	5.89	5.15
Russell Middle	5.60	5.33
Russell Middle	10.29	8.39
Russell Middle	10.57	8.17
Russell Middle	7.79	7.94
Russell Middle	7.87	7.86
Russell Middle		10.85
Russell Middle		11.04

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Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
Russell Middle	Psiloconcha	0.50	20.00
Russell Middle	Psiloconcha	0.50	28.00
Russell Middle	Psiloconcha	0.50	20.00
Russell Middle	Psiloconcha	1.00	17.00
Russell Middle	Psiloconcha	1.00	21.00
Russell Middle	Psiloconcha	1.00	28.00
Russell Middle	Psiloconcha	1.00	22.50
Russell Middle	Psiloconcha	0.50	15.00
Russell Middle	Psiloconcha	0.50	18.00
Russell Middle	Psiloconcha	0.50	25.00
Russell Middle	Psiloconcha	0.50	26.00
Russell Middle	Psiloconcha	0.50	27.00
Russell Middle	Rhytimya	0.50	19.00
Russell Middle	Rhytimya	0.50	20.00
Russell Middle	Rhytimya	0.50	22.00
Russell Middle	Rhytimya	0.50	35.00
Russell Middle	Rhytimya	0.50	11.50
Russell Middle	Sinuites	1.00	43.00
Russell Middle	Sinuites	1.00	32.00
Russell Middle	Sinuites	1.00	38.00
Russell Middle	Sinuites	1.00	16.10
Russell Middle	Sinuites	1.00	31.00
Russell Middle	Sinuites	1.00	23.50
Russell Middle	Sinuites	1.00	26.00
Russell Middle	Sinuites	1.00	17.00
Russell Middle	Sinuites	1.00	29.00
Russell Middle	Sinuites	1.00	24.00
Russell Middle	Sinuites	1.00	33.70
Russell Middle	Sinuites	1.00	36.00
Russell Middle	Sinuites	1.00	24.00
Russell Middle	Sinuites	1.00	26.00
Russell Middle	Sinuites	1.00	37.00
Russell Middle	Sinuites	1.00	22.00
Russell Middle	Sinuites	1.00	30.00
Russell Middle	Whiteavsia	1.00	35.50
Russell Top	Ambonychia	0.50	25.00
Russell Top	Ambonychia	0.50	28.00
Russell Top	Corallidomus	0.50	52.00
Russell Top	Cuneamya	0.50	20.50
Russell Top	Cuneamya	0.50	26.50
Russell Top	Cuneamya	0.50	30.13
Russell Top	Cuneamya	0.50	33.00
Russell Top	Cuneamya	1.00	50.00
Russell Top	Cyrtolites	1.00	15.00
Russell Top	Psiloconcha	0.50	13.50
Russell Top	Psiloconcha	1.00	18.00
Russell Top	Psiloconcha	0.50	19.50
Russell Top	Psiloconcha	0.50	20.00
Russell Top	Psiloconcha	0.50	21.00
Russell Top	Psiloconcha	0.50	25.00
Russell Top	Psiloconcha	0.50	32.00
Russell Top	Sinuites	1.00	34.00
Russell Top	Sinuites	0.50	34.00
Russell Top	Whiteavesia	0.50	22.10
Russell Top	Ambonychia	1.00	24.25
Russell Top	Ambonychia	0.50	48.00
Russell Top	Ambonychia	1.00	48.00
Russell Top	Ambonychia	0.50	60.00
Russell Top	Cleidophorus	0.50	10.00
Russell Top	Cleidophorus	0.50	12.50

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
Russell Middle		8.97
Russell Middle		8.90
Russell Middle		5.72
Russell Middle	5.68	5.96
Russell Middle		6.93
Russell Middle		6.80
Russell Middle		5.35
Russell Middle		6.46
Russell Middle		7.81
Russell Middle	6.50	7.78
Russell Middle		6.50
Russell Middle		6.27
Russell Middle	8.40	8.33
Russell Middle	3.02	2.79
Russell Top		6.09
Russell Top		4.82
Russell Top	5.49	
Russell Top	5.61	
Russell Top		4.64
Russell Top	3.00	
Russell Top	6.00	
Russell Top	7.00	
Russell Top		7.00
Russell Top		4.00
Russell Top	5.50	
Russell Top	4.00	
Russell Top	8.00	
Russell Top	7.00	
Russell Top	6.00	
Russell Top		7.00
Russell Top	5.00	
Russell Top		7.00
Russell Top		5.00
Russell Top	3.00	
Russell Top	7.00	
Hannah Creek	5.00	
Hannah Creek	4.64	
Hannah Creek	5.27	5.05
Hannah Creek		6.70
Hannah Creek	6.65	6.45
Hannah Creek		4.59
Hannah Creek	5.72	4.83
Hannah Creek		6.13
Hannah Creek	4.96	
Hannah Creek		3.69
Hannah Creek	5.94	6.47
Hannah Creek		5.43
Hannah Creek		7.63
Hannah Creek		2.81
Hannah Creek		2.56
Hannah Creek	1.16	1.01
Hannah Creek		7.30
Hannah Creek	5.38	7.72
Hannah Creek		8.25
Hannah Creek		6.83
Hannah Creek	5.74	6.59
Hannah Creek	6.24	7.67
Hannah Creek	4.62	4.22
Hannah Creek	4.95	4.97

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Mollusk Measurements

Locality	Genus	#Individuals	Measurement (mm)
Russell Top	Corallidomus	0.50	20.00
Russell Top	Corallidomus	0.50	40.00
Hannah Creek	Ambonychia	0.50	35.00
Hannah Creek	Ambonychia	0.50	45.00
Hannah Creek	Ambonychia	0.50	45.00
Hannah Creek	Ambonychia	1.00	46.00
Hannah Creek	Ambonychia	0.50	47.00
Hannah Creek	Ambonychia	0.50	50.00
Hannah Creek	Caritodens	0.50	13.00
Hannah Creek	Caritodens	0.50	65.00
Hannah Creek	Caritodens	0.50	70.00
Hannah Creek	Corallidomus	0.50	43.50
Hannah Creek	Corallidomus	0.50	51.00
Hannah Creek	Corallidomus	1.00	38.00
Hannah Creek	Corallidomus	1.00	47.00
Hannah Creek	Corallidomus	0.50	49.50
Hannah Creek	Cuneamya	0.50	15.50
Hannah Creek	Cuneamya	1.00	16.50
Hannah Creek	Cuneamya	0.50	38.00
Hannah Creek	Cuneamya	1.00	24.00
Hannah Creek	Cuneamya	0.50	50.00
Hannah Creek	Cymatonota	1.00	58.00
Hannah Creek	Cymatonota	1.00	26.00
Hannah Creek	Cymatonota	1.00	55.00
Hannah Creek	Cyrtolites	1.00	13.50
Hannah Creek	Cyrtolites	1.00	15.00
Hannah Creek	Modiolopsis	0.50	37.00
Hannah Creek	Modiolopsis	0.50	48.00
Hannah Creek	Modiolopsis	1.00	65.50
Hannah Creek	Pholadomorph	1.00	64.00
Hannah Creek	Rhytimya	1.00	23.00
Hannah Creek	Rhytimya	1.00	31.00
Clear Fork	Caritodens	0.50	7.75
Clear Fork	Caritodens	0.50	14.00
Clear Fork	Caritodens	0.50	16.00
Clear Fork	Caritodens	0.50	20.00
Clear Fork	Deceptrix	1.00	7.50
Clear Fork	Deceptrix	0.50	8.50
Clear Fork	Deceptrix	0.50	10.50
Clear Fork	Deceptrix	0.50	10.50
Clear Fork	Deceptrix	1.00	12.00
Clear Fork	Deceptrix	0.50	13.50
Clear Fork	Psiloconcha	0.50	12.50

***Flexicalymene* Measurements**

Locality	Glabella Length (mm)	Pygidium Length (mm)
Hannah Creek		
Hannah Creek	3.04	3.20
Hannah Creek	6.50	
Hannah Creek		5.99
Hannah Creek	6.56	
Hannah Creek	1.46	1.62
Hannah Creek		6.20
Hannah Creek		7.06
Hannah Creek	3.40	3.51
Hannah Creek	3.07	3.28
Hannah Creek	6.98	
Hannah Creek		2.83
Hannah Creek		2.94
Hannah Creek	6.12	6.78
Hannah Creek		6.61
Hannah Creek	5.61	
Hannah Creek		9.01
Hannah Creek		6.00
Hannah Creek	6.26	
Hannah Creek	5.79	
Hannah Creek		7.03
Hannah Creek		5.76
Hannah Creek		7.65
Clear Fork		1.71
Clear Fork		2.16
Clear Fork		2.61
Clear Fork	3.22	
Clear Fork	3.13	
Clear Fork	1.52	
Clear Fork		2.38
Clear Fork		2.03
Clear Fork		2.08
Clear Fork	2.00	
Clear Fork	1.50	
Clear Fork	2.00	
Clear Fork	2.50	
Clear Fork	2.23	2.36
Clear Fork	2.00	
Clear Fork		2.00
Clear Fork	3.00	
Clear Fork	2.50	
Clear Fork	2.81	2.00

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Appendix 5

Rock Volume, Ichnofabric, and Taphonomic Data

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Appendix 5

Rock Volume, Ichnologic, and Taphonomic Data

Estimation of Rock Volume Excavated

Site	Sample	Position	Volume (cm^3)
Backbone Creek	1a	135-150 cm	4,800
Backbone Creek	1b	0-30 cm	3,600
Dornbusch	1a	20-30 cm	37,800
Dornbusch	1b	0-20 cm	50,400
Dornbusch	2a	20-40 cm	39,600
Dornbusch	2b	0-20 cm	42,000
Russell Lower	1	0-40 cm	5,605
East Fork Blue Creek	1a		5,040
East Fork Blue Creek	1b		1,500
Russell Middle	1a	160-180 cm	9,900
Russell Middle	1b	140-160 cm	10,230
Russell Middle	1c	115-140 cm	14,145
Russell Middle	1d	100-112 cm	7,560
Russell Middle	1e	80-100 cm	7,900
Russell Middle	1f	70-80 cm	3,150
Russell Middle	1g	50-70 cm	7,000
Russell Middle	1h	30-50 cm	5,200
Russell Middle	1i	0-20 cm	8,685
Russell Top	1a	10-13 cm	1,440
Russell Top	1b	0-10 cm	13,875
Hannah Creek	1a	30-50 cm	21,250
Hannah Creek	1b	0-30 cm	15,600
Hannah Creek	2a	30-50 cm	18,000
Hannah Creek	2b	0-30 cm	14,400
Clear Fork	1a	50-60 cm	4,800
Clear Fork	1b	0-50 cm	14,580

Burrow Diameters

Site	Formation	Max. Diameter	Mean Diameter	Standard Deviation
Kentucky Rt. 17	Kope	4.25	2.41	0.82
Kentucky Rt. 17	Kope	5.06	2.83	1.15
Kentucky Rt. 17	Kope	2.88	1.71	0.61
Kentucky Rt. 17	Kope	2.65	1.41	0.49
Backbone Creek	Kope	1.98	1.13	0.42
Backbone Creek	Kope	2.83	1.64	0.64
Backbone Creek	Kope	2.98	1.89	0.66
Backbone Creek	Kope	2.65	1.07	0.54
Backbone Creek	Kope	1.98	1.16	0.38

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Burrow Diameters

Site	Formation	Max. Diameter	Mean Diameter	Standard Deviation
Backbone Creek	Kope	4.54	2.41	0.62
Backbone Creek	Kope	1.79	0.82	0.38
Backbone Creek	Kope	4.21	2.21	0.89
Other Backbone Mudstones	Fairview	2.23	1.49	0.48
Other Backbone Mudstones	Fairview	2.69	1.45	0.58
Other Backbone Mudstones	Fairview	3.65	1.14	0.66
Other Backbone Mudstones	Fairview	3.55	1.43	0.64
Dornbusch	Corryville	1.77	0.88	0.39
Dornbusch	Corryville	1.77	1.02	0.43
Dornbusch	Corryville	1.27	0.79	0.31
Dornbusch	Corryville	1.80	1.17	0.39
Monroe	Corryville	4.03	1.85	0.89
Monroe	Corryville	2.42	1.36	0.39
Russell Lower	Waynesville	1.54	1.12	0.31
Russell Lower	Waynesville	1.98	1.04	0.38
Russell Lower	Waynesville	1.42	0.82	0.28
Russell Lower	Waynesville	8.24	2.20	1.77
Russell Middle	Waynesville	2.56	1.73	0.56
Russell Middle	Waynesville	6.66	2.94	2.70
Russell Middle	Waynesville	3.00	2.08	0.44
Russell Top	Waynesville	2.50	1.67	0.45
Russell Top	Waynesville	3.31	3.42	6.22
Russell Top	Waynesville	3.06	1.52	0.69
Russell Top	Waynesville	3.06	1.70	0.75
Russell Top	Waynesville	1.04	0.74	0.22
Hannah Creek	Waynesville	2.04	1.37	0.35
Hannah Creek	Waynesville	4.82	3.29	1.22
Hannah Creek	Waynesville	2.17	1.28	0.55
Hannah Creek	Waynesville	5.63	3.26	1.36
Hannah Creek	Waynesville	2.32	1.38	0.53
Hannah Creek	Waynesville	4.87	2.17	0.97
Hannah Creek	Waynesville	4.26	1.52	0.78
Hannah Creek	Waynesville	6.24	2.49	1.48
Hannah Creek	Waynesville	4.24	3.38	0.65
Hannah Creek	Waynesville	1.42	0.90	0.30
Hannah Creek	Waynesville	1.82	1.23	0.40
Hannah Creek	Waynesville	4.67	3.35	0.77
Hannah Creek	Waynesville	1.33	0.68	0.32
Clear Fork	Liberty	3.56	2.81	0.61
Clear Fork	Liberty	8.22	4.91	1.89
Clear Fork	Liberty	6.37	3.88	1.38

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Taphonomic Data

Articulation of *Flexicalymene*

Site	Prone	Rolled	Cranidia	Pygidia	% Articulated
Backbone Creek	4	0	16	11	20.0%
Backbone Upper	0	0	2	1	0.0%
Dornbusch	4	1	8	6	38.5%
Russell Lower	0	1	5	8	11.1%
Russell Middle	18	4	207	203	9.6%
Russell Top	2	0	11	8	15.4%
E. Fk. Blue Creek	1	4	17	29	14.7%
Hannah Creek	25	7	48	65	33.0%
Clear Fork	1	2	8	3	27.3%

Articulation of Mollusks

(Note: Due to inconsistencies in collecting, number of individuals listed here will not always add to total from site)

Site		*Ambonychia*	*Caritodens*	*Cleidophorus*	*Corallidomus*	*Cuneamya*	*Cymatonota*	*Deceptrix*	*Modiolopsis*	*Psiloconcha*	*Pholadomorpha*	*Rhytimya*
Backbone Creek	Articulated	0	0	0	0	0	1	2	1	4	0	5
Backbone Creek	Single Valves	5	1	9	0	1	1	13	1	7	0	0
Backbone Upper	Articulated	1	0	0	0	0	0	0	1	0	0	0
Backbone Upper	Single Valves	3	0	0	0	0	0	0	1	0	0	0
Dornbusch	Articulated	0	2	0	0	0	0	0	0	1	0	0
Dornbusch	Single Valves	0	6	0	0	0	0	0	1	0	0	0
Russell Lower	Articulated	0	0	1	0	1	0	0	0	0	0	1
Russell Lower	Single Valves	0	0	10	0	0	0	0	0	7	0	0
Russell Middle	Articulated	11	0	0	43	2	1	0	0	10	1	1
Russell Middle	Single Valves	38	12	7	34	7	3	0	0	15	2	6
Russell Top	Articulated	2	0	2	0	1	0	0	0	0	0	1
Russell Top	Single Valves	7	0	2	3	8	1	0	0	8	0	1
E. Fk. Blue Creek	Articulated	1	0	0	3	0	0	1	0	0	0	2
E. Fk. Blue Creek	Single Valves	5	2	2	3	6	1	1	0	10	0	1
Hannah Creek	Articulated	1	0	0	3	2	5	0	1	0	2	2
Hannah Creek	Single Valves	9	6	0	5	5	0	0	0	2	2	0
Clear Fork	Articulated	0	0	0	0	0	0	3	0	0	0	0
Clear Fork	Single Valves	1	9	0	0	0	0	7	0	0	0	0

Appendix 6

Mineralogic Composition Data

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Appendix 6

X-Ray Powder Diffraction Data

Maximum counts (cps) for each mineral are listed
Data not calibrated to a known standard

Key

Mineral	**d-spacing value (Å)**
Chlorite	14.0-14.3
Illite	9.6-10.1
Quartz	3.34
Calcite	3.032
Dolomite	2.9
Pyrite	1.633
Feldspar	3.74-3.79

		Mineral						
Locality	**Sample**	**Chlorite**	**Illite**	**Quartz**	**Calcite**	**Dolomite**	**Pyrite**	**Feldspar**
Clear Fork	CF1 sample 1	169	248	1576	1180	459	88	93
	CF1 sample 4	199	305	1838	2202	607	no peak	no peak
	CF1 sample 3	191	333	2039	596	576	no peak	112
	CF1 sample 2	232	418	1888	1157	1079	81	81
Oldenberg	Oldenberg sample 3	200	340	2091	635	663	996	98
	Oldenberg sample1b	183	332	1860	667	699	84	no peak
	Oldenberg sample 1a	202	306	1848	496	581	100	no peak
Hannah Creek	hc site1 sample 2	205	333	1821	757	570	74	112
	hc site 9 sample 10	194	256	2163	437	448	~84	96
	hc site 7 sample 8	211	385	2039	372	615	127	110
	hc site 7 sample 6	245	414	1994	351	405	105	105
	hc site 7 sample 6b	257	455	2114	370	501	94	101
	hc site 1 sample 1	268	453	1988	391	569	107	106
	hc site 7 sample 9	236	394	2370	235	457	~90	110
	hc site 1 sample 4	210	357	2191	382	498	~85	110
	hc site 1 sample 3	202	336	1717	1055	533	87	92
	hc1 sample 5	189	323	2013	246	424	100	no peak
Salt Creek	Salt Creek sample 1	196	311	2192	682	738	106	109
	Salt Creek sample 2	220	350	2276	759	778	108	102
	Salt Creek sample 3	181	255	1979	405	621	116	92
Russell Top	RB2:17	223	369	2049	441	135	142	102
	RB2 sample 1B	236	347	2060	201	302	122	111
	RB2 sample 1A	270	455	2184	222	428	141	106
Bon Well Hill	BWH sample 2	250	466	2030	225	717	110	108
	BWH sample 4	222	321	1974	179	272	105	112
	BWH sample 1	257	370	1984	201	535	136	105
Russell Middle	RB1 *sample 5 no. 2*	273	486	2017	486	276	129	93
	RB1 sample 5	233	518	2164	730	456	134	103
	RB1:179	238	331	1812	545	136	103	107
	RB1 *sample 4*	255	388	2006	540	131	~95	*no peak*
	RB1 sample 3	267	478	2180	390	781	90	no peak
	RB1 sample 2	289	417	1821	287	749	105	111
	RB1 sample 1	242	419	1782	285	789	127	no peak
Russell Lower	RB3 sample 1b	214	319	1869	454	129	149	102
	RB3 sample 1	221	332	1897	460	159	133	113
	RB3 sample 2	269	419	2013	309	314	142	113
	RB3 sample 3	214	353	2103	238	167	148	102
Mt. Orab	Mt. Orab sample 2a nodule	136	230	1302	1832	205	no peak	no peak
	Mt. Orab Kurt's sample	218	323	2181	299	242	85	111
	Mt. Orab sample 1	192	265	2258	689	535	96	98
	Mt. Orab sample 203	230	309	2297	544	324	98	103
Monroe	Monroe sample 1	207	273	2213	718	322	no peak	116
	Monroe sample 2 no. 2	188	256	2646	610	359	no peak	114
	Monroe sample 2	208	285	2158	712	365	60	120
Dornbusch	DB1:15	251	318	2254	163	256	no peak	121
	DB1:13	249	322	2555	167	360	no peak	114
	DB2 sample 4	239	349	2471	191	255	no peak	118
	DB2 sample 4 no. 2	228	286	2495	242	232	no peak	128
	DB site 2 sample 3	231	321	2539	179	243	126	138
	DB site 1 sample 2	256	355	2346	165	272	113	105
Orphanage Rd.	Orphanage Rd. sample 1	310	475	2186	220	114	no peak	no peak

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		Mineral						
Locality	**Sample**	**Chlorite**	**Illite**	**Quartz**	**Calcite**	**Dolomite**	**Pyrite**	**Feldspar**
	Orphanage Rd. sample 3	246	390	2537	306	126	no peak	119
	Orphanage Rd. sample 2	274	530	2684	252	185	no peak	122
Backbone Cree	Backbone sample 1A	220	358	2659	224	232	67	126
	Backbone sample 3A	318	593	2858	146	249	90	144
	BB1 sample 1	246	353	1939	164	117	117	79
	BB2 sample 1	212	342	1975	296	122	102	106
	Backbone sample 3B	207	292	2622	147	178	89	143
	BB2 sample 2	322	598	2232	278	163	94	no peak
	Backbone sample 4a	238	412	2221	116	126	101	116
	BB1 sample 2 no. 2	273	434	2106	217	113	105	no peak
	BB3	234	367	2580	360	195	71	131
	Backbone sample 2B	223	354	2551	182	363	93	99
	Backbone sample 1B	252	397	2347	194	235	111	124
	BB1 sample 2A	341	607	2198	203	138	100	105
	BB1 sample 3	389	731	2347	350	181	125	113
Second Creek	SC shale 1	140	168	1381	1660	203	79	104
	SC shale 3	199	284	2527	312	310	79	106
	SC sample 4B	294	515	2612	330	627	116	118
	SC sample 4A	215	286	2101	309	333	96	91
	SC shale 2	221	380	2688	269	466	90	108

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Appendix 7

Cluster Analysis Results

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Appendix 7

Cluster Analysis Results, Q-Mode

Percent transformation, range transformation, Quantified Dice coefficient of similarity

Key		Clustering		
Sample	Number	Low	High	Level of clustering
Orphanage	1	7	8	0.7802
Backbone 1	2	9	10	0.7899
Backbone 2	3	11	12	0.8853
Backbone Upper	4	16	17	0.7330
Reading A	5	18	25	0.6949
Reading B	6	20	21	0.7438
Springdale A	7	22	23	0.7074
Springdale B	8	26	28	0.7674
Harrison 12-13	9	29	30	0.6547
Harrison 14-16	10	1	2	0.5369
Dornbusch 1	11	6	7	0.7285
Dornbusch 2	12	11	24	0.6500
Russell Low	13	14	18	0.6433
East Fork Upper	14	19	20	0.6817
East Fork Lower	15	26	27	0.6981
Russell Middle A	16	6	9	0.7002
Russell Middle B	17	11	26	0.5957
Russell Middle C	18	16	19	0.6319
Bon Well Hill A	19	5	6	0.6676
Bon Well Hill B	20	15	16	0.6123
Bon Well Hill C	21	3	5	0.5972
Harpers Run	22	14	15	0.5421
US Rt 42	23	1	3	0.4314
Russell Top B	24	13	14	0.4629
Russell Top A	25	1	22	0.3406
Hannah Creek A	26	11	13	0.3759
Hannah Creek B	27	1	11	0.2599
Hannah Creek 3-7	28	1	29	0.1905
Clear Fork A	29	1	4	0.1703
Clear Fork B	30			

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Appendix 7

Cluster Analysis Results, R-Mode

Percent transformation, range transformation, Quantified Dice coefficient of similarity

Key		Clustering		
Genus	**Number**	**Low**	**High**	**Level of clustering**
Stromotoporoidea	1	1	2	0.7881
Tetradium	2	4	45	0.5648
Conularia	3	5	44	0.5344
Spatiopora	4	6	25	0.5940
Lingulid	5	7	10	0.4454
Trematis	6	17	18	1.0000
Rafinesquina	7	20	21	1.0000
Zygospira	8	24	48	1.0000
Hebertella	9	28	35	0.6382
Platystrophia	10	36	47	0.5856
Plectorthis	11	38	53	0.8566
? Brachiopod	12	40	41	0.9290
Sinuites	13	1	33	0.6361
Cyrtolites	14	3	49	0.5075
Liospira	15	6	31	0.4972
Loxoplucus	16	12	20	0.6886
Lophospira	17	13	37	0.5642
Ruedemannia	18	14	24	0.6004
Fusispira	19	17	19	1.0000
Sphenospira	20	34	36	0.5540
? Gastropod	21	40	43	0.8358
Treptoceras	22	1	22	0.5558
Trocholites	23	5	29	0.4612
? Cephalopod	24	12	52	0.6741
Technophorus	25	13	38	0.5242
Cleidophorus	26	17	23	1.0000
Deceptrix	27	30	39	0.5899
Ambonychia	28	1	32	0.4983
Caritodens	29	8	12	0.5381
Corallidomus	30	13	34	0.4439
Modiolopsis	31	15	27	0.4263
Orthodesma	32	17	42	1.0000
Pholadomorpha	33	30	40	0.4696
Cymatonota	34	8	9	0.2368
Psiloconcha	35	17	46	1.0000
Cuneamya	36	26	28	0.4321
Rhytimya	37	3	5	0.3749
Lyrodesma	38	13	26	0.3882
Whiteavesia	39	3	13	0.2798
Eridonychia	40	3	50	0.2351
Cycloconcha	41	7	11	0.2047
Cyrtodontula	42	3	15	0.2056
Obalinas	43	3	16	0.1769
Flexicalymene	44	3	6	0.1700
Platycorphe	45	3	7	0.1364
Homotelus	46	3	4	0.1226
Isotelus	47	1	3	0.0968
Amphilichas	48	1	30	0.0895
Ancienta	49	1	51	0.0379
Cornulites	50	1	14	0.0355
Iocrinus	51	1	8	0.0260
Cincinnaticrinus	52	1	17	0.0249
Hyolithes	53			

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Appendix 8

Factor Analysis Results

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Appendix 8

Factor Analysis Results

	Principle Factor Loadings						Varimax Factor Matrix, Rotated Factors			
Sample	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	lotated Factor 1	lotated Factor 2	lotated Factor 3	lotated Factor 4
Orphanage	0.4219	0.6477	-0.4131	-0.0513	0.0621	-0.0819	-0.0088	0.6558	-0.5807	0.0598
Backbone 1	0.3291	0.5350	-0.7339	0.1796	0.0501	-0.0686	-0.0366	0.3834	-0.9004	0.0794
Backbone 2	0.5992	0.6597	-0.1386	-0.1511	-0.0293	-0.1052	0.0998	0.8308	-0.3294	0.1663
Backbone Upper	0.2377	0.1906	0.0009	0.1669	0.4630	0.8017	-0.0063	0.1899	-0.1286	0.2609
Reading A	0.5434	0.6869	0.0997	-0.2058	-0.3206	0.0557	0.0258	0.8822	-0.0942	0.1778
Reading B	0.6231	0.6986	0.1504	-0.0342	-0.1804	0.0376	0.0064	0.8656	-0.1122	0.3715
Springdale A	0.6068	0.7004	0.2123	-0.0580	-0.1826	0.0648	-0.0075	0.8781	-0.0468	0.3658
Springdale B	0.5937	0.6990	0.0801	-0.0185	-0.2588	-0.0038	-0.0089	0.8352	-0.1769	0.3448
Harrison 12-13	0.6709	0.6445	0.0320	-0.1155	-0.1029	0.1060	0.1196	0.8636	-0.1907	0.2888
Harrison 14-16	0.7012	0.5758	0.1629	-0.0376	-0.1767	0.1894	0.1340	0.8127	-0.0816	0.4077
Dornbusch 1	0.7482	-0.5578	-0.1827	-0.1892	-0.1882	0.0745	0.9547	-0.0163	-0.0861	0.1450
Dornbusch 2	0.7333	-0.5607	-0.1839	-0.1543	-0.2066	0.1236	0.9339	-0.0403	-0.0946	0.1643
Russell Low	0.7790	-0.4094	-0.0613	-0.1748	0.0004	-0.0823	0.8630	0.1232	-0.0197	0.2201
East Fork Upper	0.8743	-0.2769	0.0178	-0.0435	0.1371	0.0805	0.7918	0.2270	-0.0317	0.4049
East Fork Lower	0.8470	0.0238	0.0728	0.3278	0.1123	-0.1448	0.4532	0.2977	-0.1583	0.7153
Russell Middle A	0.8220	-0.0627	0.2271	0.3181	0.1697	-0.0493	0.4664	0.2464	0.0101	0.7443
Russell Middle B	0.8176	-0.0127	0.2930	0.2830	0.3012	-0.1404	0.4352	0.3065	0.0691	0.7392
Russell Middle C	0.8580	-0.2248	0.1229	0.1116	-0.0800	-0.0448	0.6779	0.2101	0.0090	0.5572
Bon Well Hill A	0.8209	0.0994	0.2772	0.3064	0.0750	-0.0948	0.3647	0.3815	0.0202	0.7587
Bon Well Hill B	0.7526	-0.0597	0.2711	0.4409	0.0782	-0.0565	0.3659	0.1713	0.0239	0.8210
Bon Well Hill C	0.8822	-0.1811	0.1744	0.3099	-0.0437	-0.0676	0.5909	0.1807	-0.0158	0.7453
Harpers Run	0.4151	0.3539	0.1521	-0.5883	0.4923	-0.1779	0.2615	0.7329	0.1644	-0.1851
US Rt 42	0.5774	0.1485	0.1432	-0.5189	0.5421	-0.1226	0.4755	0.6240	0.1620	-0.0596
Russell Top B	0.8124	-0.4845	-0.0595	-0.0837	-0.2236	0.0304	0.8991	0.0446	-0.0314	0.3062
Russell Top A	0.8565	-0.4026	0.0405	0.0019	-0.0043	-0.0482	0.8350	0.1073	0.0088	0.4340
Hannah Creek A	0.7954	-0.5012	-0.1737	-0.1977	-0.0479	0.0342	0.9554	0.0541	-0.0960	0.1678
Hannah Creek B	0.7857	-0.4538	-0.2199	-0.2355	-0.0495	0.1134	0.9408	0.0945	-0.1373	0.1192
Hannah Creek 3-7	0.7858	-0.5283	-0.0980	-0.2066	-0.0439	0.0597	0.9560	0.0437	-0.0163	0.1808
Clear Fork A	0.2003	0.2811	-0.8618	0.2483	0.1927	-0.0720	0.0215	0.0815	-0.9572	0.0133
Clear Fork B	0.4806	-0.0161	-0.8487	0.1402	0.0575	-0.0192	0.4322	0.0354	-0.8828	0.0625

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Appendix 8

Factor Analysis Results

	Principal Factor Scores						Varimax Factor Score Matrix, Rotated Factors			
Genus	**Factor 1**	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**	**Factor 6**	**Rotated Factor 1**	**Rotated Factor 2**	**Rotated Factor 3**	**Rotated Factor 4**
Stromotoporoidea	0.004	0.006	0.007	-0.040	0.045	-0.023	0.033	-0.055	0.027	-0.126
Tetradium	0.002	0.002	0.003	-0.017	0.021	-0.009	0.056	-0.093	0.046	-0.194
Conularia	0.029	-0.014	0.006	-0.003	0.007	-0.004	-0.044	-0.230	-0.139	-0.101
Spaticpora	0.021	-0.012	0.018	0.021	0.031	-0.038	-0.078	-0.053	-0.234	0.034
Lingulid	0.716	-0.579	-0.148	-0.160	-0.237	0.083	-0.103	-0.058	-0.111	0.333
Trematis	0.067	0.055	0.032	0.093	0.237	0.820	0.050	-0.022	-0.019	-0.026
Rafinesquina	0.030	-0.007	-0.004	-0.030	-0.029	0.027	0.026	-0.132	0.009	-0.074
Zygospira	0.164	0.271	-0.884	0.237	0.179	-0.060	0.111	0.012	0.032	0.409
Hebertella	0.002	0.000	-0.017	0.004	0.002	-0.001	0.010	-0.025	0.027	0.212
Platystrophia	0.006	-0.002	-0.004	-0.015	-0.013	0.009	0.033	-0.216	0.075	-0.087
Plectorthis	0.003	0.009	0.003	-0.007	-0.016	0.004	0.105	-0.012	0.044	0.004
? Brachiopod	0.001	0.001	-0.013	0.005	0.004	-0.002	0.022	-0.017	0.033	0.330
Sinuites	0.335	0.673	0.095	-0.209	-0.389	-0.015	0.433	0.087	0.001	0.048
Cyrtolites	0.003	-0.005	-0.003	-0.007	-0.003	0.005	-0.030	-0.217	0.017	-0.019
Liospira	0.007	0.016	-0.009	-0.013	-0.005	-0.006	0.115	-0.014	0.037	0.006
Loxoplucus	0.001	0.003	0.002	-0.001	-0.004	0.005	0.157	0.025	0.045	0.017
Lophospira	0.005	0.016	-0.022	-0.004	0.007	-0.014	0.016	0.008	0.000	0.010
Ruedemannia	0.010	0.035	-0.048	-0.010	0.015	-0.031	0.016	0.008	0.000	0.010
Fusispira	0.003	0.011	-0.015	-0.003	0.005	-0.009	0.016	0.008	0.000	0.010
Sphenospira	0.001	0.002	-0.013	0.006	0.006	-0.003	0.013	0.005	0.009	0.139
? Gastropod	0.000	0.001	-0.006	0.003	0.003	-0.002	0.013	0.005	0.009	0.139
Treptoceras	0.104	0.067	0.053	-0.388	0.587	-0.197	0.054	-0.102	-0.030	-0.150
Trocholites	0.002	0.008	-0.011	-0.002	0.003	-0.007	0.016	0.008	0.000	0.010
? Cephalopod	0.004	-0.006	-0.002	-0.008	-0.002	0.005	-0.023	-0.083	0.006	-0.007
Technophorus	0.005	0.013	-0.011	0.012	0.055	0.131	0.030	0.007	-0.009	-0.036
Cleidophorus	0.099	0.056	-0.001	0.005	0.055	-0.129	0.086	0.056	-0.183	0.062
Deceptrix	0.037	0.077	-0.046	0.010	-0.020	-0.038	0.224	0.109	-0.006	0.209
Ambonychia	0.282	0.147	0.233	0.390	0.279	0.146	0.165	0.054	-0.425	-0.057
Caritodens	0.047	0.023	0.009	-0.029	-0.012	0.007	0.119	-0.320	0.053	0.271
Corallidomus	0.018	-0.041	0.214	0.462	0.257	-0.250	-0.081	0.057	-0.476	-0.076
Modiolopsis	0.042	0.063	0.027	0.032	0.018	0.225	0.147	0.016	-0.036	-0.046
Orthodesma	0.015	0.010	0.026	-0.008	0.059	-0.046	0.010	-0.003	-0.097	-0.169
Pholadomorpha	0.039	0.016	0.044	-0.137	0.209	-0.110	0.035	-0.140	-0.022	-0.267
Cymatonota	0.053	0.052	0.030	-0.066	0.004	0.011	0.221	-0.149	0.001	-0.065
Psiloconcha	0.315	0.125	0.214	0.316	-0.102	-0.181	0.165	0.015	-0.398	0.128
Cuneamya	0.144	0.181	0.127	-0.199	0.052	-0.027	0.380	-0.076	-0.019	-0.168
Rhytimya	0.078	0.084	0.026	0.063	-0.046	-0.040	0.267	0.109	-0.136	0.159
Lyrodesma	0.016	0.040	0.016	-0.012	-0.055	0.028	0.262	0.050	0.061	0.014
Whiteavesia	0.024	-0.004	0.023	0.061	0.021	-0.023	-0.008	0.620	-0.254	-0.024
Eridonychia	0.016	-0.004	0.026	0.069	0.011	-0.019	-0.020	0.061	-0.126	-0.006
Cycloconcha	0.011	-0.003	0.017	0.046	0.006	-0.013	-0.026	0.074	-0.157	-0.002
Cyrtodontula	0.002	0.008	-0.011	-0.002	0.003	-0.007	0.016	0.008	0.000	0.010
Obalinas	0.002	0.000	0.004	0.012	0.003	-0.003	-0.012	0.041	-0.080	-0.011
Flexicalymene	0.225	-0.008	0.010	-0.310	0.313	-0.068	0.078	-0.467	-0.073	-0.118

Appendix 8

Factor Analysis Results

	Principal Factor Scores						Varimax Factor Score Matrix, Rotated Factors			
Genus	**Factor 1**	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**	**Factor 6**	**Rotated Factor 1**	**Rotated Factor 2**	**Rotated Factor 3**	**Rotated Factor 4**
Platycorphe	0.010	-0.008	0.002	-0.003	0.009	-0.014	-0.035	-0.042	-0.089	0.039
Homotelus	0.002	0.008	-0.011	-0.002	0.003	-0.007	0.016	0.008	0.000	0.010
Isotelus	0.099	0.134	0.045	-0.238	0.117	0.174	0.359	-0.157	0.107	-0.209
Amphilichas	0.001	-0.002	-0.001	-0.003	-0.001	0.002	-0.023	-0.083	0.006	-0.008
Ancienta	0.093	-0.049	0.061	0.117	0.083	-0.094	-0.067	-0.070	-0.324	-0.017
Cornulites	0.017	0.009	0.015	0.011	-0.016	0.002	0.054	-0.012	-0.057	0.030
Iocrinus	0.001	0.000	0.002	0.004	0.003	-0.001	-0.031	0.008	-0.101	-0.023
Cincinnaticrinus	0.003	-0.001	-0.014	0.002	0.005	-0.006	0.007	-0.006	-0.013	0.234
Hyolithes	0.045	0.101	0.049	-0.018	-0.138	0.095	0.285	0.056	0.057	0.019

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