ABUNDANCE AND EXTINCTION AT THE ORDOVICIAN/SILURIAN BOUNDARY OF THE CINCINNATI ARCH, USA

by

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(Under the Direction of Steven M. Holland)

ABSTRACT

This study tests the relationship between fossil abundance and extinction. Samples were collected from the Late Ordovician type-Cincinnatian Series and the earliest Silurian Brassfield Formation of the Cincinnati Arch. The abundance of brachiopod genera and families was assessed with nine different metrics to account for differences across spatial and temporal scale. Each of these metrics was compared to global duration in the fossil record and survivorship across the Ordovician/Silurian boundary.

The results indicate that survivors were more abundant than victims, and are further evidence that the Ordovician/Silurian extinction was not accompanied by a macroevolutionary selectivity regime shift. Furthermore, abundances during this interval are not correlated with duration in the fossil record, a finding that is interpreted as further evidence of changing selectivity patterns through time.

INDEX WORDS: Mass extinction, Selectivity, Brachiopods

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B.A. The College of William and Mary, 2008

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2010

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August 2010

DEDICATION

To Karen, Rowan, and Laura

ACKNOWLEDGEMENTS

First and foremost, I am very grateful to my parents who have always been supportive of me and my education. Special thanks also go out to Karen Layou, Rowan Lockwood, Heather MacDonald, and Brent Owens for fostering my interest in the geological sciences and supporting me every step of the way in my pursuit of a graduate education.

I would also like to thank Patrick McLaughlin, Morgan Rosenberg, Max Christie, and Dylan Radford for their help in finding, collecting, and processing my field data. I also owe an especially large debt to Sarah Kolbe and Jay Zambito, who kindly opened their home to me and Morgan Rosenberg during our very strenuous time in the field.

Lastly, I want to thank my advisor, Steve Holland, for all of the time and dedication he has invested in me, this thesis, and my future career. His help and insight has been a great boon to me, not only in the production of this thesis, but also all of his contributions in helping me move forward with my career.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

This thesis is written as a manuscript intended for submission to the academic journal *Paleobiology*. Because of this, it is best read as a single chapter. The second chapter discusses in detail the previous literature, geological setting, methods, results, and conclusions.

The null model of extinction theory predicts that taxa with higher abundances will have lower extinction rates (Rosenzweig and Lomolino 1997), which should manifest in longer fossil-record durations and higher survivorship during major extinction events for more abundant taxa. This expectation can be independently derived from the multiple perspectives of metapopulation ecology (Connell 1983; Bengtsson 1989), conservation biology (Gaston and Kunin 1997), statistics (Raup 1992), population genetics (Karlin 1968), and biostratigraphy (Signor and Lipps 1982); but this prediction has not extended well into the larger spatial and temporal scales of the fossil record. Various paleontologic studies have found conflicting results, indicating a more complex relationship between abundance and extinction patterns in the geologic past (McClure and Bohonak 1995; Lockwood 2003; Harnik 2007; Lockwood and Barbour Wood 2007; Leighton and Schneider 2008; Simpson and Harnik 2009).

This study tests whether the null model of extinction theory applies across the Ordovician/Silurian boundary of the Cincinnati Arch, USA. Specifically, it tests whether more abundant brachiopods have longer fossil-record durations and increased survivorship across the Ordovician/Silurian mass extinction. Samples of macroinvertebrate marine fossils were collected from the Late Ordovician type-Cincinnatian Series and from the earliest Silurian Brassfield Formation. The abundance of brachiopod genera and families was calculated with nine different metrics that explicitly take into account differences in spatial and temporal scale, to determine if any observed patterns were scale driven. Each of these abundance metrics was compared to global duration in the fossil record and survivorship through the Ordovician/Silurian extinction.

A comparison of survivors and victims directly across the boundary indicates more abundant taxa survived better across the extinction boundary. Although the statistical significance of each test varied, survivors always have a greater abundance than victims. This is in keeping with the null model of extinction theory, but has not been observed previously at a mass extinction boundary. This may be further evidence that the Ordovician/Silurian extinction was not accompanied by a macroevolutionary selectivity regime shift (*sensu* Jablonski 1986).

Statistical testing shows no significant relationship between brachiopod abundance and duration – excluding a single case. Mean alpha-level abundance is negatively correlated with duration in the fossil record ($p \leq 0.05$). This suggests that rare genera (at the alpha-level) survive for longer periods of time. This may be further evidence of changing abundance selectivity through time (Simpson and Harnik 2009); but may be an artifact of differential sampling along each taxon's history of rise and fall (Foote et al. 2007; Liow and Stenseth 2007) or reflect true changes in the correlation of different ecological properties (e.g., geographic range) with abundance.

CHAPTER 2

ABUNDANCE AND EXTINCTION AT THE ORDOVICIAN/SILURIAN BOUNDARY OF THE CINNCINATI ARCH, USA

Zaffos, A. To be submitted to *Paleobiology*

INTRODUCTION

The null model of extinction theory treats abundance as an advantageous trait that buffers taxa against extinction (Rosenzweig and Lomolino 1997). In contrast, recent paleontological studies have not found any evidence to support this null model in the geologic record. Some studies have found no relationship between abundance and survivorship (McClure and Bohonak 1995; Lockwood 2003; Harnik 2007; Lockwood and Barbour Wood 2007), others have found that abundance can act as a disadvantageous trait (Leighton and Schneider 2008), and still others have found a more complex non-linear relationship (Simpson and Harnik 2009). This has led to the general view the effect of abundance on extinction is inconsistent on geologic time scales, particularly during mass extinction intervals (Jablonski 1986, 2004, 2005; Simpson and Harnik 2009).

Here, brachiopod abundances were measured in the Late Ordovician type-Cincinnatian Series (Holland and Patzkowsky 2007) and earliest Silurian Brassfield Formation (Katian-Telychian; ~17 Myr) of the Cincinnati Arch, USA to answer two different questions about abundance and extinction patterns. First, does increased abundance promote survivorship in brachiopods directly across the Ordovician/Silurian boundary? Second, does increased abundance produce longer durations for brachiopods in the global fossil record?

Previous Work

The idea that certain ecological characteristics are preferentially selected against during extinction is one of the oldest ideas in the life sciences (see review by McKinney 1997b). Abundance, in particular, has always been at the forefront of proposed selectivity characteristics, as the fields of conservation biology (Gaston and Kunin 1997), metapopuluation ecology (Connell 1983; Bengtsson 1989), population genetics (Karlin 1968), statistical population dynamics (Raup 1992), and biostratigraphy (Signor and Lipps 1982) unanimously predict a positive relationship between abundance and survival. This prediction is the null model of extinction theory, and has been widely applied to the field of conservation biology. Both empirical and theoretical ecology studies affirm that increased abundance is correlated with a lower extinction risk (Tracy and George 1992; Rosenzweig and Clark 1994; Mace and Kershaw 1997; O'Grady et al. 2004).

The pattern observed in these modern studies, however, does not scale up well into the longer temporal perspective of the fossil record. While there is evidence in ecology that rare species stay rare on decadal scales (McGowan and Walker 1985, 1993), recent work in the fossil record indicates a more complex rise and fall pattern over millions years, wherein all taxa are rare at the earliest and latest portions of their history (Foote et al. 2007; Liow and Stenseth 2007). Thus, modern and ancient studies capture different portions of each taxon's abundance history due to differing temporal resolution. Such differences in the spatial or temporal scale of observation may be the reason that a positive relationship between abundance and survival has not been found in studies by paleontologists (McClure and Bohonak 1995; Lockwood 2003; Harnik 2007; Lockwood and Barbour Wood 2007; Leighton and Schneider 2008; Simpson and Harnik 2009).

Therefore, attention must be paid to scaling issues to determine if this conflict between studies is an artifact of differences in temporal or spatial resolution. Leighton and Schneider (2008) addressed this possibility by using a modification of Whittaker's (1960) alpha, beta, and gamma paradigm to partition their abundance measurements into spatially finer (alpha) and coarser (gamma) scales. An alpha, beta, and gamma partitioning scheme can also be used to quantify changes of temporal scale (Fig. 2.1), which are equally important to consider when examining abundance patterns (Simpson and Harnik 2009). The unified partitioning scheme outlined in Figure 2.1 (see **Data Metrics**) tests whether differences in abundance-extinction patterns through time are scale-driven; that is, whether these patterns change in response to the geographic or temporal extent of the study.

Alternatively, the discrepancy between the findings of paleontological studies and the null model may reflect true changes in selectivity patterns through time (Simpson and Harnik 2009). Particularly important to consider is Jablonski's (1986) alternating selectivity regimes hypothesis, which predicts that each extinction event will have its own set of ecological traits (a regime) that are selected against. These traits are hypothesized to be relatively constant among background intervals, but may change drastically during the widespread environmental changes of mass extinctions. Thus, background intervals are predicted to have comparable selectivity patterns, while mass extinctions are expected to have unique selectivity patterns (e.g., Payne and Finnegan 2007).

Jablonski's (1986) hypothesis has been supported by studies showing non-selectivity for many hypothesized background traits during the end-Cretaceous mass extinction (Jablonski and Raup 1995; McClure and Bohonak 1995; Jablonski 2004, 2005), end-Permian mass extinction (Leighton and Schneider 2008; Clapham 2009), and other selectivity shifts during most major extinction events (e.g., changing importance of geographic range, Payne and Finnegan 2007). Studies of abundance at these mass extinctions (McClure and Bohonak 1995; Lockwood 2003; Leighton and Schneider 2008) have consistently demonstrated abundance selectivity patterns at odds with background interval expectations. In particular, the work of Simpson and Harnik (2009) demonstrated that the correlation between abundance and extinction of Mesozoic-

Cenozoic bivalves varies through time, and that abundance does not always positively correlate with longer durations in the fossil record.

In this study, abundance was measured with nine different metrics. Each metric examined abundance at different temporal and spatial resolutions, because there is no single, optimal measure of taxonomic abundance that can account for changes in the scale of observation or differential sampling. Extinction was examined in two ways: survival through the Ordovician/Silurian mass extinction and global duration in the fossil record. Each metric was compared against each measure of extinction to determine the relationship between abundance extinction during the Ordovician/Silurian extinction.

SETTING

Global Perspective

The Late Ordovician was typified by major climatic disturbances and large-scale extinction of taxa at global and regional levels (Harper and Rong 1995; Sheehan 2001). These major shifts can be broken down into two pulses. The first pulse began during the earliest Hirnantian, during which widespread global glaciation led to rapid cooling of oceanic waters, changes in circulation patterns, and a fall in eustatic sea level (Brenchley et al. 1991; Brenchley et al. 2001; Sheehan 2001). A second pulse of extinction occurred towards the very end of the Hirnantian as the glaciations ended, followed by a rapid return to warmer tropical and sub-tropical conditions. The magnitude of extinction for brachiopods is complicated by tracking of preferred environments by some genera (e.g. *Dolerorthis*, *Dicoelosia*), which caused them to go extinct in some regions but survive globally (Rong et al. 2006). Brachiopods and corals suffered the greatest extinction during the first pulse (Scrutton 1997; Rong et al. 2006).

The long-term impact of the extinction was mixed, with little meaningful re-organization of ecological relationships following the extinction (Droser et al. 2000; Bottjer et al. 2001; Brenchley et al. 2001). Every major taxonomic group from this period suffered from increased extinction rates, yet no major group went completely extinct (Sheehan 2001). Brachiopods and echinoderms both suffered heavily from extinction at the generic level, but they continued to remain important throughout the remainder of the Paleozoic (Sheehan 1996). Corals, bryozoans, and trilobites suffered the most long-term damage, with numerous clades disappearing completely or failing to recover to their pre-extinction levels of abundance or diversity (Sepkoski 1981; Sheehan 1996, 2001; Adrain et al. 2000).

Interpretations of the Silurian recovery focus heavily on the lower abundance, lower diversity, and cosmopolitanism of the Silurian fauna (Berry and Boucot 1973). In particular, the substantial decline in inarticulate brachiopods and the rise of pentamerid and spire-bearing clades (e.g. *Virgiana, Plectatrypa*) is considered emblematic of changes occurring during the Ordovician/Silurian transition (Droser et al. 2000; Rong and Harper 2000; Harper and Rong 2001; Sheehan 2001). This is not true for the earliest Silurian, however, as orthid and strophomenid clades continued to be major constituents (Baarli and Harper 1986; Rong and Zhan 2006; Rong et al. 2006; Cocks and Rong 2008), and many pentamerid clades (e.g. the Lazarus superfamily Pentameroidea) are temporarily absent from the earliest Silurian fossil record (Rong and Harper 2000).

Regional Perspective

The type-Cincinnatian Series of the Cincinnati Arch (Fig. 2.2) has received much study of its stratigraphy, lithofacies, biofacies, regional correlation, and faunal tracking patterns (Tobin 1986; Holland 1993; Holland and Patzkowsky 1996; Pope and Read 1997; Holland et al. 2001;

Miller et al. 2001; Brett et al. 2007). Its six third-order sequences, C1-C6 (Holland and Patzkowsky 1996), cover the interval prior to the onset of glaciation (Brenchley et al. 1997). The region maintains a diverse fauna dominated by orthid and strophomenid brachiopods and an assortment of trilobites, gastropods, solitary rugose corals, favositids, and diverse bryozoans (Holland and Patzkowsky 2007).

The earliest Silurian Brassfield Formation (Fig. 2.2) is a complex stratigraphic unit that has had numerous revisions to its lithostratigraphy and regional correlations (e.g., O'Donnell 1967; Peterson 1981; McDowell 1983; Brett et al. 1990; Norrish 1991; Hettinger 2001), without yet producing a consensus (McLaughlin et al. 2008). This is partially due to so-called state-line stratigraphy, but is also a product of several different erosional and diagenetic gradients throughout the region (McLaughlin et al. 2008). This complexity is compounded by several distinct units within the Brassfield (Belfast, Brassfield, Oldham, Lulbegrud, and Plum Creek) that have occasionally been assigned as members, formations, or groups (see Peterson 1981 vs. McDowell 1983, for example). These differences provide several different options in how to define the Brassfield Formation.

Here, the Brassfield Formation of Kentucky and Ohio is considered to include all of the strata overlying the Ordovician/Silurian unconformity up to the contact with the Dayton or Waco Formations (e.g., O'Donnell 1967), an interval that has traditionally been interpreted as a single, condensed third-order depositional sequence (Norrish 1991). More recent work in the Brassfield, however, suggests this interval may be two separate condensed third-order sequences (McLaughlin et al. 2008). Here, the more traditional interpretation of Norrish (1991) is used, and all of the analyses (Table 2.1; see **Data Metrics**) treat the Brassfield as a single third-order sequence.

The Brassfield maintains a fauna strikingly similar to that of the type-Cincinnatian at the family level, yet drastically different at the genus level (Fuentes 2003). Most orthid, strophomenid, and rhynchonellid families of the type-Cincinnatian Series survive into the Brassfield (Appendix A and B). The relative abundances of higher taxonomic groups, however, are strikingly different immediately across the boundary. Large portions of the Brassfield Formation in Ohio and Kentucky are dominated by low diversity camerate crinoid thickets (Frest et al. 1999), mostly represented by ossicles, but, occasionally, fully or well preserved calyxes (e.g. Sumrall 2002; Schneider and Ausich 2002; Blake and Ettensohn 2009). Bryozoan abundance plummets across the boundary, except for cryptostomes, and rugose corals are strikingly abundant in some horizons (Laub 1979). These rugose corals and camerate crinoids decline in abundance in the higher portions of the Brassfield, as a greater variety of taxonomic assemblages arise.

METHODS

Data Collection

The dataset used in this study comprises 783 samples (>46,500 individuals) of marine macroinvertebrate fauna taken across seven third-order depositional sequences from the Katian-Telychian of the Cincinnati Arch in southwestern Ohio and northern Kentucky (Fig. 2.2). Samples from the C1-C6 sequences of the type-Cincinnatian Series were obtained from Holland and Patzkowsky's (2007) dataset and are available from the Paleobiology Database (paleodb.org). Forty-three additional samples were collected from nine outcrops of the Silurian Brassfield Formation specifically for this study (Fig. 2.3; Appendix A and C).

The volume and size of individual samples was determined by the availability of exposed bedding planes and slabs. Most taxonomic groups were identified to the genus level, but several bryozoans and horn corals were identified by morphotype (Appendix A). Counting protocols were different for each higher taxonomic group, but each attempted to minimize instances of double-counting of individuals. For example, the number of individuals for each brachiopod genus within a sample was counted as the total number of articulated shells, plus the greater of the pedicle or brachial valves, plus half the number of any indeterminate valves.

The Ordovician samples ranged in size from 100 cm^2 to 16,200 cm^2, with a mean of 1,780 cm^2. The Silurian samples ranged in size from 100 cm^2 to 16,000 cm^2 with a mean of 2,033 cm^2. The variation in sample size did not produce a strong correlation between abundance and sample size or diversity and sample size, but all of the metrics use some method to standardize for differential sampling intensity: ranking, percent-transformation, averaging, or combinations thereof (see **Data Metrics**). Only in the case of the Brassfield data was there a strong correlation between abundance and diversity. A standard bootstrap procedure was used to correct for this correlation in the Brassfield data by re-sampling the Silurian data with replacement 10,000 times.

The bootstrap procedure required a minimum of 24 individuals per sample, and samples with less than 24 individuals were culled from all of the data for consistency. Singleton taxa (taxa with only one counted individual) were also culled from the dataset. This was done since singletons do not add any additional information to measures of relative abundance. It is arguable that in a study of abundance, singleton taxa should have been kept; but this culling procedure did not noticeably affect the final analyses, since only one of the studied brachiopod genera, *Strophonella*, was removed for being a singleton. Additionally, three epiboles in the Brassfield (two horn coral epiboles; one epiole of *Helopora*, a delicate branching cryptostome bryozoan) were culled from the data, as their extremely high local abundances skewed many of the abundance metrics. A total of 71 samples were culled from the data, leaving 712 remaining samples for the final analysis.

Holland and Patzkowsky's (2007) data and the bootstrapped Brassfield data were combined into a single dataset. This dataset was then reorganized into three variations: Dataset 1 included Ordovician-Silurian taxa at the genus level, Dataset 2 included Ordovician-Silurian taxa at the family level, and Dataset 3 included Ordovician-only taxa at the genus level. Each of these dataset variants included all counted macroinvertebrate groups, but the statistical analyses of abundance vs. duration and abundance vs. survivorship were limited to the articulate brachiopods. The statistical analyses were limited to the articulate brachiopod genera to alleviate concerns of strong differences in preservation potential arising from different skeletal compositions. In addition, brachiopods had the highest genus richness (29) and abundance of any taxonomic group, making them the most robust for statistical analysis. Therefore, the other macroinvertebrate groups were used only to calculate the relative abundances of the brachiopods and for sample size standardizations.

Data Metrics

Nine metrics were used to quantify abundance (Table 2.1), because any given metric has the potential to produce different trends if abundance patterns are decoupled with the temporal or spatial scales of observation. For example, Simpson and Harnik (2009) showed that correlations of abundance with extinction rate are dependent on temporal resolution. When they treated the post-Paleozoic as a single interval, a strong non-linear relationship between abundance and extinction rates was observed. When they partitioned this interval into separate 10 million-year bins, however, they found that each bin had its own set of relationships, which produced the very strong non-linear relationship when aggregated. Furthermore, certain metrics may capture different ecological relationships; for example, occurrence data (number of samples containing a taxon) is a reflection of both abundance and range (Kunin 1997; Gaston et al. 1997; Gaston et al 2000). Thus, a multiple-metric analysis provides numerous benefits for ecological interpretation, decoupling the effects of scale, and limits the effects of temporal and spatial biases.

The first of the nine metrics, Gamma (Total), is the total number of individuals of a taxon within the entire dataset. This metric is equivalent to the cumulative “Raw” and “Rank” metrics used by Lockwood (2003) and the “Gamma” metric used by Leighton and Schneider (2008). This metric suffers from some temporal bias, because as more time is added to the dataset, the relative importance of organisms that went extinct earlier in the dataset is decreased, even though they may have been very abundant while extant. The same bias applies to taxa that originate towards the end of the dataset.

Gamma (Proportional) addresses this temporal bias by partitioning the data by sequences (α_2 in Fig. 2.1) to correct for time. The total number of individuals of a taxon within a sequence is divided by the total number of individuals for all taxa within that same sequence to measure what proportion of a sequence’s entire biota a taxon represents. This proportion is then averaged across all sequences in which that taxon occurs, thus eliminating the edge-effects caused by the origination or extinction of taxa at the beginning or end of the dataset.

Gamma (Dominance) measures a taxon’s abundance rank within an entire sequence, e.g. the most abundant taxon is assigned rank one, the second most abundant taxon is assigned rank two etc. These ranks are then averaged across all sequences in which the taxon occurs. This differs from ranking Gamma (Proportional) or Gamma (Total), since the ranking process for those metrics occurs after averaging or totaling through time, whereas Gamma (Dominance) measures sequence to sequence changes in the rank-abundance structure.

Alpha (Mean) is the average abundance of a taxon across all samples in which it occurs within a sequence. This average is then itself averaged across all sequences in which the taxon occurs. The average only includes samples in which a taxon occurs in order to limit the influence of abundance-occurrence relationships (Gaston et al. 1997). This metric is sensitive to any correlations between sample size and abundance.

Alpha (Proportional) accounts for sample size-abundance biases by standardizing each taxon's abundance within a sample by the total abundance of all taxa in that sample. As long as there is no sample-size bias, Alpha (Mean) and Alpha (Proportional) should give similar results. Neither of these metrics is equivalent to the "Alpha" of Leighton and Schneider (2008), as they did not temporally partition alpha abundance by stratigraphic units.

Alpha (Dominance) is similar to Gamma (Dominance) in that it measures changes in ranked abundance across sequences. Alpha (Dominance) is calculated by taking a taxon's average rank among samples in which it occurs and then averaging those means across all sequences.

Occurrence (Total) is the total number of samples containing a taxon, and is equivalent to the "occurrence" metric used in Leighton and Schneider (2008). This metric suffers from the same temporal bias and sampling intensity bias as Gamma (Total). As with Gamma (Proportional), this bias is corrected by expressing occurrence as a proportion of the total number of samples within a sequence, and then averaging across all sequences containing that taxon. This corrected metric is called Occurrence (Proportional).

The Gamma vs. Stenotopy metric is a combination of abundance (number of individuals) and occurrence (number of samples) data. The total individuals of a taxon within a depositional sequence (α_2 in Fig. 2.1) is divided by the number of samples in which it is absent (plus one to avoid dividing by zero). This creates a ratio that rewards taxa for having a high total abundance within a sequence, while penalizing taxa that occur in few samples within a sequences (i.e. stenotopic taxa). Higher ratios represent a state of simultaneous eurytopy and abundance; while lower ratios are closer to a state of simultaneous rarity and stenotopy.

Each of these metrics uses a different scheme to standardize for differential sampling from sequence to sequence or sample to sample (Table 2.1). For example, the Gamma (Proportional) metric places a greater weight on taxa that only occur in sequences with few samples. Conversely, the Gamma (Total) metric places more weight on some taxa that occur in depositional sequences with many samples. Each metric will inevitably place more weight on more heavily or less heavily sampled sequences if there is any differential sampling effect. Because of these differential effects, multi-metric analysis is necessary for abundance studies.

Abundance vs. Survivorship

Any brachiopod genus that was present in the type-Cincinnatian Series and survived across the Ordovician/Silurian boundary anywhere on Earth (as determined from Tapanila's (2006) modified version of Sepkoski's (2002) compendium) is considered a survivor of the Ordovician/Silurian extinction (Appendix B1). Although many brachiopods limited to the Silurian strata of the Cincinnati Arch occurred elsewhere in the Ordovician (Appendix B1, "Immigrants"), their absence from the type-Cincinnatian Series prevents measurement of their pre-extinction abundance. Tests of survivorship were limited to those brachiopod genera for which their pre-extinction abundance on the Cincinnati Arch could be measured.

Although it would be interesting to know how abundance correlates with survival across the Ordovician/Silurian boundary on the Cincinnati Arch, only four genera survived across the boundary regionally, too few for a meaningful statistical analysis. Similarly a survivorship test could not be performed on Dataset 2, as too few Cincinnatian families went extinct (globally or regionally) for analysis.

A two-tailed Student's *t*-test comparison of means was used to determine the comparative abundance of victims and survivors for each of the nine abundance metrics. Since all abundance metrics consistently display a strong log-normal distribution the abundance metrics were log-transformed. The non-parametric Mann-Whitney's U-test was used to compare the median abundance for each of the nine metrics.

Abundance vs. Duration

Duration is measured here as the millions of years from a taxon's first global occurrence to its last global occurrence. Genus durations are based on Tapanila's (2006) modified version of Sepkoski's (2002) compendium for genus-level data (Appendix B2). Family-level durations were taken from the intervals in the *Treatise on Invertebrate Paleontology*.

The non-parametric Spearman's-rho ranked correlation test was used to test for a monotonic relationship between abundance and duration. This was necessary for two reasons. First, taxonomic durations in the fossil record are strongly right-skewed (Sepkoski 1989), violating the requirements of a parametric test. Second, recent live-dead assemblage studies indicate that ranked or relative abundance conserves the best represents abundance relationships in the fossil record (Kidwell 2001; Olszewski and Kidwell 2007).

When non-parametric tests are used on relatively small sample sizes (<29), there is a risk of Type II error owing to the low power of non-parametric tests (Johnson 1995). To compensate for this, p-values were evaluated at the traditional 95% level, as well as at the 90% and 85% level to compensate for the lower power. Here, p-values ≤ 0.05 are labeled as significant, $0.05 \leq p \leq$

0.15 are considered weakly significant, and all values where $p > 0.15$ are considered non-significant.

RESULTS

Abundance and Survivorship

The comparison of survivors versus victims is depicted in Tables 2.2 and 2.3, which list each of the abundance metrics used and the corresponding mean and median abundance of survivors and victims. Survivors always have a higher mean and median abundance than victims, excluding the single case of Alpha (Proportional) in Dataset 1. This indicates abundant organisms preferentially survived the Ordovician/Silurian extinction. Although p-values vary from metric to metric, abundance metrics with a $p \leq 0.15$ in Dataset 1 tend to also have a $p \leq 0.15$ in Dataset 3.

Abundance vs. Duration

A majority of the correlations for abundance and duration return non-significant p-values ($p > 0.15$), but almost all are non-positive (rho ≤ 0). This non-positive relationship is generally strengthened by the genera *Leptaena* and *Petrocrania,* which are strong outliers in terms of duration (Fig. 2.4; Appendix B). These two genera are considered outliers because the duration of *Leptaena* is double that of the second closest genus *Dolerorthis* (~60 Myr), and the genus *Petrocrania*'s duration is almost twice as long as *Leptaena*'s (~220 Myr). Not only does an extremely long duration have a disproportionate effect on the correlations, it is also doubtful that the abundances observed over the ~17 Myr interval of this study adequately represent abundance of these genera over their entire histories. Furthermore, these long durations may be artifacts of the so-called "taxonomic wastebasket" effect (Plotnick and Wagner 2006), wherein different genera with similar morphology are grouped together under a single name.

The analyses were re-run without *Leptaena* and *Petrocrania* for all datasets (Figs. 2.5, 2.6, and 2.7). The impact of removing the outliers is minimal (Appendix E), and the overall pattern of non-significant ($p > 0.15$), non-positive correlations remains. This is generally true regardless of the metric used, but there is some sensitivity to the dataset used. The rho values for Datasets 1 and 2 are relatively strong and always negative or non-positive, except for Occurrence (Proportional); while Dataset 3 had rho values closer to zero generally indicating no relationship. In only one instance (Alpha (Mean) vs. Duration) is abundance significantly ($p \leq 0.05$) and strongly correlated with extinction (Figs. 2.4 and 2.5).

DISCUSSION

Does a higher abundance for survivors mean no selectivity shift?

Ordovician and Silurian genera (Dataset 1) and Ordovician-only genera (Dataset 2) show multiple weakly-significant cases ($p \leq 0.15$) in which more abundant taxa survived better across the boundary (Tables 2.2 and 2.3). Furthermore, the mean and median abundance of survivors is always, excluding a single case, higher than that of victims; regardless of the metric used or the associated *p*-value. This finding matches the null expectations of modern extinction theory, but has not been described previously at a mass extinction boundary. The leading hypothesis is that mass extinctions differ from background extinction (Jablonski 2004, 2005), because periods of dramatic global stress may introduce selectivity patterns different than those in background intervals.

Since abundance is considered to be a background trait, the findings of this study seem to contradict the notion that the Ordovician/Silurian, as a mass extinction, should substantially differ from background events in selectivity. This begs the question if the climatic shift at the Ordovician/Silurian is truly comparable to the dramatic conditions during the end-Permian or end-Cretaceous that overrode the background selectivity regime for multiple traits (e.g. Jablonski and Raup 1995; Clapham 2009). In other words, these data suggest that the Ordovician/Silurian extinction represents an intensification of background-style selection, not a shift to a different macroevolutionary regime.

The lack of a selectivity regime shift for abundance in the Ordovician matches well with other lines of evidence suggesting that the Ordovician/Silurian extinction was a mass extinction in magnitude only (Droser et al. 1997). Payne and Finnegan's (2007) examination of geographic range and extinction rates throughout the geologic record showed that geographic range is less important for selectivity during most major extinction events, and that geographic range alone cannot explain all of the observed extinction during these periods. A strange outlier from their trend is the Ordovician/Silurian extinction, which has a geographic selectivity pattern more like background intervals than major extinctions. Similarly, Peters (2006) showed that the Ordovician/Silurian does not deviate substantially from the best-fit expected rate of background extinction, while the end-Permian and end-Cretaceous extinctions had residuals from the overall trend more than twice that of the Ordovician/Silurian.

A background selectivity regime may explain many of the ecological patterns observed during the Ordovician-Silurian transition (Droser et al. 1997). The lack of ecological restructuring following the extinction (Droser et al. 2000; Bottjer et al. 2001; Brenchley et al. 2001) may indicate that the extinction did not target different traits or niches than those in background times. The continuation of the orthid and strophomenid clades well past the Ordovician/Silurian boundary (Baarli and Harper 1986; Rong et al. 2006; Rong and Zhan 2006; Cocks and Rong 2008) may be specific evidence that extinction among articulate brachiopods during the Late Ordovician did not substantially differ in selectivity from the Middle Ordovician, and was only magnified in intensity. If niche-specific selectivity was applied equally across each of these two clades, which make up a majority of this study's dataset, then the differentiating factor may only have been abundance and geographic range as would be expected under background extinctions or under the fair-game model of extinction, in which the least abundant taxa are more likely to go extinct (Raup 1992).

Why is there a non-positive relationship between Abundance and Duration?

Alpha (Mean) is the only statistically-significant ($p \leq 0.05$) ranked correlation between abundance and duration (Fig. 2.4). This relationship is part of a more general non-significant, negative trend between abundance and duration in Datasets 1 and 2 (Figs. 2.4 and 2.5). This trend is generally indifferent to the metric used, though in some cases the correlations are better interpreted as indicative of no-relationship whatsoever (Figs. 2.5, 2.6 and 2.7: $0.1 \leq \text{rho} \leq -0.1$), particularly in the case of Dataset 3.

A non-positive relationship goes against the null model of extinction theory, but there is precedent in the fossil record. Simpson and Harnik (2009) found a non-linear relationship between abundance and duration for the entire non-Paleozoic. They showed, however, that this non-linear relationship throughout the entire interval is actually built upon multiple linear trends on smaller 10-million-year intervals. These linear trends range from positive to negative and change through time, thus providing empirical precedent for non-positive relationships.

Although there is Simpson and Harnik's (2009) empirical precedent, a negative relationship is still difficult to justify within a theoretical context. The null model of extinction theory assumes a fair-game world (Raup 1992). In such a world each taxon's duration is solely a function of its abundance, and rare taxa will go extinct sooner than more abundant taxa (Raup 1992). Any relationship between duration and abundance other than that predicted by this null model must, by definition, imply an unfair game wherein rare taxa have some additional advantage – i.e. extinction is applied unequally across taxa. Within the context of this model there must then be some extinction-resistant trait correlated with rarity (or an extinction-prone trait correlated with abundance) that is causing extinction to be applied unequally between abundant vs. rare groups.

The problem with this is that the majority of hypothesized traits that might cause unfair selection are also positively correlated with rarity: rare taxa tend to be homozygous, stenotopic, have larger body sizes, and are more restricted in global and local geographic range (Gaston and Kunin 1997; McKinney 1997a, 1997b). Each of these traits is considered deleterious, and should only further strengthen any positive linear correlation between abundance and duration. Especially important is geographic range, which is hypothesized to be the most important trait affecting probability of extinction (e.g. Jablonski 2004, 2005; Payne and Finnegan 2007) and it has been shown to be bi-directionally linked with duration in the fossil record (Foote et al. 2008). Geographic range is generally strongly correlated with abundance (Gaston and Kunin, 1997; Gaston et al. 2000), and this three-way positive relationship between duration, geographic range, and abundance should be observable.

Studies examining geographic range during the Ordovician/Silurian extinction show that it was an important selectivity parameter that explains much of the observed extinction pattern (Payne and Finnegan 2007). There must, therefore, be a breakdown between the range and abundance correlation during this interval. Theoretical consideration suggests that such a breakdown occurred in the Silurian. In general, Silurian marine invertebrates are thought to be rarer than their Ordovician or Devonian counterparts, but they are also more cosmopolitan and wide-ranging, particularly in the case of brachiopods (Harper and Rong 2001; Rong et al. 2006;

Rong and Zhan 2006; Cocks and Rong 2008). It may be that the rarer, but more cosmopolitan Silurian brachiopods viewed in Datasets 1 and 2 drive the observed negative relationship between abundance and duration.

An alternative explanation may come from recent work that suggests genera and species follow a roughly symmetrical pattern of rise and fall in occupancy over millions of years (Foote et al. 2007; Liow and Stenseth 2007). Although no evidence for such a pattern of rise and fall exists in the Upper Ordovician strata of the Cincinnati Arch (Holland and Zaffos 2009), such a pattern may exist in the Silurian strata. Thus, it is possible that many Brassfield-only brachiopods appear rare because Silurian sampling was limited to the earliest period of rise immediately following origination, and some of these genera may be more abundant in later stratigraphic intervals.

Both explanations can be evaluated by examining the results of the analyses without the Silurian data (Ordovician-only, Fig. 2.7). All negative trends between abundance and duration disappear when the Silurian data is removed, suggesting that the comparatively rarer Silurian organisms have some effect. It remains unclear, however, whether or not their effect is an artifact of incomplete sampling or reflects a change in the correlation of ecological properties during the Silurian (e.g., simultaneous cosmopolitanism and rarity).

What can be inferred for certain, however, is that the genera in this interval did not meet the expectations of the null model, since a perfectly fair world would produce a positive linear relationship between abundance and duration (Raup 1992; McKinney 1997b). The observed correlations, whether including or omitting the Silurian data, are non-positive (Figs. 2.5, 2.6, and 2.7). A non-positive relationship requires rare organisms to have a different probability of extinction than abundant organisms, which implies that rarity is correlated with some extinction-resistant trait during this interval.

Is there a decoupling of abundance patterns with scale?

Survivors always show a higher abundance than victims (Tables 2.2 and 2.3), excluding the case of Alpha (Proportional) in Dataset 1. Thus, the abundance selectivity pattern does not change with geographic or temporal scale during this interval, and strongly implies that ranked abundance does not change with scale either. This latter implication can be examined by correlating each metric to each other, once all metrics have been rescaled to show ranked abundance (Fig. 2.8).

A general consistency across metrics is expected. For example, a strong correlation between occurrence (the number of samples a taxon is present in) and abundance (the total number of individuals) is common in both modern and ancient systems (Blackburn and Gaston 1997; Gaston et al. 1997; Gaston et al. 2000). This correlation is easily visible in this study between the Gamma-level and Occurrence metrics (Fig. 2.8). Furthermore, evidence specifically from the Cincinnati Arch suggests that ecological properties among the marine fauna, including peak abundance and ranked abundance, are strongly conserved through time (Holland and Zaffos 2009) and space (Novack-Gottshall 2003).

Nevertheless, the correlations among metrics are not perfect (Fig. 2.8), and it is likely that this, albeit limited, decoupling between scales is one source of the varying p-values for each metric in the survivorship tests (Tables 2.2 and 2.3). For example, the decoupling between Gamma (Proportional) and Alpha (Proportional) demonstrates a disconnect between the alpha-level and gamma-level; that is, taxa that are rare throughout the sequence (α_2 in Fig. 2.1), but are dominant in individual samples ($\overline{\alpha_1}$ in Fig. 2.1) will cause the rank abundances of the two metrics to be different.

Metrics differ even within the same temporal and spatial scales, suggesting differences in underlying ecological patterns. Taxa that tend to make up large proportions of samples (high Alpha (Proportional) rankings) do not necessarily tend to dominate the samples they occur in (low Alpha (Dominance) ranking), which means that some taxa are highly abundant in nearly monospecific patches, but are rarer when they occur in more diverse samples (Fig. 2.8).

Even limited decoupling across scales highlights the importance of using multiple metrics and levels of scale when analyzing patterns of abundance and extinction. Changes within the same scales of observation can also be utilized to infer certain ecological interaction by proxy. Future work examining abundance and extinction will benefit from multi-scale, multi-metric analysis.

CONCLUSIONS

1) The preferential survival of more abundant Ordovician brachiopods during the Ordovician/Silurian extinction suggests an intensification of background-type extinction, in which survivorship correlates positively with abundance. This correlation suggests that there was no selectivity regime shift (*sensu* Jablonski 1986). The lack of a selectivity regime shift during the Ordovician/Silurian is supported by previous selectivity and extinction studies (Peters 2006; Payne and Finnegan 2007), and may explain the lack of ecologic restructuring during this interval (Droser et al. 2000; Bottjer et al. 2001; Brenchley et al. *200*1).

2) Abundance and duration are not correlated in this study, contrary to the null model of extinction theory. The relatively brief study interval may fail to adequately capture the abundance history (*sensu* Foote et al. 2007; Liow and Stenseth 2007) of longer-lived taxa.

Alternatively, a breakdown of the relationship between cosmopolitanism and abundance during the Silurian (Baarli and Harper 1986; Rong et al. 2006; Rong and Zhan 2006; Cocks and Rong 2008) may explain the lack of a correlation between abundance and duration, as geographic range may have a more powerful effect on duration (Jablonski 2004, 2005; Payne and Finnegan 2007; Foote et al. 2008).

3) If the observed relationship between abundance and duration during this interval is correct, than some trait or traits correlated with rarity must have conferred an advantage over abundant organisms (McKinney 1997a). Future theoretical work on the identification of extinction-resistant traits in rare taxa would benefit conservation biology and the interpretation of ancient selectivity patterns.

4) Multiple abundance metrics that explicitly treat time and space differently can capture changes in ecological relationships that happen between or within temporal or spatial scales. Comparison of metrics revealed decoupling among temporal and spatial scales in this study interval, but this decoupling was only severe for the Alpha (Proportional) metric. Evidence for lack of strong decoupling has been reported in other studies on the Cincinnatian Arch fauna (Novack-Gottshall and Miller 2003; Holland and Zaffos 2009). This decoupling may be more severe during intervals with more complex and diverse fauna, and future studies should take advantage of multiple metrics to capture decoupling effects.

CHAPTER 3

CONCLUSIONS

The relationship between abundance and extinction in the geologic past remains a complex question, and there is mounting evidence that multi-metric, multi-resolution analyses are necessary to properly investigate this question (Leighton and Schneider 2008; Simpson and Harnik 2009). Here, a comparison of articulate brachiopods from the Katian-Telychian interval of the Cincinnati Arch, USA was performed with multiple metrics that partitioned time and space differently.

A comparison of survivors and victims across the Ordovician/Silurian boundary showed that survivors of the extinction were more abundant than victims, but that more abundant genera do not have longer fossil-record durations. These results differ from patterns observed during other mass extinction intervals (McClure and Bohonak 1995; Lockwood 2003; Leighton and Schneider 2008; Simpson and Harnik 2009); but the consistency of this study's results across multiple abundance metrics suggests that findings of this study are not artifacts of measuring abundance at different spatial or temporal resolutions, or with different standardization techniques.

The first finding regarding abundance and survivorship is interpreted as further evidence that the Ordovician/Silurian extinction was only severe in terms of magnitude (Droser et al. 1997), and was not accompanied by a change in macroevolutionary selectivity as seen in the end-Cretaceous and end-Permian mass extinctions (*sensu* Jablonski 1986). This may explain the lack of ecologic reorganization following the extinction as compared to other mass extinction events (Droser et al. 2000; Bottjer et al. 2001; Brenchley et al. 2001).

The second finding of a non-positive relationship between Ordovician/Silurian brachiopod abundances and fossil record duration has several possible interpretations. A larger portion of each taxon's abundance history (Foote et al. 2007; Liow and Stenseth 2007) may be required, suggesting that the non-positive relationship between abundance and duration is an artifact of temporal resolution. Alternatively, a breakdown of the relationship between cosmopolitanism and abundance during the Silurian (Baarli and Harper 1986; Rong et al. 2006; Rong and Zhan 2006; Cocks and Rong 2008) may drive this pattern, which would imply that the observed non-positive relationship between abundance and duration is a result of changes in ecological relationships, such as the relationship between geographic range and abundance. Other factors may also be produce this relationship, but many traits (e.g. homozygosity, larger body-size) correlated with abundance are considered deleterious (Gaston and Kunin 1997).

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Table 2.1. Data Metrics

Abundance Metric	Formula
Gamma (Total)†	Total number of individuals (abundance) of a taxon in the entire dataset.
Gamma (Proportional)*	The among-sequence mean of the proportional abundance of a taxon within a sequence.
Gamma (Dominance)*	The among-sequence mean of the rank abundance of a taxon within a sequence.
Alpha (Mean)*	The among-sequence mean of the within-sequence mean abundance of a taxon within a sample.
Alpha (Proportional)*	The among-sequence mean of the within-sequence mean proportional abundance of a taxon within a sample.
Alpha Dominance)*	Among sequence mean of the within-sequence mean rank abundance of a taxon within a sample.
Occurrence (Total)†	Total number of samples containing a taxon in the entire dataset.
Occurrence (Proportional)*	The among-sequence mean of the proportion of samples containing a taxon within a sequence.
Gamma vs. Stenotopy	The total number of individuals of a taxon within a sequence, divided by the number of samples lacking that taxon in that sequence, averaged over all sequences.

Metrics marked with an † will more heavily weight taxa that are very abundant in sequences with many samples. Metrics marked with an * will more heavily weight taxa that are very abundant in sequences with few samples. See text (**Data Metrics**) for an explanation of why each metric was necessary.

Table 2.2. Survivors vs. Victims at the O/S. Dataset 1: Ordovician and Silurian genera.

Abundance Metric	**Means**		**Medians**	
	Survivors	**Victims**	**Survivors**	**Victims**
Gamma (Total)	**399.87**	76.85*	**221.50**	152.50*
Gamma (Proportional)	**0.02**	0.01*	**0.05**	0.01*
Gamma (Dominance)	**13.26**	16.18	**11.50**	14.25
Alpha (Mean)	**4.94**	4.43	**4.86**	4.36
Alpha (Proportional)	0.08	**0.09**	**0.10**	0.09
Alpha (Dominance)	**7.52**	8.27	**7.68**	8.61*
Occurrence (Total)	**67.77**	17.00*	**64.00**	31.00*
Occurrence (Proportional)	**0.24**	0.08**	**0.33**	0.14*
Gamma vs. Stenotopy	**2.58**	0.46*	**6.08**	0.79*

Significance: $p \leq 0.15$ *; $p \leq 0.10$**; $p \leq 0.05$***. The value representing a higher abundance is bolded. Note: For Alpha (Dominance) and Gamma (Dominance), a lower value means a higher abundance.

Table 2.3. Survivors vs. Victims at the O/S. Dataset 3: Ordovician-only genera

Abundance Metric	**Means**		**Medians**	
	Survivors	**Victims**	**Survivors**	**Victims**
Gamma (Total)	**386.84**	76.85*	**212.00**	152.50*
Gamma (Proportional)	**0.02**	0.01	**0.05**	0.01*
Gamma (Dominance)	**11.98**	16.18	**11.50**	14.25
Alpha (Mean)	**5.64**	4.43	**5.69**	4.36
Alpha (Proportional)	**0.24**	0.09	**0.24**	0.09
Alpha (Dominance)	**7.03**	8.61*	**7.03**	8.61*
Occurrence (Total)	**59.67**	17.00	**64.00**	31.00*
Occurrence (Proportional)	**0.20**	0.08	**0.33**	0.14
Gamma vs. Stenotopy	**2.53**	0.46*	**6.08**	0.79*

Significance: $p \leq 0.15$ *; $p \leq 0.10$**; $p \leq 0.05$***. The value representing a higher abundance is bolded. The means have been un-logged for easier interpretation. Note: For Alpha (Dominance) and Gamma (Dominance), a lower value means a higher abundance.

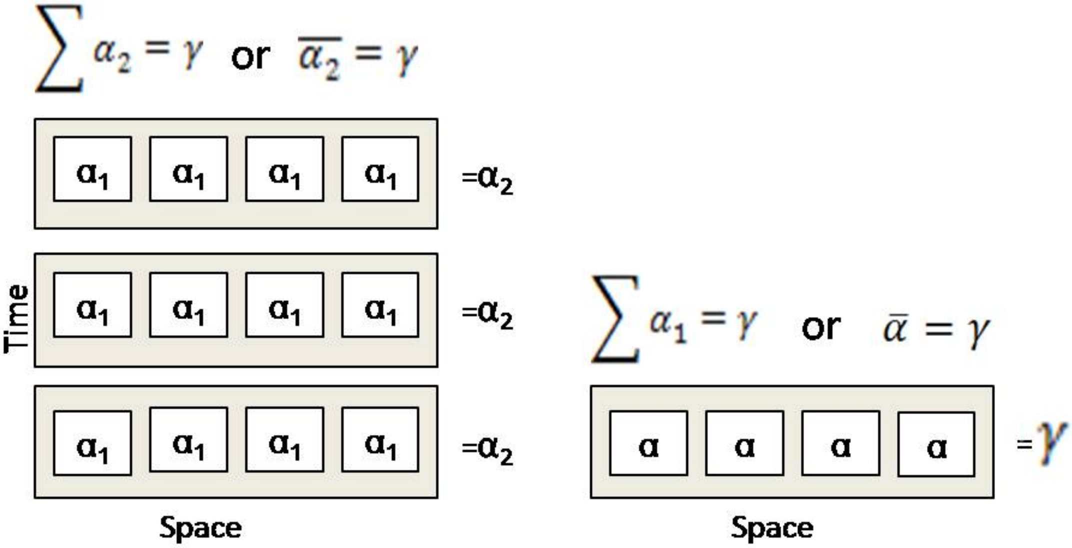
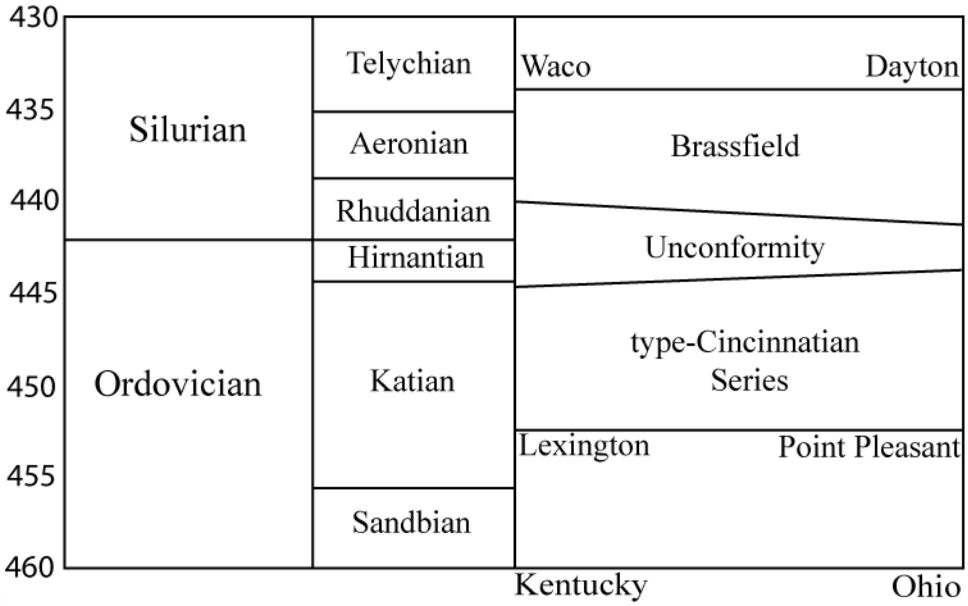


Figure 2.1. Depicts spatial and temporal partitions. A partitioning scheme that only captures changes in spatial scale is represented on the right (e.g., mean sample-level abundances ($\bar{\alpha}$) or the entire region's ($\sum \alpha = \gamma$) total abundance). A partitioning scheme that partitions along both spatial and temporal scale is depicted on the left (e.g., sample-level abundance within a sequence (α_1), regional sequence-level abundance ($\sum \alpha_1 = \alpha_2\ or\ \overline{\alpha_1} = \alpha_2$), and among-sequence total regional abundance ($\sum \alpha_2 = \gamma\ or\ \overline{\alpha_2} = \gamma$).



c

Figure 2.2. Studied interval of the Cincinnati Arch. The Lexington Formation and Point Pleasant Formation grade into the type-Cincinnatian Series, which is followed by the Ordovician/Silurian unconformity. This unconformity is longest is Kentucky and shortest in Ohio. The Brassfield contains all strata until the sharp erosional contact between the Dayton Formation and Waco Formation.

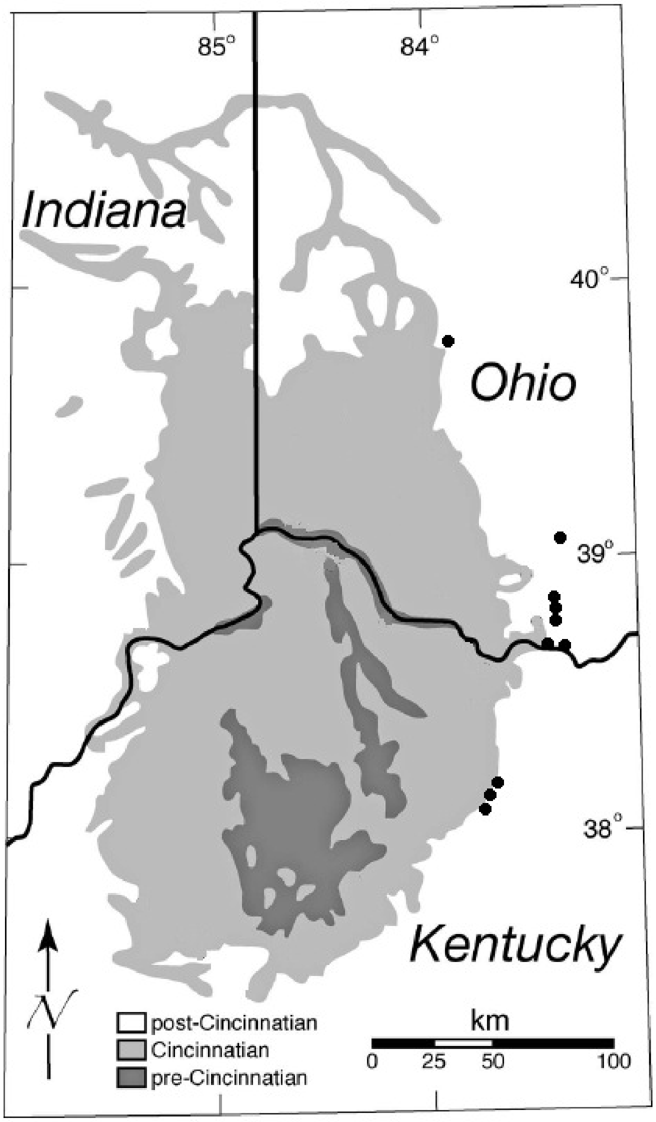


Figure 2.3. Map of sampled Brassfield localities (black dots). Specific coordinates and locality descriptions are included in Appendix C. Base map adapted from Holland and Patzkowsky (2007).

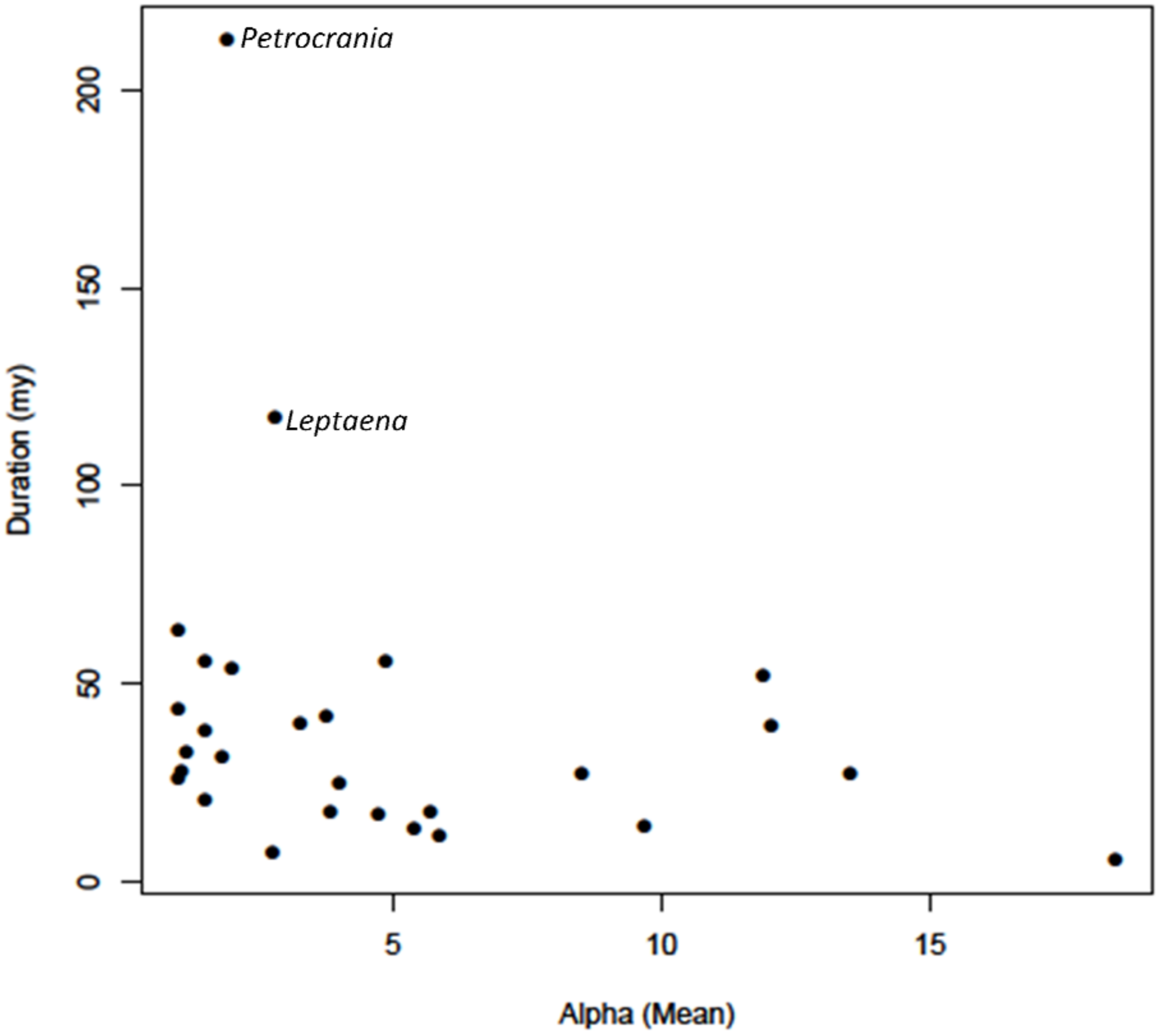


Figure 2.4. Sample of Dataset 1 results with the outliers *Leptaena* and *Petrocrania*, which had disproportionately long durations (see **Results**). These outliers were removed from Figs. 5, 6, and 7.

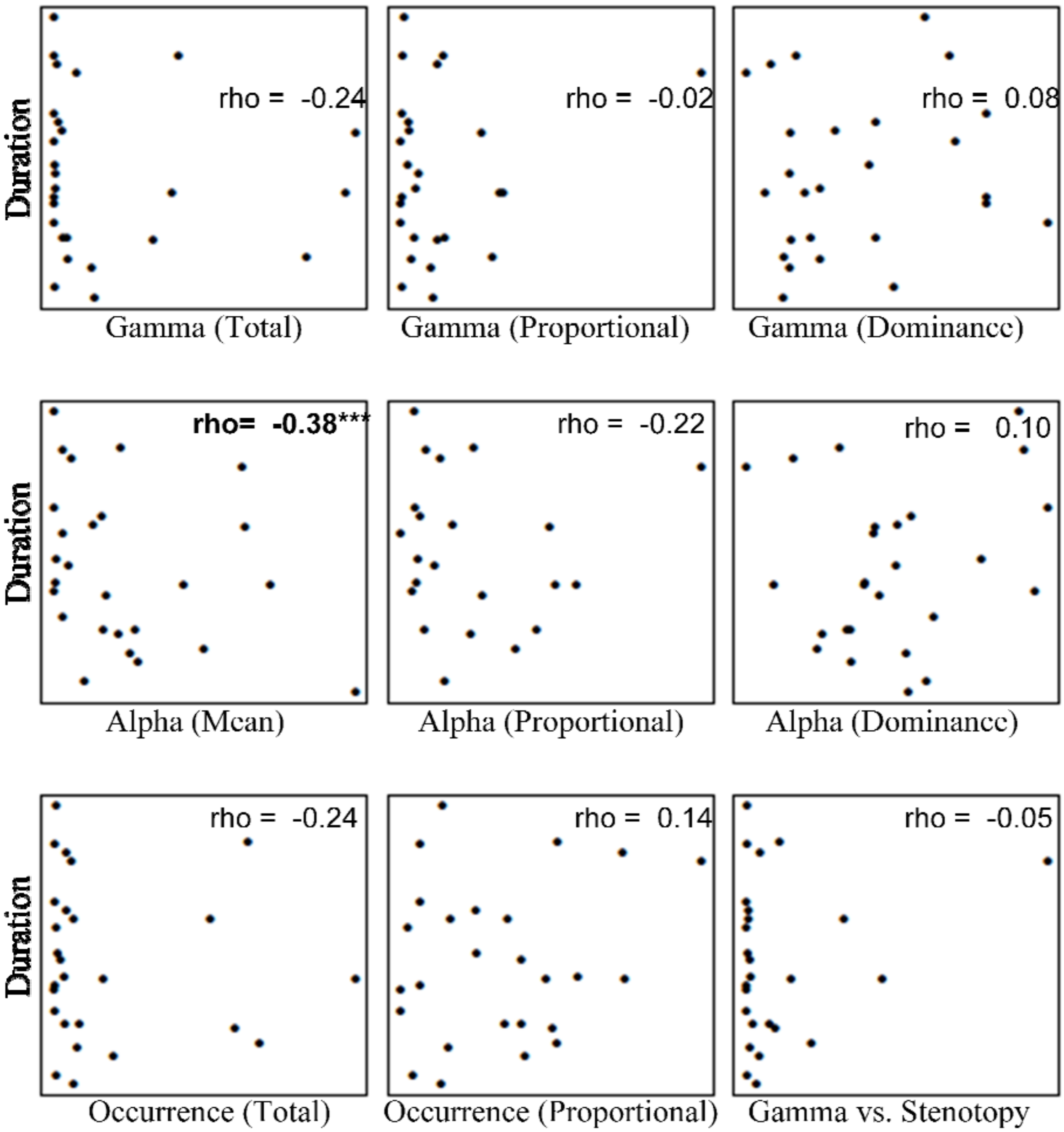


Figure 2.5. Abundance vs. Duration, Dataset 1: Ordovician-Silurian genera. Significance: *p*≤0.15 *; *p*≤0.10**; *p*≤0.05***. Note: a positive rho for Gamma (Rank) or Alpha (Dominance) indicates a negative relationship.

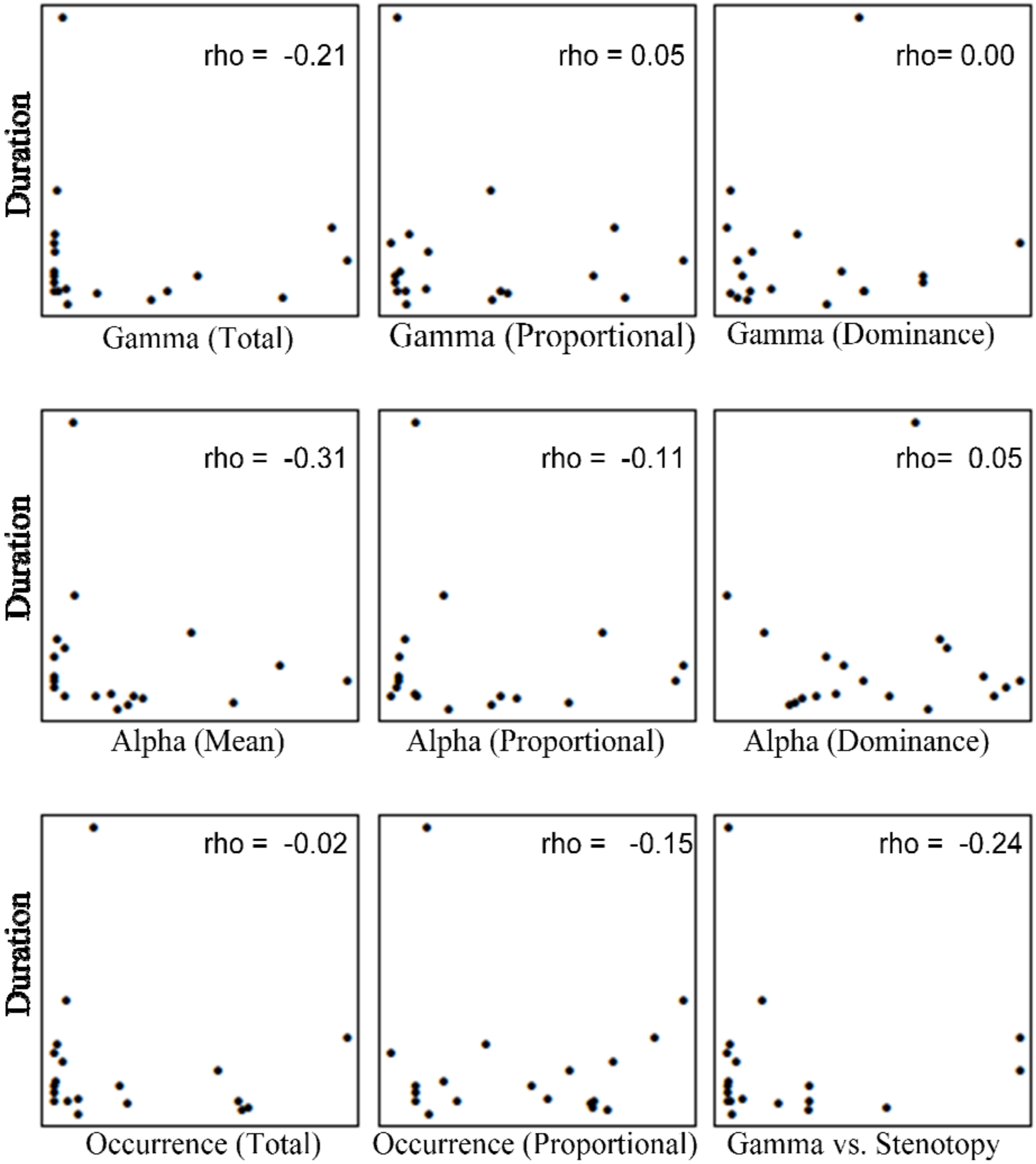


Figure 2.6. Abundance vs. Duration, Dataset 2: Ordovician-Silurian families. Significance: *p*≤0.15 *; *p*≤0.10**; *p*≤0.05***. Note: a positive rho for Gamma (Rank) or Alpha (Dominance) indicates a negative relationship.

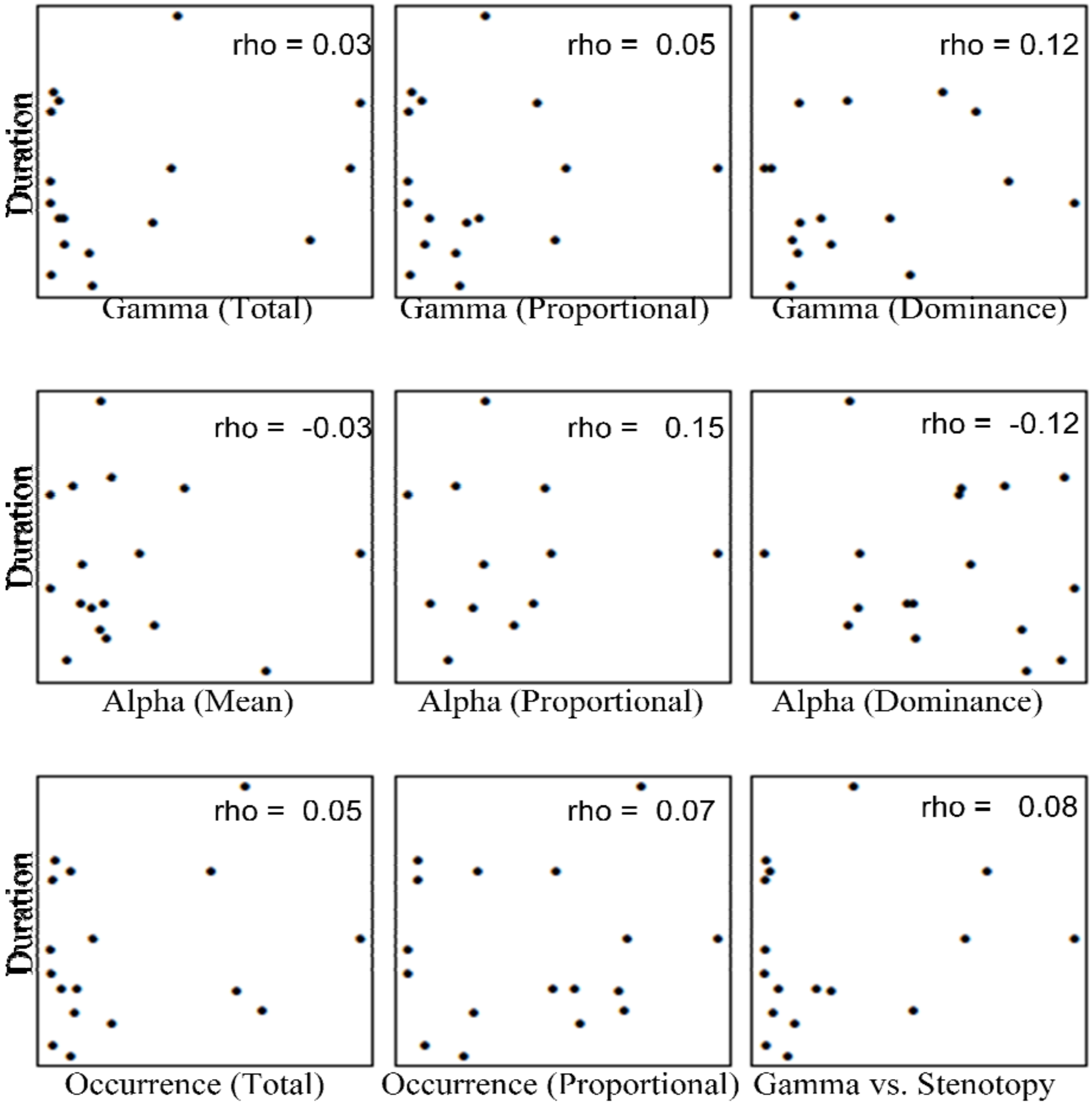


Figure 2.7. Abundance vs. Duration, Dataset 3: Ordovician-only genera. Significance: *p*≤0.15 *; *p*≤0.10**; *p*≤0.05***. Note: a positive rho for Gamma (Rank) or Alpha (Dominance) indicates a negative relationship.

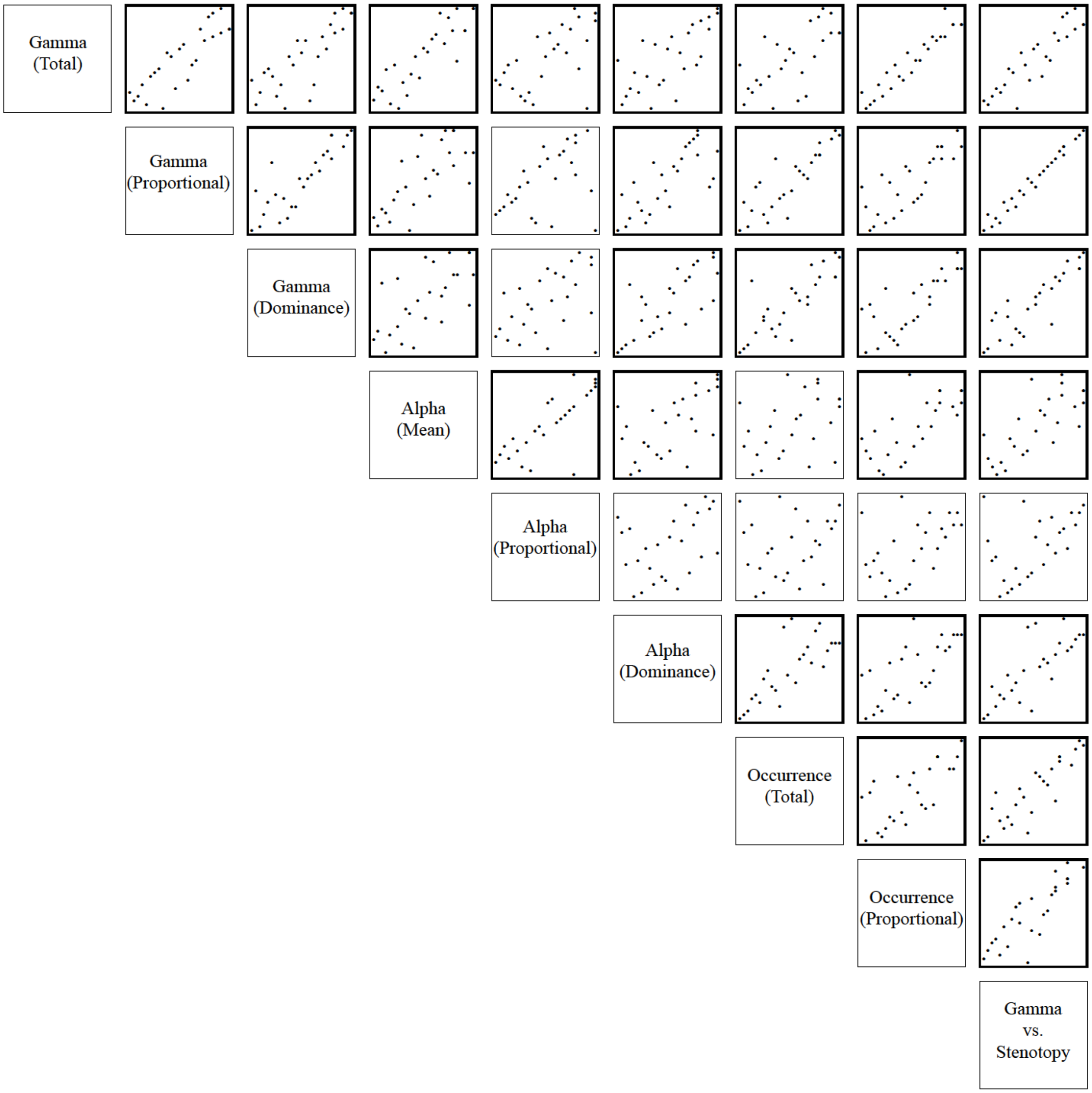


Figure 2.8. Correlation of Data Metrics. Each metric has been rescaled to show ranked abundance, with the most abundant taxa represented as number 1 etc. Correlations with a Pearson's coefficient greater than 0.5 are shown in boldface.

APPENDIX A

BRASSFIELD FORMATION COLLECTION DATA

	Alveolites Tabulate Coral	*Arachnophyllum* Rugose Coral	*Aspidopora* Trepostome	*Bellerophontina* Gastropod	*Bumastus* Corynexochida	Calymenid Phacopod	*Chasmatopora* Fenestrate	*Coenites* Tabulate Coral	Conularida Cnidaria	Cornulites Tentaculid
09-Oakes-01	0	1	1	0	0	0	0	0	0	0
09-Oakes-04	0	0	0	0	0	0	0	0	0	0
09-Oakes-35	0	0	9	0	0	0	11	0	0	0
09-Oakes-06	0	0	24	0	0	0	57	0	0	0
09-Oakes-08	3	0	21	0	0	0	23	0	0	1
09-Oakes-09	1	1	20	0	0	0	1	3	0	1
09-Oakes-10	0	0	2	0	0	0	0	0	0	0
09-WestUnion1-01	0	0	0	0	0	0	0	0	0	0
09-WestUnion1-02	0	0	4	0	0	0	0	0	0	1
09-WestUnion1-03	0	1	1	0	0	1	0	0	0	0
09-WestUnion1-05	0	0	1	1	0	3	0	0	0	0
09-WestUnion2-01	0	0	2	0	0	0	0	0	0	0
09-WestUnion2-02	3	0	9	0	0	0	0	0	0	0
09-WestUnion2-03	0	0	0	0	0	0	0	0	0	0
09-WestUnion2-04	0	0	12	0	1	0	0	1	0	31
09-WestUnion3-01a	0	0	2	0	0	1	1	0	0	3
09-WestUnion3-01b	0	0	1	0	0	0	0	0	1	0
09-WestUnion3-02	0	0	0	0	1	0	0	0	1	0
09-WestUnion3-03	0	0	0	0	0	0	0	0	0	0
09-WestUnion3-04	0	0	0	1	0	0	0	0	0	0
09-WestUnion3-05	0	0	6	2	0	3	1	0	0	1
09-BrushCreek-01	0	0	15	0	0	0	0	0	0	0
09-BrushCreek-02	0	0	1	0	0	0	0	0	0	1
09-Cuckoo-01	0	0	0	0	0	0	1	0	0	0
09-Cuckoo-02	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-03	0	0	2	0	0	0	0	0	0	2
09-Cuckoo-04	0	0	0	1	0	0	0	0	0	0
09-Manchester-01	1	0	1	0	0	0	0	0	0	0
09-Manchester-03	0	0	3	0	0	0	0	0	0	0
09-Manchester-05	0	0	0	0	0	2	0	0	1	0
09-SugarGrove-01	0	0	8	0	0	0	0	8	4	0
09-SugarGrove-02	0	0	8	0	0	0	0	5	0	0
09-Orescue-01	0	0	0	0	0	0	0	0	0	0
09-Owingsville1-01	0	0	0	0	0	0	0	0	0	0

	Clathropora Cryptostome	*Cyathophyllum* Rugose Coral	*Dalejina* Orthid	*Dalmanites* Phacopod	*Dinophyllum* Rugose Coral	*Dolerorthis* Orthid	*Eospirifer* Spiriferid	*Encrinurus* Phacopod	*Fardenia* Orthotedia	*Favosites* Tabulate Coral
09-Oakes-01	0	0	0	0	0	0	0	0	0	1
09-Oakes-04	0	0	1	0	0	2	0	0	0	0
09-Oakes-35	0	0	4	0	0	1	0	0	0	2
09-Oakes-06	10	0	3	0	0	0	0	0	2	9
09-Oakes-08	1	0	0	0	0	0	0	0	0	3
09-Oakes-09	0	0	0	0	0	2	0	0	0	5
09-Oakes-10	0	0	7	0	0	0	0	0	0	0
09-WestUnion1-01	0	0	0	0	0	0	0	0	0	0
09-WestUnion1-02	0	0	1	0	6	0	0	0	0	0
09-WestUnion1-03	0	0	2	0	1	0	0	0	0	0
09-WestUnion1-05	0	0	3	1	0	0	0	0	0	0
09-WestUnion2-01	1	0	2	0	1	0	0	0	0	0
09-WestUnion2-02	0	0	0	0	4	0	0	0	0	2
09-WestUnion2-03	0	0	5	0	0	0	0	0	5	0
09-WestUnion2-04	3	0	3	0	0	0	0	0	0	0
09-WestUnion3-01a	4	0	4	0	5	1	0	0	0	6
09-WestUnion3-01b	0	0	9	0	1	0	0	0	0	2
09-WestUnion3-02	1	0	19	0	0	0	0	1	8	0
09-WestUnion3-03	0	0	0	0	0	0	0	0	2	0
09-WestUnion3-04	0	0	1	0	0	0	0	0	0	0
09-WestUnion3-05	8	0	2	0	0	0	1	0	3	12
09-BrushCreek-01	0	0	1	0	1	3	0	0	0	1
09-BrushCreek-02	0	0	5	0	1	0	2	0	0	1
09-Cuckoo-01	0	0	13	0	4	0	0	0	0	3
09-Cuckoo-02	0	0	1	0	0	0	0	0	0	1
09-Cuckoo-03	0	0	3	0	0	0	0	0	1	2
09-Cuckoo-04	0	0	0	0	1	0	0	0	0	1
09-Manchester-01	0	1	0	1	0	0	0	0	0	0
09-Manchester-03	0	0	1	0	0	0	0	0	0	0
09-Manchester-05	0	0	0	0	0	0	0	0	0	0
09-SugarGrove-01	0	1	0	0	39	0	0	0	0	4
09-SugarGrove-02	0	4	0	0	12	0	0	0	1	1
09-Orescue-01	0	0	0	0	2	0	0	0	5	0
09-Owingsville1-01	0	0	0	0	11	0	0	0	0	0

	Fenestellid Bryozoan	*Glyptorthis* Orthid	*Hallopora* Trepostome	*Heliolites* Tabulate Coral	*Helopora* Cryptostome	*Hemitrypa* Fenestrate	*Hormotoma* Gastropod	Horn Coral	*Illaenus* Corynexochida	*Leptaena* Strophomenid	*Lyellia* Tabulate Coral
09-Oakes-01	0	0	0	0	0	0	0	0	0	0	0
09-Oakes-04	0	1	0	0	0	0	0	0	0	0	0
09-Oakes-35	14	6	0	0	0	10	0	0	0	0	0
09-Oakes-06	11	0	21	0	0	30	1	7	0	16	0
09-Oakes-08	1	0	0	1	5	6	0	0	0	0	0
09-Oakes-09	0	0	0	0	6	1	0	0	0	0	0
09-Oakes-10	0	0	0	0	0	0	0	0	0	0	0
09-WestUnion1-01	2	0	0	0	0	0	0	0	0	1	0
09-WestUnion1-02	8	1	2	0	5	0	0	0	0	0	0
09-WestUnion1-03	0	3	0	0	0	3	0	0	0	0	0
09-WestUnion1-05	1	0	0	0	0	0	1	3	0	2	0
09-WestUnion2-01	0	0	0	0	0	2	0	0	0	0	0
09-WestUnion2-02	14	0	0	0	0	0	0	0	0	0	0
09-WestUnion2-03	2	0	0	0	0	3	0	0	0	0	0
09-WestUnion2-04	11	1	8	0	4	3	0	0	0	1	0
09-WestUnion3-01a	7	2	1	1	621	17	8	3	2	0	4
09-WestUnion3-01b	0	6	0	0	0	0	0	3	0	1	1
09-WestUnion3-02	0	2	0	0	75	0	9	0	1	1	0
09-WestUnion3-03	0	2	0	0	0	0	0	0	0	0	0
09-WestUnion3-04	0	3	0	0	1	0	1	10	0	0	0
09-WestUnion3-05	1	3	0	2	44	3	2	0	0	5	1
09-BrushCreek-01	4	0	0	0	0	1	0	0	0	0	0
09-BrushCreek-02	1	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-01	1	2	0	0	0	4	0	2	0	0	0
09-Cuckoo-02	0	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-03	2	0	0	0	0	0	0	6	0	0	0
09-Cuckoo-04	1	1	0	0	0	0	0	0	0	0	0
09-Manchester-01	0	0	0	0	1	0	0	1	0	0	0
09-Manchester-03	1	0	0	0	0	1	0	0	0	0	0
09-Manchester-05	0	0	0	0	0	0	0	0	0	0	0
09-SugarGrove-01	27	0	5	2	1	19	0	40	0	3	0
09-SugarGrove-02	14	0	4	1	0	7	0	7	0	4	0
09-Orescue-01	0	0	0	0	0	0	0	0	0	0	0
09-Owingsville1-01	0	1	0	0	0	0	0	1	0	0	0

	Nautiloid	*Oxydiscus* Gastropod	*Pachydictya* Cryptostome	*Phaenopora* Cryptosome	*Platystoma* Gastropod	*Platystrophia* Orthid	*Plectatrypa* Atrypid	*Pterinea* Bivalve	*Ptilodictya* Cryptostome	Ramose Bryozoan
09-Oakes-01	1	1	0	1	2	0	0	0	0	0
09-Oakes-04	2	0	0	0	0	0	0	0	0	0
09-Oakes-35	2	0	0	0	1	7	0	0	0	2
09-Oakes-06	0	0	0	0	0	2	0	0	0	14
09-Oakes-08	0	0	1	0	0	0	1	0	0	21
09-Oakes-09	0	0	0	0	0	0	5	0	0	11
09-Oakes-10	1	1	0	0	0	1	0	0	0	1
09-WestUnion1-01	0	0	0	0	0	0	0	0	0	1
09-WestUnion1-02	0	0	2	0	0	0	0	0	0	0
09-WestUnion1-03	2	0	0	0	0	0	0	0	0	1
09-WestUnion1-05	0	0	0	0	0	0	0	0	3	0
09-WestUnion2-01	0	0	0	0	0	0	0	0	0	0
09-WestUnion2-02	0	0	8	0	0	0	0	0	0	3
09-WestUnion2-03	1	0	0	0	0	0	0	0	0	0
09-WestUnion2-04	0	0	0	0	0	0	0	0	1	0
09-WestUnion3-01a	4	1	4	0	0	1	0	0	7	0
09-WestUnion3-01b	0	1	0	0	0	2	0	0	0	0
09-WestUnion3-02	0	0	0	0	0	0	0	0	0	0
09-WestUnion3-03	0	0	0	0	1	0	0	0	0	0
09-WestUnion3-04	0	0	0	0	1	3	0	0	0	1
09-WestUnion3-05	0	0	0	0	0	0	0	1	3	0
09-BrushCreek-01	0	0	1	0	0	0	0	0	0	0
09-BrushCreek-02	0	0	1	0	0	0	0	0	0	0
09-Cuckoo-01	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-02	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-03	0	0	0	0	0	0	0	0	0	0
09-Cuckoo-04	0	0	0	0	0	0	0	0	0	0
09-Manchester-01	0	0	0	0	0	0	0	0	0	0
09-Manchester-03	0	0	0	0	0	0	0	0	1	0
09-Manchester-05	0	0	0	0	0	0	0	0	0	0
09-SugarGrove-01	0	0	4	1	0	0	0	0	1	2
09-SugarGrove-02	0	0	0	0	0	0	0	0	1	1
09-Orescue-01	0	0	0	0	0	4	0	0	0	0
09-Owingsville1-01	0	0	0	0	0	0	0	0	0	0

	Resserella Orthid	*Rhegmaphyllum* Rugose Coral	*Rhinopora* Cystopora	*Rhynchotreta* Rhynchonellid	*Sowerbyella* Strophomenid	*Stegerhynchus* Rhynchonellid	*Streptelasma* Rugose Coral	Streptelasmiid	*Strohonella* Strophomenid	*Syringopora* Tabulate Coral
09-Oakes-01	32	0	0	0	0	0	0	10	0	0
09-Oakes-04	20	0	0	1	0	0	0	0	0	0
09-Oakes-35	0	0	0	3	1	6	0	19	0	0
09-Oakes-06	3	0	3	4	0	4	0	0	0	0
09-Oakes-08	6	0	0	2	0	3	0	0	0	0
09-Oakes-09	3	0	0	1	0	0	0	0	0	0
09-Oakes-10	40	0	0	0	2	2	2	0	0	0
09-WestUnion1-01	6	0	0	2	0	0	0	17	0	0
09-WestUnion1-02	14	0	0	1	1	6	0	1	0	0
09-WestUnion1-03	7	0	0	0	1	0	2	8	0	0
09-WestUnion1-05	5	0	0	0	0	3	0	0	0	0
09-WestUnion2-01	15	0	0	3	0	0	4	1	0	0
09-WestUnion2-02	3	0	0	2	0	1	6	8	0	0
09-WestUnion2-03	22	0	0	0	1	0	0	9	0	0
09-WestUnion2-04	29	0	0	0	1	0	0	3	0	0
09-WestUnion3-01a	19	0	0	1	0	1	0	0	0	2
09-WestUnion3-01b	12	0	0	0	1	0	4	1	0	0
09-WestUnion3-02	14	0	0	0	2	0	0	2	0	0
09-WestUnion3-03	28	0	0	0	0	0	0	7	0	0
09-WestUnion3-04	13	0	0	0	1	8	3	0	0	0
09-WestUnion3-05	30	0	2	1	5	1	2	4	0	0
09-BrushCreek-01	7	2	0	2	0	0	8	4	0	0
09-BrushCreek-02	6	1	0	0	0	0	0	3	0	1
09-Cuckoo-01	29	0	0	7	0	2	1	21	0	0
09-Cuckoo-02	18	0	0	0	0	0	0	14	0	0
09-Cuckoo-03	4	0	0	1	0	2	0	0	0	0
09-Cuckoo-04	18	0	0	2	0	0	0	0	2	0
09-Manchester-01	4	0	0	0	0	0	3	6	0	0
09-Manchester-03	26	0	1	2	0	0	0	3	0	0
09-Manchester-05	12	0	0	0	0	0	5	4	0	0
09-SugarGrove-01	0	0	0	0	0	0	7	604	0	2
09-SugarGrove-02	0	0	0	0	0	0	0	180	0	0
09-Orescue-01	0	0	0	1	0	0	0	33	0	0
09-Owingsville1-01	0	0	0	0	1	0	0	25	0	0

	Thin Ramose Bryozoan	Trepostome	*Trimerus* Phacopod	*Triplesia* Orthotetida
09-Oakes-01	0	1	0	0
09-Oakes-04	0	0	0	0
09-Oakes-35	0	0	0	0
09-Oakes-06	0	0	0	0
09-Oakes-08	2	7	0	0
09-Oakes-09	9	3	0	0
09-Oakes-10	0	0	0	0
09-WestUnion1-01	0	0	0	0
09-WestUnion1-02	0	1	0	1
09-WestUnion1-03	0	2	0	0
09-WestUnion1-05	0	0	0	1
09-WestUnion2-01	0	1	0	0
09-WestUnion2-02	0	0	0	0
09-WestUnion2-03	0	0	0	0
09-WestUnion2-04	0	0	0	0
09-WestUnion3-01a	8	1	0	1
09-WestUnion3-01b	1	2	0	0
09-WestUnion3-02	0	2	0	0
09-WestUnion3-03	0	0	0	0
09-WestUnion3-04	0	1	0	0
09-WestUnion3-05	0	3	0	0
09-BrushCreek-01	0	2	0	0
09-BrushCreek-02	1	0	0	0
09-Cuckoo-01	0	0	0	0
09-Cuckoo-02	0	0	0	0
09-Cuckoo-03	0	0	0	0
09-Cuckoo-04	0	1	0	0
09-Manchester-01	0	2	1	0
09-Manchester-03	1	3	0	0
09-Manchester-05	0	2	0	0
09-SugarGrove-01	3	0	0	0
09-SugarGrove-02	0	0	0	0
09-Orescue-01	0	0	0	0
09-Owingsville1-01	0	0	0	0

Included above is a table depicting the faunal data collected from the Silurian Brassfield Formation of Southwestern Ohio and Northern Kentucky for this study. A total of 43 samples were collected from the area. Nine of these fell below the minimum number (24) of individuals required for a valid sample, and were culled from the dataset. These nine are not included in the above table.

The remaining 34 samples shown above do not include any of the other data culling procedures performed in the study – i.e. removal of singletons, removal of epiboles, and the bootstrap re-sampling process (see **Methods**).

Similar data tables depicting Holland and Patzkowsky's (2007) Ordovician data from the underlying type-Cincinnatian Series can be accessed from the Paleobiology Database (www.paleodb.com).

APPENDIX B
BRACHIOPODS AND TAXONOMIC EXPLANATIONS

Appendix B1. List of Tested Brachiopod Genera and Extinction Status at the Ordovician/Silurian

Genus	Global	Regional	Genus	Global	Regional
Dalmanella	Survivor	Victim	*Platystrophia*	Survivor	Survivor
Resserella	**Survivor**	**Immigrant**	***Dalejina***	**Originated**	**Originated**
Plectorthis	Victim	Victim	***Fardenia***	**Survivor**	**Immigrant**
Hebertella	Victim	Victim	***Dolerorthis***	**Survivor**	**Immigrant**
Sowerbyella	Survivor	Survivor	***Triplesia***	**Originated**	**Originated**
Eochonetes	Victim	Victim	***Eospirifer***	**Originated**	**Originated**
Leptaena	Survivor	Survivor	*Zygospira*	Survivor	Victim
Rafinesquina	Victim	Victim	***Plectatrypa***	**Survivor**	**Immigrant**
Eridorthis	Survivor	Victim	***Rhynchotreta***	**Originated**	**Originated**
Glyptorthis	Survivor	Survivor	*Orthorhynchula*	Victim	Victim
Plaesiomys	Victim	Victim	*Trematis*	Victim	Victim
Retrosirostra	Victim	Victim	*Rhynchotrema*	Victim	Victim
Holtedahlina	Survivor	Victim	***Stegerhynchus***	**Originated**	**Originated**
Hiscobeccus	Victim	Victim	***Strophonella***	**Originated**	**Originated**
Petrocrania	Survivor	Victim			

The above table lists the Brachiopod genera tested in this study. Global extinction-status was determined with Tapanila's (2006) modified version of Sepkoski's (2002) compendium of genera. Regional extinction-status was based on presence or absence in the collection data used in this study (Holland and Patzkowsky 2007, and the new Brassfield data).

A taxon was considered a "Survivor" if it was present in both the Ordovician and Silurian. A taxon was considered a "Victim" if it was present in the Ordovician, but not in the Silurian. A taxon was considered "Originated" if it was present in the Silurian, but not in the Ordovician. A taxon was considered an "Immigrant" if it was present in the Ordovician and Silurian according to Tapanila (2006), but was not present in Holland and Patzkowsky's (2007) type-Cincinnatian Series dataset.

Taxa that "Originated" or were "Immigrants" from a regional perspective (shown in boldface) were omitted from the survivorship analyses, since these taxa had no pre-extinction abundance data available. Once these taxa were removed from the dataset, status as a victim or survivor was based solely on the Global column.

Appendix B2. List of Tested Brachiopod Genera and Durations

Genus	Duration (my)	Genus	Duration (my)
Dalmanella	39.6	*Platystrophia*	55.7
Resserella	51.9	*Dalejina*	53.8
Plectorthis	39.8	*Fardenia*	32.7
Hebertella	17.2	*Dolerorthis*	63.4
Sowerbyella	27.3	*Triplesia*	43.4
Eochonetes	05.3	*Eospirifer*	55.5
Leptaena	117.4	*Zygospira*	13.9
Rafinesquina	27.3	*Plectatrypa*	26.0
Eridorthis	38.0	*Rhynchotreta*	27.8
Glyptorthis	41.6	*Orthorhynchula*	25.0
Plaesiomys	13.2	*Trematis*	20.8
Retrosirostra	07.3	*Rhynchotrema*	17.9
Holtedahlina	17.9	*Stegerhynchus*	31.3
Hiscobeccus	11.3	*Strophonella*	41.5
Petrocrania	212.5		

The above table lists the brachiopod genera tested in this study. Duration in the fossil record was taken by subtracting the recorded time of global first occurrence from the recorded time of global last occurrence. Occurrence data was taken from Tapanila's (2006) modified version of Sepkoski's (2002) compendium.

The following is an explanation of several caveats associated with the taxonomic identification of the genera: *Dalmanella*, *Platystrophia*, *Strophonella*, and *Leptaena.* These caveats did not meaningfully affect the analyses or substantially change any results.

Dalmanella. - The identification of the Cincinnati Arch's Late Ordovician dalmanellid has undergone numerous revisions, particularly between the genera *Dalmanella* and *Onniella*. The latest taxonomic revision of this genus suggests that it may be an entirely new genus more closely related to *Paucicrura* than *Dalmanella* or *Onniella* (J. Jin: personal communication 2010). This study uses the range of *Dalmanella* (~40 my) for the analyses. This did not meaningfully affect the analyses since all members of the subfamily dalmanellinae have roughly equivalent ranges.

Platystrophia.- Holland and Patzkowsky's (2007) original dataset of the C1-C6 distinguished between *Platystrophia ponderosa* and *Platystrophia sp*. based on the distinctiveness of *P. ponderosa* relative to other *Platystrophia* species. This study, however, combined *P. ponderosa* counts with all other *Platystrophia species* in order to keep the analyses at the genus level.

Strophonella.- This genus was removed from the dataset following the culling and re-sampling procedures, as the number of observed individuals fell below the minimum (<2).

Leptaena and Petrocrania.- The genera *Leptaena* and *Petrocrania* had to be culled from the duration analyses (see **Results, Appendix E**) due to their extraordinarily long range and the possibility that they are so-called "taxonomic wastebaskets" (Plotnick and Wagner 2006).

APPENDIX C

LOCALITIES LIST

1. Sugar Grove Church, Kentucky - 38°6'11.4″ N, 83°49'43.3″ W

Located on Stepstone Road in the town of Owingsville, north of Sugar Grove Church (~500 ft), on east and west bluffs before the Interstate-64 underpass. Laub (1979)

Owingsville1, Kentucky - 38°7'24″ N, 83°45'30.8″ W

Located ½ mile west of the Owingsville exit off of Interstate 64, on the south side of the highway. Blake and Ettensohn (2009)

2. Owingsville Rescue, Kentucky - 38°8'39.6″ N, 83°44'26.6″ W

Located 1.3 miles east of Owingsville on U.S. Route 60, about 200 ft. east of Karrick Drive, on both the north and south sides of the road. Rexroad (1967); Laub (1979)

3. Oakes Quarry Park, Ohio - 39°48'50.7″ N, 83°59'21.9″ W

Oakes Quarry Park, 1267 E. Xenia Drive, Fairborn, Ohio. A former quarry now converted into a fossil collecting park. Formerly known as the Reed North Quarry. Schneider and Ausich (2002)

4. West Union 1, Ohio - 38°49'38.9″ N, 83°30'20.3″ W

Located on the west side of Ohio State Highway 41, north of West Union. Approximately 0.5 miles north of the intersection at Lick Run Road at Ohio State Highway 41. Fuentes (2003)

5. West Union 2, Ohio - 38°49'23.9″ N, 83°30'28.5″ W

Located on the west side of Ohio State Highway 41, north of West Union. Approximately 0.5 miles south of West Union 1, on the north side of the intersection at Lick Run Road and Ohio State Highway 41. Fuentes (2003)

6. West Union 3, Ohio - 38°49'19.4″ N, 83°30'38.8″ W

Located on the west side of Ohio State Highway 41, north of West Union. Just south of the intersection at Lick Run Road and Ohio State Highway 41

7. Cuckoo Roadcut, Ohio - 39°1'54.6″ N, 83°28'52.2″ W

A large roadcut located at the intersection of Ohio State Highway 73 and Cuckoo Road, one mile west of Serpent Mound State Park. McLaughlin et al. (2008)

8. Manchester, Ohio - 38°44'34.2″ N, 83°36'44.6″ W

A roadcut on the east side of the road, approximately six miles north of Manchester, Ohio on Ohio State Highway 136, near the intersection with Ohio State Highway 41. Laub (1979)

9. Brush Creek, Ohio - 38°41'2″ N, 83°27'31.8″ W

A large roadcut near the intersection of Brush Creek road and U.S. Route 52 near Manchester, Ohio. Rexroad (1967) describes several other Brassfield roadcuts in this area, but this roadcut was the only one seen.

APPENDIX D
[R] CODE

Bootstrap Resampling Technique

The FixSample function re-samples (g) taxa from each sample within a matrix (x). Samples must be represented as rows and taxa must be represented as columns.

```
FixSample<-function (x,g)
{
     FixMatrix<-
     matrix(1:ncol(x),ncol=1,nrow=ncol(x),dimnames=list(c(colnam
     es(x)),c("Assignment")))
     for (i in 1:nrow(x))
     {
          SampleVector<-vector()
          for (j in 1:ncol(x))
          {
               SpeciesAbundance<-x[i,j]
               if (SpeciesAbundance>0)
               {
                    Counts<-vector()
                    for (t in 1:SpeciesAbundance)
                    {
                         Counts[t]<-j
                         SampleVector<-c(SampleVector,Counts)}
                    }
               }
               Sampled<-sample(SampleVector,g,replace=T)
               Tabled<-as.data.frame(table(Sampled))
               colnames(Tabled)<-c("Assignment")
               FixMatrix<-
          merge(FixMatrix,Tabled,by='Assignment',all=T)
          }
     }
     FixMatrix[is.na(FixMatrix)]<-0
     FixMatrix$Assignment<-NULL
     FixMatrix
}
```

The Replacement function runs the FixSample function (z) times on dataset (y). The output from this function is stored as a 3-dimensional array, where the y-axis is samples, x-axis is taxa, and the z-axis is the iteration of the bootstrap.

```
Replacement<-function (y,z)
{
     FixArray<-array(NA,c(nrow(y),ncol(y),z))
     for (i in 1:z)
     {
          print(i)
          TempMatrix<-FixSample(y)
          TempMatrix<-as.data.frame(t(TempMatrix))
          for (j in 1:nrow(y))
          {
               for (t in 1:ncol(y))
               {
                    FixArray[j,t,i]<-TempMatrix[j,t]
               }
          }
     }
     FixArray
}
```

The LastMatrix function calculates the mean number of each taxon from all 10,000 simulations. The 3D-Array from the Replacement function is (x), the original matrix is (y), and the number of iterations of the bootstrap is (z).

```
LastMatrix<-function (x,y,z)
{
     FinalMatrix<-
     matrix(NA,nrow=nrow(y),ncol=ncol(y),dimnames=list(c(rowname
     s(y)),c(colnames(y))))
     for (i in 1:nrow(y))
     {
          for (j in 1:ncol(y))
          {
               FinalMatrix[i,j]<-ceiling(mean(x[i,j,1:z]))
          }
     }
     FinalMatrix
}
```

Abundance Calculations

The function AbundanceFunction calculates the metrics “Gamma”, “Alpha”, “Density”, Gamma (Proportional)”, “Alpha (Proportional)”, “Alpha (Dominance)”, “Occurrence”, “Occurrence (Proportional)”, and “Gamma (Dominance)” for each sequence. This function must be run once for each sequence, and the outputs of each run merged into a single dataset using the merge function (w/ all=T). This mater dataset of all sequences must then be merged with another table that lists each brachiopod genera or family to be statistically analyzed, and their durations and survivorship status (similar to the table shown in Appendix B).

```
AbundanceFunction<-function (x)
{
     AbundanceMatrix<-
     matrix(NA,nrow=ncol(x),ncol=8,byrow=T,dimnames=list(c(names
     (x)),c("Gamma","Alpha","Density","GammaProportional","Alpha
     Proportional","AlphaDominance","Occurrence","OccurrenceProp
     ortional")))
     NAVariant<-x    #Creates a copy of the original matrix
     PAVariant<-x    #Creates a copy of the original matrix
     OVariant<-x      #Creates a copy of the original matrix
     NAVariant[x==0]<-NA  #Replaces all zeroes with NA
     OVariant[x>0]<-1  # Replaces all number >0 with 1
     for (i in 1:ncol(x))
     {
          GammaTemp<-sum(x[[i]])   #Sums the number of each taxa
     across all samples
          AlphaTemp<-mean(NAVariant[[i]],na.rm=T)  #Averages
          number of each taxon across all samples
          TLength<-x[,i]
          TLength<-length(TLength[TLength==0])
          DensityTemp<-GammaTemp/(TLength+1) #Calculates density
          GammaPropTemp<-(Gamma/sum(x)) #Calculates Gamma
     (Proportional)
          Occurence<-sum(OVariant[[i]])
          OccurenceProportional<-Occurence/nrow(x)
          AbundanceMatrix[i,1]<-GammaTemp
          AbundanceMatrix[i,2]<-AlphaTemp
          AbundanceMatrix[i,3]<-DensityTemp
          AbundanceMatrix[i,4]<-GammaPropTemp
```

```
          AbundanceMatrix[i,7]<-Occurrence
          AbundanceMatrix[i,8]<-OccurrenceProportional
     }
     for (i in 1:ncol(x))
     {
          for (j in 1:nrow(x))
          {
               PATemp<-x[j,i]/sum(x[j,])
               PAVariant[j,i]<-PATemp
          }
     }
     PAVariant[PAVariant==0]<-NA
     for (i in 1:ncol(x))
     {
          AlphaPropTemp<-mean(PAVariant[[i]],na.rm=T)
          AbundanceMatrix[i,5]<-AlphaPropTemp
     }
     Trans<-t(x)
     NewT<-
     matrix(NA,nrow=nrow(Trans),ncol=ncol(Trans),dimnames=list(c
     (names(x)),c(rownames(x))))
     for (i in 1:ncol(Trans))
     {
          RTemp<-rank(Trans[,i],ties.method="max")
          NewT[,i]<-RTemp
     }
     for (i in 1:ncol(Trans))
     {
          NewT[,i]<-1+abs(NewT[,i]-length(NewT[,i]))
     }
     RankAlphasNA<-t(NewT)
     RankAlphasNA[RankAlphasNA==min(RankAlphasNA)]<-NA
     for (i in 1:ncol(RankAlphasNA))
     {
          DominanceTemp<-mean(RankAlphasNA[,i],na.rm=T)
          AbundanceMatrix[i,6]<-DominanceTemp  # Alpha Dominance
     }
     AbundanceMatrix<-as.data.frame(AbundanceMatrix)
     AbundanceMatrix
     GammaRanked<-rank(AbundanceMatrix[,1],ties.method="max")
     Truth<-cbind(AbundanceMatrix,GammaRanked)
     Truth$GammaRanked<-1+abs(Truth$GammaRanked-
length(Truth$GammaRanked))
     Truth
}
```

Cross Sequence Abundance Calculations

The AbundanceMaster formula must be applied once to the master dataset created from applying the AbundanceFunction to each sequence. This formula simply totals or averages across each sequence, depending on the metric involved.

```
AbundanceMaster<-function (x)
{
     MeanMatrix<-
     matrix(NA,ncol=nrow(x),nrow=15,dimnames=list(c("Gamma(Mean)
     ","Alpha(Mean)","Density","Gamma(Proportional)","Alpha(Prop
     ortional)","Occurrence(Total)","Gamma(Total)","Gamma(Domina
     nce)","Alpha(Dominance)","Occurrence(Mean)","Occurrence(Pro
     portional)","SepkoskiRange","SepkoskiVictimsSurviviors","PB
     DRange","PBDVictimsSurvivors"),c(rownames(x))))
     for (i in 1:nrow(x))
     {
          Trans<-
          mean(c(x$Gamma[i],x$Gamma.1[i],x$Gamma.2[i],x$Gamma.3[
          i],x$Gamma.4[i],x$Gamma.5[i],x$Gamma.6[i]),na.rm=T)
          MeanMatrix[1,i]<-Trans
          Trans.1<-
          mean(c(x$Alpha[i],x$Alpha.1[i],x$Alpha.2[i],x$Alpha.3[
          i],x$Alpha.4[i],x$Alpha.5[i],x$Alpha.6[i]),na.rm=T)
          MeanMatrix[2,i]<-Trans.1
          Trans.2<-
          mean(c(x$Density[i],x$Density.1[i],x$Density.2[i],x$De
          nsity.3[i],x$Density.4[i],x$Density.5[i],x$Density.6[i
          ]),na.rm=T)
          MeanMatrix[3,i]<-Trans.2
          Trans.3<-
          mean(c(x$GammaProportional[i],x$GammaProportional.1[i]
          ,x$GammaProportional.2[i],x$GammaProportional.3[i],x$G
          ammaProportional.4[i],x$GammaProportional.5[i],x$Gamma
          Proportional.6[i]),na.rm=T)
          MeanMatrix[4,i]<-Trans.3
          Trans.4<-
          mean(c(x$AlphaProportional[i],x$AlphaProportional.1[i]
          ,x$AlphaProportional.2[i],x$AlphaProportional.3[i],x$P
          ropAlpha.4[i],x$AlphaProportional.5[i],x$AlphaProporti
          onal.6[i]),na.rm=T)
          MeanMatrix[5,i]<-Trans.4
```

```
        Trans.5<-
        sum(c(x$Occurence[i],x$Occurrence.1[i],x$Occurrence.2[
        i],x$Occurrence.3[i],x$Occurrence.4[i],x$Occurrence.5[
        i],x$Occurrence.6[i]),na.rm=T)
        MeanMatrix[6,i]<-Trans.5
        Trans.6<-
        sum(c(x$Gamma[i],x$Gamma.1[i],x$Gamma.2[i],x$Gamma.3[i
        ],x$Gamma.4[i],x$Gamma.5[i],x$Gamma.6[i]),na.rm=T)
        MeanMatrix[7,i]<-Trans.6
        Trans.7<-
        mean(c(x$GammaRanked[i],x$GammaRanked.1[i],x$GammaRank
        ed.2[i],x$GammaRanked.3[i],x$GammaRanked.4[i],x$GammaR
        anked.5[i],x$GammaRanked.6[i]),na.rm=T)
        MeanMatrix[8,i]<-Trans.7
        Trans.8<-
        mean(c(x$AlphaDominance[i],x$AlphaDominance.1[i],x$Alp
        haDominance.2[i],x$AlphaDominance.3[i],x$AlphaDominanc
        e.4[i],x$AlphaDominance.5[i],x$AlphaDominance.6[i]),na
        .rm=T)
        MeanMatrix[9,i]<-Trans.8
        Trans.9<-
        mean(c(x$Occurence[i],x$Occurence.1[i],x$Occurence.2[i
        ],x$Occurence.3[i],x$Occurence.4[i],x$Occurence.5[i],x
        $Occurence.6[i]),na.rm=T)
        MeanMatrix[10,i]<-Trans.9
        Trans.10<-
        mean(c(x$OccurrenceProportional[i],x$OccurrenceProport
        ional.1[i],x$OccurrenceProportional.2[i],x$OccurrenceP
        roportional.3[i],x$OccurrenceProportional.4[i],x$Occur
        renceProportional.5[i],x$OccurrenceProportional.6[i]),
        na.rm=T)
        MeanMatrix[11,i]<-Trans.10
        Trans.15<-x$SRange[i]
        MeanMatrix[18,i]<-Trans.15
        Trans.16<-x$SEOE[i]
        MeanMatrix[19,i]<-Trans.16
        Trans.17<-x$PBDRange[i]
        MeanMatrix[20,i]<-Trans.17
        Trans.18<-x$PBDEOE[i]
        MeanMatrix[21,i]<-Trans.18
    }
    MeanMatrix
}
```

APPENDIX E

DURATION TESTS WITH OUTLIERS INCLUDED

APPENDIX E. Comparison of Dataset 1 results with and without *Leptaena* and *Petrocrania*

	With Outliers		Without Outliers	
Abundance Metric	*p*-values	rho values	*p*-values	rho values
Gamma (Total)	0.37	-0.18	0.23	-0.24
Gamma (Proportional)	0.58	-0.11	0.92	-0.02
Gamma (Dominance)	0.45	0.15	0.64	0.10
Alpha (Mean)	0.04	-0.39	0.05	-0.38
Alpha (Proportional)	0.25	-0.25	0.33	-0.22
Alpha (Dominance)	0.39	0.17	0.63	0.10
Occurrence (Total)	0.67	-0.08	0.32	-0.20
Occurrence (Proportional)	0.93	0.02	0.51	0.14
Gamma vs. Stenotopy	0.54	-0.12	0.82	-0.05