Exploring Predator-Prey Interactions in Devonian Strophomenate Brachiopods

by

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Abstract

Predation is an important process that helps to shape community structure. The study of predation in the fossil record has often used repair scars – traces of failed predatory attacks left on prey individuals – to identify differences in predation pressure across space, time, and taxa. However, fossil studies of communities and predation are often conducted at very different scales: paleocommunities may be sampled over millions of years while the effects of predation can be tested within a single bed or assemblage. Here, I used repair scars on brachiopod prey to evaluate: 1) whether predation is detectable as a driver of fine-scale community structure in the fossil record, and 2) which prey and environmental characteristics most strongly influence the likelihood of an individual being repaired over a broad spatio-temporal scale.

Paleocommunity studies have historically focused on depth and other environmental processes over ecological processes such as predation. This may be due to sampling at large spatio-temporal scales, at which environmental processes overprint finer-scale ecological ones. I directly tested predation and depth as drivers of Late Devonian brachiopod paleocommunities from Iowa over a time interval of ~ 1 My. Ordination of sampled communities revealed that both predation and depth influenced species distribution, but predation was the primary driver.

Individual characteristics such as prey size, ornament, and latitude have been identified as having an influence on the frequency and outcome of predatory attacks. However, these characteristics have infrequently been evaluated for their relative effect size on predation and only at small scales. Here, I examined Mid- to Late Devonian concavo-convex brachiopods from across North America for repair scars and created generalized linear mixed models including six candidate variables to explain and predict the likelihood of an individual being repaired. I found that prey size, shell convexity, and paleolatitude were most strongly associated with repairs, and the effect of size was greater than that of both convexity and paleolatitude. The effect of each of these variables on the likelihood of repair can be attributed to differences in attack frequency: attacks were more frequent on larger, less convex (flatter) individuals living at lower latitudes. The rate of success may have had an additive effect of attacks on larger prey being less successful, resulting in a greater likelihood of repair for these individuals.

As a whole, these studies revealed that predation can have a detectable influence on species distribution in the fossil record, and that prey and environmental characteristics – size, convexity, and paleolatitude in particular – can be used to explain and predict the likelihood of prey individuals being repaired.

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Chapter 1

Introduction

Predation is an important process that influences evolution and community structure. Predation pressure can influence the morphology and behaviour of prey (Bertness, 1977; Palmer, 1990; Chivers et al., 2008; Gravem and Morgan, 2017), and in turn, characteristics of the prey can affect success rates of predatory attacks (Savino and Stein, 1989; Thirgood et al., 2002; Hostetter et al., 2012; Stafford et al., 2015; Mendonca et al., 2021). In the fossil record, it is obviously impossible to witness a predatory attack as it happens, so we depend on predation traces to evaluate predation. Repair scars are common predation traces that result when a crushing predator fails to crush a shelled prey individual (such as a bivalve, gastropod, or brachiopod) and instead breaks off a piece of the shell (Alexander, 1986; Kowalewski, 2002). The prey individual survives and is able to regrow the shell, leaving a scar that is characterized by thinning in the immediate damage area, alteration to any external ornament in the regrown portion, and possible thickening of the regrown portion of the shell. As repair scars track failed attacks, and not mortality, there is ambiguity in their interpretation: a greater frequency of scars in one sample may reflect either an increased rate of attacks – resulting in both an increase in repairs as well as successfully crushed shells – or a decrease in the success rate of the predator (Stafford and Leighton, 2011). Regardless of the cause, detectable differences in repair rates reflect changes to some aspect of predation in or between systems. Here, my goals were to use repair scars to 1) determine whether predation can be detected as a driver of species distribution in fossil communities, and 2) identify which characteristics of prey and their environment are most strongly associated with the likelihood of an individual being repaired and are therefore influential on the rates of predatory attacks and success.

The Devonian is an exciting time to study predation as it was a period of intensifying predation pressure due to the evolution of stronger, more specialized predators (Signor and Brett, 1984). During this time, brachiopods were common and abundant prey (Leighton, 2003a). As sessile animals, brachiopods depend on characteristics of their shells that would either 1) deter a predator from attempting an attack, 2) physically prevent a predator from crushing the shell, or 3) hide the prey animal completely to avoid death by predation. These defensive characteristics are primarily morphological and can be observed even in fossils. During the Paleozoic, brachiopods of varying morphologies commonly lived together as communities, resulting in within-community differences in success and attack rates. As paleocommunities changed through time or across space, the differences in predation rates would become detectable between communities, with greater success frequencies occurring in paleocommunities with more abundant fragile taxa.

Surprisingly, the influence of predation on community structure has never been tested in the fossil record. This may be due to scale, as paleocommunities are commonly sampled across onshore-offshore gradients or very long time intervals (Boucot, 1975; Springer and Bambach, 1985; Brett et al., 1993; Patzkowsky and Holland, 2012). Environmental processes have historically been the primary focus as drivers of paleocommunities (Patzkowsky and Holland, 2012) and there is some evidence that fine-scale processes, such as predation, can be overprinted by these larger-scale environmental processes when sampling scales are large (Lafferty et al., 1994; Forcino et al., 2012). Ecological and other fine-scale processes may, however, still be detectable where sampling is conducted at a finer temporal or spatial resolution (Olszewski and

Patzkowsky, 2001). In chapter 2, I tested predation as a driver of community structure for a suite of brachiopod assemblages from the Late Devonian (Frasnian) of Iowa. A positive result would indicate that predation has had a significant control on community structure since the Paleozoic, and that our understanding of paleocommunities can benefit from the examination of ecological controls.

As previously mentioned, not only can predation exert an influence on prey species, the prey and environments they live in can also influence the attack and success rates of predators. As predators were evolving throughout the Devonian, it is expected that their prey similarly evolved to adapt to these new threats (Vermeij, 1987). Fossils of prey that were better defended against their predators would likely show greater repair rates, as predators would be less successful against strong prey. A number of individual characteristics that influence predation have been identified (Palmer, 1979; Vermeij, 1987; Alexander, 1989; Alexander, 1990; Brett and Walker, 2002; Leighton, 2003b; Johnsen et al, 2013; Harper and Peck, 2016; Leighton and Tyler, 2021 among others) but have infrequently been tested against one another for the strength of their effects. Stafford et al. (2015) did compare the effects of predator abundance, prey size, prey shell thickness, and water energy; finding that predator abundance was the strongest predictor of an individual being repaired. However, this study was limited by its spatial scale, only examining the coastline along Vancouver Island, Canada. In chapter 3 of this thesis, I assessed broad-scale trends in predation on concavo-convex brachiopods from across North America during the Mid- to Late (Givetian to Frasnian) Devonian. I tested six candidate variables to determine which had the strongest influence on the likelihood of an individual brachiopod being repaired. This study can provide understanding into how morphological and environmental characteristics influence predation as well as determine whether characteristics that have previously been identified on local scales have an equal influence on a broader spatio-temporal scale. The goals of this thesis were to 1) determine whether predation can be detected as a driver of species distribution and community structure in fossil communities, and 2) identify which prey and environmental characteristics are most influential on the likelihood of a prey individual having a repair scar.

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Chapter 2

Assessing the relative influence of biotic and environmental processes on paleocommunities

2.1 Introduction

The distribution of fossils in rock packages has frequently been used to aid in the interpretation of paleoenvironments (Savrda and Bottjer, 1991; Brett, 1998; Patzkowsky and Holland, 2012). Examinations of fossil assemblages through time or space commonly identify water depth as the primary variable that separates marine biofacies (Boucot, 1975; Springer and Bambach, 1985; Brett et al., 1993; Scarponi and Kowalewski, 2004; Patzkowsky and Holland, 2012). This is an advantageous result as depth is a single variable that correlates with many other environmental properties including water temperature, water energy, oxygenation, salinity, light, and nutrient content. The identification of biofacies and their associated depths can then provide a basic understanding of a system. Despite these promising results from paleontological studies, many modern studies identify properties other than depth as the drivers of species distribution (Feder et al., 1994; McKinney and Hageman, 2006; Freestone et al., 2020). Ecological (biotic), rather than physical, properties are often identified as drivers by modern studies and this disconnect with the fossil data may be due to scale. If so, paleontological studies may be missing important information that could further improve our understanding and recognition of biofacies. The goal of the present study is to test for the influences of both depth and a biotic variable (predation) on a suite of fossil assemblages through time.

Fossil studies have commonly compared paleocommunities (recurring fossil assemblages of multiple interacting species) over large geographic or temporal scales such as entire basins or millions of years. Sampling at scales at which transgressive-regressive (T-R) cycles or onshore-offshore gradients can be detected may increase the likelihood of depth-associated biofacies due to the different organisms that inhabit varying depths. Several studies have directly examined the effects of scale on community structure and its drivers. Lafferty et al. (1994) compared faunal transitions within temporally constrained beds and found that variation in community structure is greater between outcrops than within them. In a similar study, Forcino et al. (2012) determined that lateral variation was only significant when fossil assemblages were studied at finer temporal scales. These results both suggest that fine-scale variation in community structure – and the processes driving this variation – are important influences on communities but may become overprinted by larger-scale factors.

We do not mean to suggest that study at a fine scale is inherently better, rather that the answers to the questions we may ask about ancient life and environments may depend on the scale at which they are studied. In fact, a section that is sampled at a high frequency over a long interval may be the most beneficial to geologists and paleontologists alike as it would span a broad enough interval to detect depth changes while also having a fine enough resolution to recognize changes in ecological processes. This methodology essentially describes Olszewski and Patzkowsky (2001): within a 2.5 Myr package of meter-scale stratigraphic cycles (~50 000 years for each cycle), they identified two paleocommunities – one brachiopod-dominated, the other bivalve-dominated – driven by a depth gradient. A further examination of just the brachiopod-dominated paleocommunity revealed that differences in taxonomic composition of each sample were driven by oxygenation. Clearly then, it is possible to detect fine-scale processes as drivers of community structure, but even the above studies have limited their analyses to physical environmental factors.

Redman et al. (2007) did specifically examine ecological factors and demonstrated that life mode – and not water depth – controlled bivalve species distribution in the Pliocene of California, with a study interval of <1 Myr and area of ~0.32 km2. In this study, however, water depth did not vary significantly between the samples and so it was not surprising that depth was not a driver. The question remains, then, as to whether fine-scale ecological processes can be identified as drivers of community structure where there is also significant environmental variation.

Here, we identify whether water depth and predation were drivers of brachiopod paleocommunities in the Late Devonian (Frasnian) of Iowa. The Cerro Gordo Member of the Lime Creek Formation spanned <1 Myr (Witzke and Bunker, 1996; Kaufman, 2006) and was a period of shallowing and warming in the Iowa basin (Witzke and Bunker, 1996; van Geldern et al., 2006). Predation was tested as a possible ecological driver because brachiopods from this formation were frequent victims of crushing and drilling attacks (Leighton, 2001; Johnsen et al., 2013; personal observation); if an ecological driver were detectable in this unit, predation would be a likely candidate. This study tests whether ecological processes can be detected as drivers of species distribution in the fossil record. Such a finding would suggest that a fuller understanding of biofacies can be aided by an examination of fine scale processes.

2.2 Material and Methods

We bulk-collected and identified 4107 brachiopod fossils from the Rockford Fossil & Prairie Preserve and Bird Hill in Iowa (Figure 2.1a). We then used oxygen isotope and magnetic susceptibility data for the section reported in De Vleeschouwer et al. (2017) as environmental proxies. These measurements were taken from bulk carbonate and so the oxygen isotopes reflect temperatures throughout the water column rather than just from the sea floor (Brand et al., 2012; Reghellin et al., 2015), making them an inappropriate proxy for depth. Because of this, we used oxygen isotope data as a broad climatic indicator where increasing isotopic values are related to general cooling in the system. Magnetic susceptibility has been increasingly used as a proxy for relative sea level (Crick et al., 1997; Whalen and Day, 2010; Da Silva et al., 2015 among others), especially in carbonate platform settings where lowering sea level is associated with increased detrital input (Da Silva et al., 2009) and therefore increased magnetic susceptibility values. The Cerro Gordo Member was deposited in a carbonate platform setting (Witzke and Bunker, 1996) and so we used magnetic susceptibility as a proxy for depth, inferring an inverse relationship between the two. Following Witzke and Bunker (1996), the Cerro Gordo Member has been interpreted as a period of constant sea level fall, so we used the ranked height of each sample in the section as an additional proxy for depth wherein stratigraphic height and inferred paleodepth are inversely correlated (Figure 2.1b). Our environmental proxies were then: 1) magnetic susceptibility (MS) and 2) stratigraphic height (SH) to infer paleodepth, and 3) oxygen isotopes to infer climatic temperature conditions.

We measured predation by two metrics: repair rate (Rr) and weighted mean ornament (WMO; Leighton, 2003). Rr was calculated as the number of failed attacks divided by the number of specimens in a sample (Rf2 of Molinaro et al., 2014); failed attacks are identified by repair scars, which are formed when a crushing predator fractures the shell, but the prey animal survives and heals the shell, leaving a scar (Alexander, 1986; Kowalewski, 2002) (Figure 2.2). WMO is a measure of the relative ornamentation of all specimens in a sample and – as brachiopods rely heavily on external ornament for defense from predators (Leighton, 2003) – is a suitable proxy for overall defensive capabilities and ability to avoid successful predatory attacks; WMO also represents the prey assemblage from the predator's point of view. The calculation of WMO requires each specimen be assigned to an ornament category; the categories are given values of 1 to 4 and represent an increase in ornament with increasing value. More specifically, the categories are: 1) smooth, 2) costate or lamellose, 3) multiplicate or rugose, and 4) spinose. Where N is the number of specimens in a sample, WMO is then:

$$\mathrm{WMO} = (\Sigma\ (\mathrm{Ni} * \mathrm{categoryi}))\ /\ (\mathrm{N})$$

An important difference in the application of these two predation methods is that while WMO was performed on all members of each sample, repair rate was calculated using only the Class Strophomenata (the concavo-convex brachiopods). Biconvex brachiopods have significantly lower repair rates than the strophomenates (Alexander, 1986; Leighton, 2013; Pruden et al., 2018) and therefore repair rates would be much smaller and differences more difficult to detect between samples if all brachiopods were used. WMO can be used to verify that the measured Rr reflects the predation pressure for the assemblage as a whole – and not just the strophomenates – if the results for the two metrics conform with each other. To ensure accurate repair rates were sampled, we limited our study to only those samples with at least 30 well-preserved strophomenates. This resulted in an analysis of 3835 specimens from 12 samples.

We performed NMDS ordination using the relative Sorensen distance measure in R (vegan package, version 2.5-7) to visualize samples based on their taxonomic composition and to identify paleocommunities. NMDS is an heuristic approach and does not identify the axes in order of amount of variance explained, limiting our ability to determine which process – predation or depth – may be the primary driver in our study. To solve this problem, we performed principal components analysis (PCA) on the scores of our NMDS result. We then used the envfit function to map gradients of our environmental and predation variables onto the NMDS ordination and performed Spearman rank correlations between each variable and each axis to identify drivers. We also performed Spearman rank correlations between all variables to 1) ensure that variables we have identified as predation or depth metrics are related to each other (ie. Rr is correlated with WMO and MS is correlated with SH) and 2) determine whether predation may have been dependent on an environmental process – in which case a predation metric (Rr or WMO) would be correlated with an environmental proxy (MS, SH, or oxygen isotopes).

2.3 Results

The selected NMDS ordination used two axes (final stress = 5.721 %; stress from a three-axis result = 2.827 %). The two-axis solution was chosen as stress values < 10 % are considered reasonable (McCune and Grace, 2002), the distribution of samples across the first two axes did not change with the addition of a third axis, and no variable of interest was correlated with the third axis. The samples were divided into two major clouds in ordination space (Figure 2.3a). The separation of these clouds generally follows the height in stratigraphic section (cloud 1 [red] being lower and cloud 2 [blue] being higher in section). Fitting the variables of interest onto the ordination (Figure 2.3b) revealed Rr to be strongly correlated with the first axis while both depth proxies – MS and SH – were correlated with the second axis, and these results were replicated with Spearman rank correlations (Table 1.1). WMO had a moderate correlation with each axis, although neither relationship was statistically significant. Oxygen isotopes were not significantly correlated with either ordination axis. Spearman correlations between variables of interest (Table

1.2) showed strong relationships between predation proxies (Rr and WMO) as well as between depth proxies (MS and SH). These correlations did not reveal a relationship between repairs and any environmental variable, however, WMO was correlated with MS.

2.4 Discussion

We found that predation and depth were both drivers of community structure of Late Devonian brachiopods of Iowa. This is evidenced by the correlations between Rr and the first axis, and both MS and SH and the second axis of ordination. As Rr measures direct evidence of predation – one scar records one failed predatory attack – differences in Rr will always represent changes in predation pressure in the system. Here, the correlation of Rr and the first ordination axis indicates that predation was the primary driver of community structure within the section. While using the stratigraphic height as a proxy for depth could result in missing small changes in sea level, the fact that SH and MS are significantly correlated enables us to more confidently interpret the section as a period of constant sea level fall. This interpretation allows for the inference of depth being associated with the second axis of ordination, and therefore being a driver of community structure.

Contrasting with most other marine paleocommunity studies (summarized in Patzkowsky and Holland, 2012), depth – by means of proxy of MS and SH – was not correlated with the first axis of our ordination and so was not the primary community driver. This is potentially owing to the scale of our study. Redman et al. (2007) showed that spatiotemporal scale is important to whether depth will be detected as a driver. This effect has also been found in modern studies that examined multiple spatial scales (Grill and Zuschin, 2001; Ghiglione et al., 2005; Blanchard and

Feder, 2014). Paleocommunities are frequently studied at scales that may be biased towards the detection of larger-scale processes such as depth. This may be at the expense of overprinting finer-scale variation in community structure and its associated drivers. Time averaging also has a role in removing fine-scale variation, but as Olszewski (1999) and others have pointed out, this can be advantageous in reducing noise in the data, and high frequency sampling with a sufficient number of individuals should still enable the detection of finer-scale trends. We examined a section in which sea level was falling but the environment can still be described as the margin of the inner shelf throughout the duration of the unit (Witzke and Bunker, 1996). This implies that the change in depth was very modest relative to most paleocommunity studies and, correspondingly, depth had only a modest influence on community structure.

While Rr was clearly correlated with the first axis, the results of our two predation metrics were not consistent with one another. WMO was not strongly correlated with either ordination axis but was correlated with both Rr and MS. This suggests that ornament is not influenced by a single factor. Previous studies have shown that brachiopod ornament – specifically spines – can act as defense against predation (Alexander, 2001; Leighton, 2001; Johnsen et al., 2013) and as a mechanism to stabilize or anchor the animal on the substrate (Grant, 1966; Alexander, 1984; Garcia et al., 2018; Dievert et al., 2021). Our results support the idea that ornament serves multiple purposes for brachiopods as sessile animals. We can still, however, infer predation as a driver of species distribution due to Rr providing direct evidence for predation pressure in a system.

Predation was the primary driver of species distribution in our study. The lack of previous work examining the effect of predation on paleocommunities may be due to either 1) the difficulty of obtaining quantifiable evidence of predation in fossils or 2) the idea that predation and other ecological processes operate on finer spatiotemporal scales than can be observed in the fossil record. Our work here demonstrates the latter explanation to be false, although there may be a limit beyond which these ecological processes become overprinted by larger-scale processes. Scaling up is a hypothesis from macroecology (summarized in Teng et al., 2020) that suggests that processes that are important to ecosystem function will be observable at multiple scales. It is evident from our findings – in addition to many modern studies – that predation is a key process driving modern and fossil community structure and that failing to examine it runs the risk of losing potentially critical information.

We identified two paleocommunities – described as clouds in the ordination – that were separated by depth and predation. The first community (red cloud in Figure 2.3a) was from deeper water and generally displayed greater predation pressure compared to the second community (blue cloud in Figure 2.3a). The first community is dominated by *Pseudoatrypa* (32%) and *Theodossia* (20%) and will henceforth be referred to as the *Pseudoatrypa-Theodossia* community. The second community is dominated by *Douvillina* (30%) and *Sulcatostrophia* (22%) and as such will be referred to as the *Douvillina-Sulcatostrophia* community. Apart from two samples – R-N8 and R-E14 – these communities are separated temporally, with the *Pseudoatrypa-Theodossia* community transitioning to the *Douvillina-Sulcatostrophia* community midway through the section (Figure 2.3c). Sample R-N8 is unusual in that it is heavily dominated by *Douvillina* (83%) while other samples have a more even distribution of taxa. While sample R-E14 is distinctly part of the *Pseudoatrypa-Theodossia* community, it does have a greater relative abundance of *Douvillina* which could represent a transitional phase between the two communities.

As sea level fall is associated with stratigraphic height in the section, it could be difficult to disentangle the reasoning for the transition from the *Pseudoatrypa-Theodossia* community to the *Douvillina-Sulcatostrophia* community. If the shift in communities were due to the passage of time, we would expect (local) extinction of some species from the *Pseudoatrypa-Theodossia* community and potential evolution or recruitment of new species into the *Douvillina-Sulcatostrophia* community. This is not the case here; no taxon that was abundant in any one sample appeared or disappeared from the area within the studied section, and the differences between paleocommunities are attributed to changes in the relative abundance of taxa not presence or absence. The shift in paleocommunities, then, must be due to the environmental changes related to sea level fall.

The use of fossils as paleoenvironmental indicators is valid where environmental tolerances of a species are well defined, however, species distribution may also be limited by ecological factors. The fundamental niche of a taxon can be defined by environmental tolerances, but it is rare for species to occupy the fundamental niche space fully (MacArthur, 1972). Including biotic interactions in paleocommunity studies can help refine our understanding of the realized niche space of these organisms. This can, in turn, result in improved biofacies constructions that represent community-level responses to environmental changes. We also echo previous studies (Levin, 1992; Redman et al., 2007; Bennington et al., 2009; Forcino et al., 2012) that urge a greater focus on spatial and temporal scale when examining community structure and constructing biofacies.

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Table 2.1

Spearman rank correlations of variables of interest with each ordination axis. Significant correlations shown in bold. Rr = repair rate; WMO = weighted mean ornament; Strat = stratigraphic height; Mag = magnetic susceptibility; δ18O = oxygen isotopes.

Metric	**Axis 1**		**Axis 2**	
	r_s	p	r_s	p
Rr	**0.629**	**0.032**	0.287	0.366
WMO	0.552	0.067	0.517	0.089
Strat	-0.123	0.704	**0.820**	**0.001**
Mag	0.011	0.974	**0.687**	**0.014**
δ^{18}O	-0.221	0.491	0.427	0.166

Table 2.2

Spearman rank correlations between variables of interest. Significant correlations shown in bold. Abbreviations as in Table 1.1.

	WMO		**Strat**		**Mag**		**$\delta^{18}O$**	
	r_s	p	r_s	p	r_s	p	r_s	p
Rr	**0.692**	**0.016**	0.119	0.712	0.217	0.498	-0.245	0.442
WMO			0.550	0.064	**0.664**	**0.027**	0.081	0.804
Strat					**0.663**	**0.019**	0.530	0.076
Mag							0.530	0.076

Figure 2.1

(A) Map of Floyd County, Iowa with sample locations, 1. Rockford Fossil & Prairie Preserve, 2. Bird Hill. (B) Stratigraphic column of the Lime Creek Formation at sampling sites indicating the position of each sample. Sample names and locations are defined in the Supplemental Material[1]. Modified from Day and Witzke, 2017.

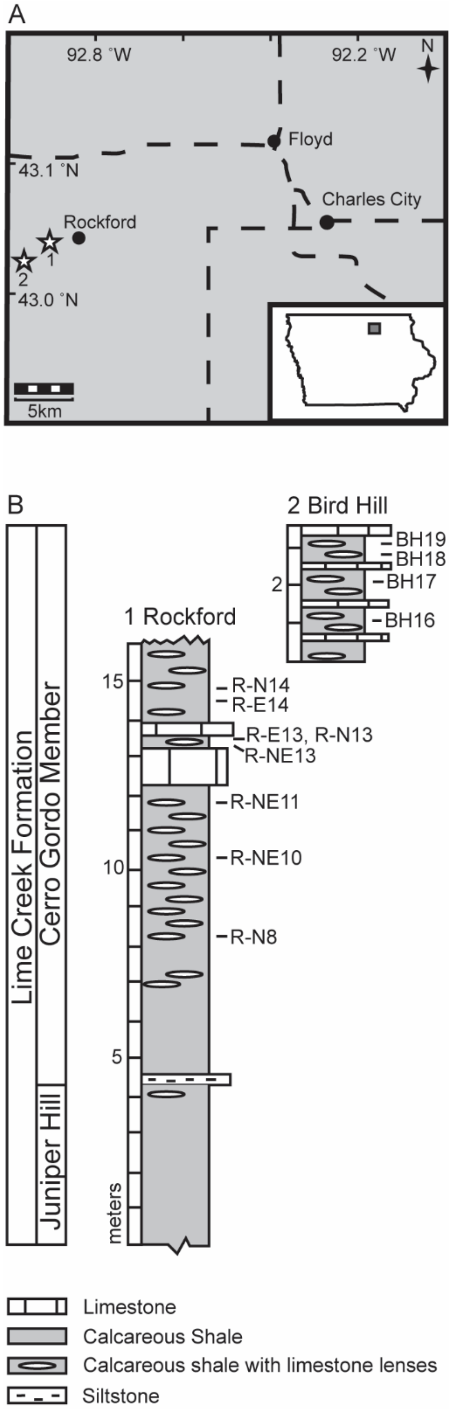
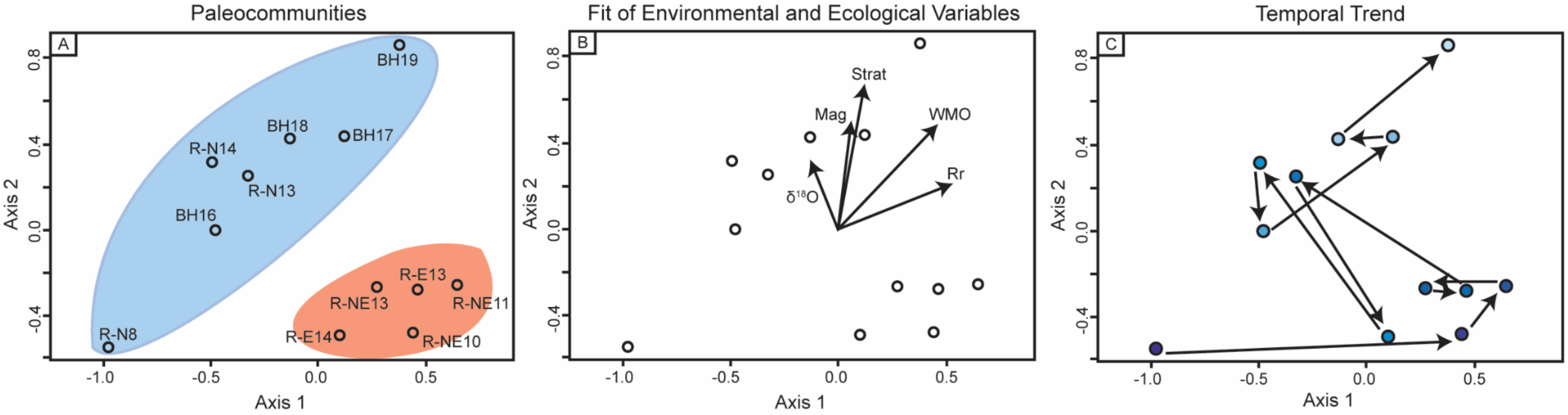


Figure 2.2

Example of a repair scar on *Douvillina arcuata*. Repair highlighted in white.

Figure 2.3

2-axis NMDS ordination of brachiopod samples. A) Sample distribution in ordination space with clouds showing paleocommunities; *Pseudoatrypa-Theodossia* community in red, *Douvillina-Sulcatostrophia* community in blue; sample names as in Figure 1.1. B) Fit of variables of interest onto ordination; arrows point in direction of maximum correlation with the ordination; arrow length represents strength of correlation. C) Temporal trend of samples in ordination space; oldest sample in bottom left, youngest sample at top right; arrows connect samples temporally; colour gradient transitions from older samples (dark blue) to younger samples (light blue).



Chapter 3

The influence of brachiopod prey and environmental characteristics on predation

3.1 Introduction

Predation is a known driver of community structure and ecology, and a significant body of research has determined that both characteristics of prey and features of their environment can have an impact on predation rates and predator success. Several modern studies have observed the effects of biological and environmental factors on individual predator-prey systems (Savino and Stein, 1989; Thirgood et al., 2002; Hostetter et al., 2012 etc.). Others have explored the various influences on predation within whole ecosystems such as seagrass communities (Orth et al., 1984), rocky intertidal communities (Menge and Sutherland, 1976, 1987) and forests (Shultz et al., 2004). Stafford et al. (2015) identified predator abundance as the most significant influence on crushing predation rates of the gastropod Tegula funebralis while prey morphology and environmental characteristics had a lesser influence. This study though was on a small geographic scale – limited to a single coastline on Vancouver Island – and only examined a single prey taxon. A recent study from Mendonca et al. (2021) suggested that differences in prey species' defenses are associated with the likelihood of a successful predatory attack. Identifying which morphological characteristics and environmental properties are correlated with predation rates may provide insight into how prey animals respond to predation and whether their responses are predictable across time, space, and taxa. In this study, we compared crushing predation rates between Devonian brachiopods from 46 communities in North America, covering 5 basins from the Northwest Territories, Canada to New York state, USA. These brachiopods were sedentary and depended primarily on the strength and size of their shells to avoid death by predation. Using generalized linear mixed models (GLMMs), we tested which characteristics most influenced the likelihood of an individual brachiopod surviving a crushing attack. This analysis may provide a general framework that can be used to predict predation pressure on Devonian brachiopods, as well as isolate morphological features that are protective against predatory attacks.

Brachiopods were a major component of marine ecosystems in the Devonian, comprising 842 genera (PaleoBioDB) and constituting an impressive 35% of Devonian fossil occurrences (PaleoBioDB). They were also very widespread, with known occurrences from 0-75 degrees of paleolatitude globally (Williams, 1965) – most likely only lacking polar occurrences due to a lack of polar fossiliferous rock. Because they were such a diverse and abundant group, brachiopods were readily available prey for many predators, including arthropods, gastropods, and recently evolved jawed fish (Signor and Brett, 1984). While it is obviously impossible to witness predation occurring in fossil systems, several distinct traces may be examined on fossilized shells: drill holes and repair scars. Researchers who study drilling predation have the advantage of a complete system: complete drill holes represent successful attacks, incomplete holes represent failed attacks, and shells without a hole have not been attacked. Drilling is not, however, a significant source of mortality for many invertebrates. Crushing predators tend to be larger and feed more often than drillers; for example, modern red rock crabs (Cancer productus) consume multiple mussels in a day (Leighton and Tyler, 2021) whereas the predatory gastropod Nucella crassilabrum rarely consumes more than a single mussel within a 7-day period (Dye, 1991). Additionally, modern gastropods can require up to several days to drill through an invertebrate shell completely (Hughes and Dunkin, 1984; citations), a time frame in which it is increasingly likely that a predator of the gastropod itself could arrive, resulting in a failed attack and an incomplete drillhole (Palmer, 1990; Chattopadhyay and Baumiller, 2007). Crushing predators, in contrast, can rapidly complete an attack once a prey individual has been found. The handling time of mussels for modern crabs is less than 30 seconds for red rock crabs (Cancer productus; Tyler and Leighton, 2021) and no more than 2 minutes for European green crabs (Carcinus maenas; Smallgange and Van der Meer, 2003), while modern shell crushing fish require an average of 20 to 80 seconds (Naddafi and Rudstam, 2014). However, even predators with high success rates require more time to attack prey with stronger defenses (Barclay et al., 2020; Mendonca et al., 2021), and this additional handling time could provide an opportunity for higher trophic level predators to arrive, resulting in the crusher either abandoning its prey or being attacked itself. As Devonian crushers were not as specialized as their modern counterparts - crabs would not evolve until the Jurassic (Krobicki and Zaton, 2008) and living arthropods at the time did not possess sophisticated mouthparts or appendages specialized for crushing (Signor and Brett, 1984 and references therein; Vermeij, 1987) - their handling time may have been greater in general, and significantly increased when encountering added shell defenses. It should, however, also be noted that brachiopod shells are much thinner than bivalve shells (Behrensmeyer et al., 2005). A successful attack, then, would depend on the capabilities of the predator relative to the anti-predatory strategies of its prey. Leighton (2003) demonstrated that crushing predators were a significant source of mortality for Devonian brachiopods so for this and the aforementioned reasons we chose crushing predation as the focus of this study.

In the fossil record, we study crushing predation using repair scars, which represent failed attacks. These are produced when a predator attempts to crush the shell of an animal such as a brachiopod but fails and is only able to break off a piece of the shell rather than crush it entirely. The surviving animal then regrows the shell but leaves a distinctive scar that may be recognized by thinning of the shell in the immediate damage area and a change or distortion of the shell ornament in the re-grown portion which may be accompanied by thickening of the shell (Figure 3.1). These scars are easily recognizable in well preserved fossils, and the frequency of repairs is often used to compare predation rates between samples (Vermeij et al., 1980; Leighton, 2002; Alexander and Dietl, 2003; Leighton et al., 2013; Molinaro et al., 2014). The repair frequency does introduce some ambiguity in that a sample with a greater repair frequency may be so due to a lower success rate – resulting in fewer crushed shells and more repairs – or to a greater attack frequency – that would result in more repaired shells but also more successfully crushed shells that are shattered completely (Stafford and Leighton, 2011) and thus likely lost to the fossil record (but see Saloman et al., 2014 and Leighton et al., 2016). However, the traits associated with failed attacks should be those that are anti-predatory – whether specifically evolved for this purpose or evolved separately with the added benefit of being protective – so there is the potential that members of communities with greater repair rates possess characteristics that are better adapted to defend against predatory attacks (Vermeij, 1987).

The characteristics on which we focused in this study include features of the brachiopod shells themselves, and regional environmental traits that may be associated with predator strength and capabilities. As brachiopods are sessile animals, they are unable to protect themselves from predatory attacks through escape so only features that would deter a predator from attempting an attack, physically prevent a predator from crushing the shell, or hide the prey completely could be anti-predatory. These defenses are typically morphological; they are observable even in the fossil record. Of the brachiopod groups that lived during the Devonian, only members of Class Strophomenata frequently preserve repair scars (Alexander, 1986; Pruden et al., 2018). This is potentially owing to their concavo-convex morphology, which may have caused them to be less likely to shatter completely than the biconvex rhynchonellates

(Alexander, 1989), but it may be more likely that they were preferred prey and attacked more frequently (Pruden et al., 2018). Strophomenates possessed a general shared external morphology that differed between members within the group mainly in 1) overall shell size, 2) shell thickness, 3) convexity, and 4) external ornament. 1) Large size can be advantageous to sessile organisms in deterring crushing predators, especially those that are gape-limited such as the ptyctodont placoderm fish that would have preyed on Devonian brachiopods (Signor and Brett, 1984; Brett and Walker, 2002; Leighton, 2003). Phyllocarid arthropods (which were much larger in the Devonian than their modern counterparts), also potential predators, may have avoided taking especially large prey that would have been difficult to manipulate in their appendages. Even a predator capable of crushing such large prey may require multiple attempts (Boulding and LaBarbera, 1986) and the increase in handling time may be undesirable to a predator such that they would abandon the attack. 2) Shell thickness impacts the strength required to crush a shelled animal (Alexander, 1990), and we may predict that a thicker-valved brachiopod species would experience fewer successful attacks than a thin-shelled species (Vermeij, 1982). 3) Convexity of the shell could also affect the result of a predatory attack: a very flat shell may be easier to grasp while a more convex shell could prevent smaller predators from attacking due again to gape limitations. Even a large enough predator may only be able to reach a small distance beyond the commissure, relying on propagation of damage across the shell in order to crush it completely. Alexander (1989) demonstrated that for Ordovician strophomenates, sublethal fractures were more common in more convex and geniculate individuals whereas, in crushing experiments, flatter individuals were more likely to break in an anterior-posterior direction. This form of breakage in planoconvex individuals, if generalizable to fractures generated by crushing predators, would result in a very low likelihood of surviving a crushing attack, as the fracture would propagate into the body cavity. 4) As for ornament, Johnsen et al. (2013) demonstrated that spinose brachiopods enter a size refuge at a smaller size than non-spinose brachiopods from the same Devonian community, suggesting spines increase the effective size of the brachiopod and deter predators from attacking. Ornament may also reduce vulnerability to predation through strengthening of the shell (Alexander, 1990; Miller and LaBarbera, 1995), and preventing the propagation of damage (Alexander, 1989). While each of these features may be useful against a general predator, variation in predator capabilities is also expected to exist over space and time.

North America in the Devonian, along with parts of Russia and Europe, was part of the larger paleo-continent of Laurussia. This paleocontinent was situated across the equator, with modern Canada's Northwest Territories in the heart of the tropics, and New York State at a paleo-latitude of ~30-40 oS throughout the period (Figure 3.2). A warmer global climate caused much of the continent to be flooded by a shallow seaway (Day et al., 1996). During intervals of relatively low sea level, this seaway was divided into multiple basins, five of which were examined in the present study: the Western Canadian Sedimentary Basin (WCSB), the Iowa Basin, the Illinois Basin, the Michigan Basin, and the Appalachian Basin. The WCSB and Iowa basin had the most limited communication owing to the Transcontinental Arch (TCA) between them. Communication between Laurussia and other paleocontinents was also limited due to the Appalachian Mountains and subduction zones to the south, open ocean to the west, and the terrestrial portion of Laurussia to the east and north. This resulted in only a narrow passage in the northwest of the continent that was flooded, allowing for migration of taxa into the WCSB from the shallow waters surrounding Siberia. Depending on their larval dispersal and mobility, these taxa may then have propagated throughout the WCSB and across the Transcontinental Arch into the southern basins. Studies of multiple higher taxa suggest that this was the common direction of migration for predators and prey during this time (Boucot et al., 1967; Oliver, 1977; Bailey, 1978).

Among the evolving and spreading taxa was the Order Ptyctodontida which was the first group composed entirely of durophagous fish. While they first appeared in the Early Devonian (Brazeau and Freidman, 2015), they did not reach the continental interior of Laurussia until the Eifelian (Young, 2010; Stack and Sallan, 2018). The ptyctodonts, along with crushing arthropods, evolved to become stronger and increasingly specialized through the Givetian and Frasnian (Signor and Brett, 1984) which may have caused an increase in predation pressure. Unfortunately, fossilized predators are exceedingly rare so we cannot easily study their features directly to estimate their capabilities. Instead, we focused on environmental characteristics which may be associated with predator strength. Modern communities living at low latitudes and high temperatures, for example, often possess stronger, more diverse, and more specialized predators than those living in high latitude, low temperature regions (Palmer, 1979; Vermeij, 1987; Harper and Peck, 2016). Lab experiments have also determined that some invertebrate predators attack prey more frequently at higher temperatures (Leighton and Tyler, 2021). While it is uncertain whether this pattern has persisted continuously since the Devonian, there is evidence for greater predation pressure near the equator in the Devonian (Leighton, 1999), even if the tropics were expanded such that the temperature gradient was much weaker from equator to poles (Brand, 1989; Copper and Scotese, 2003). North America also experienced a gradient in sedimentary regime from highly clastic in the south due to erosion from the rising Appalachian Mountains, to carbonate-dominated in the north (Cooper et al., 1942). It is unclear whether the sediment would have affected predation directly – such as by reduced visibility from a high clastic sediment load or an excess of available calcium carbonate to strengthen brachiopod shells. Sediment type may rather have been a proxy for other characteristics such as biomass, nutrient availability, or water depth. The five sedimentary basins could also exhibit differences in predation between them. During intervals of low sea level when the basins were isolated from one another, predators and their prey could have evolved independently of the other basins, resulting in different predation pressures and success rates.

If the brachiopods evolved to adapt to their new predators, we may expect trends in morphology through time selecting for larger and stronger shells. What may be more difficult to predict is how these morphological trends vary with repair rates. To test these trends, we have selected six candidate variables that we hypothesize to have an influence on predation. These variables include age, features of the brachiopod shells and characteristics of the environments in which they lived. We aim to create GLMMs that will identify which of our candidate variables are most significant in predicting the likelihood of repair (LOR) for individual brachiopods.

3.2 Methods

3.2.1 Data Collection

We obtained the brachiopods for this study through field work and museum collections, resulting in a data set of 3325 individuals (Table 3.1). These represent 16 formations across five North American basins. We collected field specimens only from beds that did not show obvious signs of taphonomic influence – either by transport (e.g., extensive fragmentation and abrasion of specimens) or time-averaging (e.g., specimens of the same species with very different preservation types). We bulk-sampled the selected beds and then identified all brachiopods to the species level upon returning to the lab. Only concavo-convex brachiopods (members of the Class

Strophomenata as well as the genus Tropidoleptus) were included in the analysis to ensure that enough scars were counted that differences in our candidate variables could be assessed in relation to likelihood of repair. We measured the length and height of all shells that were sufficiently preserved (at least 50% of the pedicle valve intact and no strong surface abrasion) and each individual was checked for the presence of repair scars under a microscope. Only the pedicle valve was examined for repairs due to the high rate of valve disarticulation and/or sediment infill in some specimens, with the brachial valve often being obscured or destroyed. Additionally, there is evidence that failed attacks on brachiopods typically result in damage to both valves (Mendonca et al., 2017), indicating that using either the pedicle or brachial valve alone is sufficient. We then measured the size at attack (SAA) for each scarred specimen as the distance perpendicular to the hingeline from the umbo to the growth line distorted by the scar (Figure 3.1; Richards and Leighton, 2012).

As we wished to assess not only which individuals were repaired but also how large they were when the attack occurred, we divided the observations of each individual into size bins. For any given size bin, an individual may be repaired (1) or not (0). As most individuals grew beyond the upper limit of the first (smallest) bin, this results in multiple observations in the dataset for most specimens. For example, a specimen may have grown through size bin 1 without being attacked, then was attacked and repaired in the size range of bin 2, and continued growing until it died with a size in the range of bin 3, resulting in 3 observations for the individual. Commonly used methods to determine the number of size bins (De Feo, 2017) that are free of bias would result in bins < 1 mm in length with our dataset. Because it is unknown, but unlikely, that Devonian predators could detect differences in prey size less than a millimeter, we performed the modelling procedure twice: once with 4 mm wide size bins, and once with bins 7 mm in width. This would ensure that our results are not biased due to an arbitrary choice of bin size. Size bins were treated as a categorical variable in order to identify whether there was a consistent trend in size of repairs, or if there may have been a size refuge (Richards and Leighton, 2012) or evidence of differences in repair likelihood between juveniles and adults (Pruden et al., 2018). A potential concern of using size bins to represent specimens is that individuals that have been repaired once may be more likely to be repaired again, in which case repairs on individuals would not be independent. To control for this, we included Individual specimen as a random effect variable in our regression models wherein each specimen is its own category (and the multiple observations of any one specimen belong to the same category).

The remaining variables included in our analysis are Convexity, Ornament, Stage, Paleolatitude, and Lithology (Table 3.2). Convexity was measured as the ratio of height to length of each individual at the time of death. Ornament was divided into two categories: individuals with spines (spinose) and those without. While some strophomenates possessed what are considered intermediate levels of ornament (costae, lamellae, plicae, and rugae), only spines have been definitively tested as a defense mechanism against crushing predation (Jonhnsen et al., 2013). Information on the stage and lithology was acquired from the literature (Table 3.3), except for the lithology of field-collected samples which was noted while in the field. Stage was a categorical variable defined by geological stage (Givetian or Frasnian), while Lithology was categorized by whether the depositional setting was siliciclastic- or carbonate-dominated. The paleolatitude was determined by inputting the modern coordinates of each sampled locality into a paleolatitude calculator (www.paleolatitude.org; van Hinsbergen et al., 2015). We then compared the results with approximate paleolatitudes from continental reconstructions by Blakey (Deep Time Maps) and Scotese (PALEOMAP Project) to ensure the latitudes were reasonable.

The continuous variables were scaled and centered as regression models can be influenced by the scale of the included variables, and this effect becomes more pronounced when variables operate on greatly different scales from one another – for example, in our dataset latitude varies from -43o to -10o while convexity has a range of 0.07-0.63.

We included the above variables in our analysis to test these hypothesized relationships with predation:

- Size: we are testing the hypothesis that attack frequency and LOR increases with size due to the amount of available tissue for predators to consume. If our results are consistent with previous studies (Harper et al., 2009, Richards and Leighton, 2012), we may identify a size refuge – a size at which the attack frequency and LOR are greatly decreased due to the high cost of breaking large shells.
- Ornament: this variable was included to test whether attacks are less frequent on spinose prey (decreased LOR) or if success rates are poorer on spinose prey due to stronger shell defenses (increased LOR). If ornament has no effect on LOR, then neither of these hypotheses are corroborated for Devonian strophomenates.
- Convexity: we hypothesize that LOR has a positive relationship with brachiopod convexity. The reason for this may be two-fold: 1) more convex shapes can better prevent the propagation of damage across the shell (Alexander, 1989), and 2) similarly to ornament, greater convexity may increase the effective size of the shell in the shortest dimension, resulting in a lower success rate against convex individuals.
- Stage: we are testing whether the frequency of attacks increased through time from the Givetian to the Frasnian, along with LOR. It is unknown whether success rates changed with the appearance of new, stronger predators. If the brachiopods evolved

to keep up with their predators, success rates would be unchanged, and LOR would increase due to the increase in attacks.

- Lithology: this variable was included to determine whether there was a difference in LOR between carbonate-dominated and siliciclastic-dominated settings. If, for example, carbonate-settings had prey with greater biomass, we might expect an increased number of attacks and LOR compared to siliciclastic-dominated settings.
- Paleolatitude: we included this variable to test for the persistence of a latitudinal predation gradient, resulting in a greater attack frequency and LOR at lower latitudes.

Two variables for which we did have data but elected not to include in our analysis were Basin and Taxon. Our decision to exclude these variables was due to their conflation with other variables included in our dataset. Because of the rotation of the continent during the Devonian, our sampled basins are strongly associated with latitude. Additionally, in our dataset these basins are separated by stage due to the availability of well-preserved fossil material in each; Frasnian material was collected from WCSB and the Iowa basin, while Givetian material was primarily collected from the Illinois, Michigan, and Appalachian basins. The inclusion of Basin in our study would therefore potentially overprint the larger-scale trends in age and environment that we wished to study. Similarly, the inclusion of a taxonomic variable would potentially override any trends in convexity or ornament because many taxa are at least partially defined by such characteristics – for example, all spinose taxa belong to the Order Productida, and the Family Leptostrophiidae is defined as being very weakly convex. To determine the influence of Basin and Taxon (at the Family level) on LOR, we performed pairwise chi-square and Fisher's exact tests respectively.

3.2.2 Data analysis

We constructed GLMMs (generalized linear mixed models) (lme4 package version 1.1-26 for R) to assess the most influential variables on whether individuals are repaired. GLMMs include both fixed effects – the variables we wish to evaluate – and random effects – variables that may account for biases in the data or contribute to the random error. The models were constructed using a binary distribution of the dependent (focal) variable as each individual was either repaired (1) or not (0), and the chosen distribution was assessed for validity using DHARMa diagnostics (DHARMa package version 0.4.1 for R). We included several random effects variables (Table 3.2): Individual, Sample, and Collection source. The variable Individual was coded as a factor with separate levels for each specimen included in the dataset. This accounted for the potential bias that might occur if specimens that had been scarred previously were more likely to be attacked and scarred again. The multiple observations of each specimen – separated by size bins – were recorded under the same level of individual. A sample refers to a collection of individuals that lived in close proximity to one another within a geologically short time frame during which measured environmental characteristics did not change. Collection source refers to either the museum an individual was obtained from, or that it was collected in the field under our collecting procedure.

We first created models including all random and fixed effect variables as a starting point for the analyses. In the case that the standard deviation of a random effect variable was less than 1, we conducted likelihood ratio tests to determine whether a model including the random effect was better than one without. Where likelihood ratio tests showed an insignificant difference, we removed that random effect variable from the modelling procedure. We next tested the fixed effect variables for multicollinearity using generalized variance inflation factors (GVIFs) from the car package for R (version 3.0-10). Multicollinear variables can be predicted by one or a combination of the other fixed effects within a model, which can result in high variance and estimated coefficients of the independent variables, bringing into question the validity of the model (O'Brien, 2007). Removing highly multicollinear variables can then result in simpler models with more reliable coefficients. There is not currently a consensus on an accepted threshold value of GVIF, however, a very commonly used method is to reject any variable with a GVIF > 10 (Vittinghoff et al., 2012), which we employed here.

We next modeled combinations of the fixed effect variables, as well as a selection of biologically relevant interaction terms (Table 3.4), to identify which combinations provided the best models. We used the Akaike Information Criterion (AIC) to assess relative model fit. Any models within 2 AIC points of the model with the lowest AIC score ($\Delta AIC \leq 2$) were considered in the results and discussion. For simplicity, we limited further analyses to a selected model composed of the fixed effect variables found in all of the equally parsimonious ($\Delta AIC \leq 2$) candidate models.

The fixed effects were then examined for their individual influences on the selected model. For continuous variables, we reviewed the estimated coefficients and tested for significance with Wald Z tests. For categorical variables, we examined the estimated marginal means (EMMs; package emmeans version 1.6.2-1 for R). EMMs give the mean value of the response variable for each level of a categorical variable based on modeled data. The use of modeled data rather than raw data removes potential biases due to differences in the number of observations for each category and allows for the investigation of interaction effects. With EMMs, we examined the differences in LOR between levels of categorical variables and performed pairwise tests to determine whether a difference between two levels was significant.

We performed this modelling procedure on the full dataset, as well as on a subset of the data that included a single widespread genus – Strophodonta (N = 1406). This genus is found in 4 of the 5 sampled basins and persists from the Givetian through the Frasnian. If the results from both analyses are consistent, we can consider the models to be robust to taxonomic differences within the Strophomenata. In addition, the Strophodonta-only models control for the taxonomic identity of the prey, potentially allowing for closer scrutiny of other variables.

3.3 Results

3.3.1 All Taxa Analysis

Modelling of the full dataset revealed Size, Convexity, and Paleolatitude to be the most significant variables in predicting whether an individual is repaired, and the selected model also included the interaction between Size and Convexity (Table 3.5). GVIFs identified no strong multicollinearity so all variables were suitable to be analysed. We did, however, remove Collection Source as a random effect (Table 3.6). While both Sample and Individual were included in the models, they each had a standard deviation < 1 and their contributions were trivial. As the results were consistent between the use of 4 mm and 7 mm size bins, only the results for the models using 7 mm size bins are shown here.

In addition to the variables from the selected model, models within $\Delta AIC \leq 2$ possessed various combinations of Ornament, Stage, and Lithology. The interactions between Convexity and Ornament, and Size and Ornament were also included in alternative models.

The effect of Paleolatitude was significant according to the Wald-Z test, indicating that at lower latitudes (nearer to or in the tropics), individuals were more likely to be repaired (Figure 3.3b). Size categories were also significant and graphical representation of the EMMs shows that the likelihood of repair increases through size bins 1-4 and then drops at size bin 5 (Figure 3.3c). The interaction of Size and Convexity reveals that in size bins 2-5 the likelihood of repair decreases with increasing convexity, but this relationship is reversed in size bin 1 (Figure 3.3a).

Size had the strongest effect on LOR, according to both Wald-Z test scores (Table 3.5) and EMM predictions of LOR (Figure 3.3). LOR varies from about 3 % in size bin 1 to a maximum of 20 % in size bin 4 (Figure 3.3c). The effect of Convexity was dependent on the Size of the individual. The smallest effect of convexity was seen in bin 2, where only a 7 % difference in LOR was seen across the range of convexity values studied. And the greatest difference was observed in bin 5, with a 24 % difference in LOR from low to high convexity (Figure 3.3a). Latitude had the smallest effect, with just over a 4 % difference in LOR predicted across the range of latitudes studied, holding size and convexity constant (Figure 3.3b).

The Fisher's exact tests of taxa at the level of Family show that the Family Leptostrophiidae has the greatest frequency of scars, possessing significantly more scars than several other families (Table 3.7). Results from chi-square tests for basins revealed that the Illinois basin has significantly more scars than the Iowa, Michigan, and Appalachian basins and WCSB has significantly more scars than the Michigan basin (Table 3.7).

3.3.2 Strophodonta-only Analysis

The Strophodonta-only dataset was modelled by a combination of Size, Convexity, Lithology, and the interaction between Size and Convexity (Table 3.8). There were again no strongly multicollinear variables so all fixed effects were included in the analysis. Of the random effects, only Individual had a non-trivial contribution (standard deviation > 1) so Sample and Collection source were removed (Table 3.6). The results using 7 mm size bins are shown as there was no difference between the results for different bin widths.

In addition to Size, Convexity, and Lithology, alternative models also possessed combinations of Paleolatitude and Stage. Unlike in the analysis of all taxa, alternative models did not include any other interaction terms. Individuals that lived in carbonate-dominated settings were significantly more likely to be repaired than those living in more siliciclastic-dominated ones (Figure 3.4b). The main effect of Size shows the same trend as in the analysis of all taxa: LOR increases through size bins 1-4 and then decreases in size bin 5 (Figure 3.4c). The interaction of Size and Convexity reveals that this pattern is mostly driven by more convex individuals as less convex (flatter) specimens that grew into bin 5 had an increased likelihood of being repaired, rather than a decrease (Figure 3.4a).

The strongest effect on LOR was produced by Size: individuals in bin 1 only had a 2 % chance of being repaired while individuals in bin 4 had a 15 % chance (Figure 3.4c). The effect of Convexity was moderated by Size. At a minimum, Convexity had practically no effect (0 % difference in LOR across convexity in bin 3), however, in bin 5 LOR ranged from 0 % (at high convexity) to 95 % (at the lowest convexity values), making Convexity the strongest predictor of LOR in the largest individuals (Figure 3.4a). The predicted trend in LOR across convexity in bin 5 is likely an artefact of our dataset though, as there were only 93 individuals that grew into bin 5 and the minimum convexity of those was 0.24 while the mean convexity was 0.36. Considering only the range of convexity for which we have measurements, the LOR in bin 5 is limited to a range of 0 % to about 40 %. Lithology meanwhile, had a very modest effect of an average 4 % LOR in siliciclastic environments while carbonate environments had just over a 6 % LOR (Figure 3.4b).

3.4 Discussion

3.4.1 All Taxa Analysis

We found that prey Size, Convexity, and Paleolatitude were the strongest predictors of LOR in Devonian strophomenate brachiopods. The effects of each variable are generally consistent with results from previous smaller-scale studies, lending support for the hypotheses of a latitudinal predation gradient and of a size refuge from predation. As with all repair scar studies, though, we are faced with the possibility of differences in LOR being due to either changes in the attack frequency or the success rate of predatory attacks on their prey. Using our results, we will attempt to determine which cause – success or attacks – is more likely to be responsible for the change in LOR from each variable in our selected model.

Our results for Size echo previous theoretical (Leighton, 2002) and empirical studies (Harper et al., 2009; Richards and Leighton, 2012) that repairs increase with size (bins 1-4) until the prey taxon reaches a size refuge (bin 5) at which time either the predator is no longer capable of taking the prey or the cost of doing so would outweigh the benefits for potential predators. This result does differ for very flat individuals, which may not reach a size refuge within the range of sizes studied, however there are very few repairs on large and flat individuals so this result requires further study to verify whether it is robust. The trend of increasing LOR through bins 1-4 either indicates a reduction in success of attacks at greater prey size or an increase in the number of attacks. Larger prey are more desirable to predators due to the greater amount of tissue available to be consumed, so it is reasonable to assume that the attack frequency would increase with bin size before the size refuge is reached. It is also possible, however, that predators are less successful at taking large prey, as shell thickness and ornament tend to increase with prey size. In addition, most durophagous predators (including ptyctodontids) are gape-limited, due to the lever mechanics required to exert sufficient force to fracture a shell; consequently, larger prey should be more difficult for predators to break. Without knowing the identities, sizes, or abilities of the predators in this system, or the costs and benefits of the prey relative to size, we cannot currently distinguish between the two explanations for the relationship between size and LOR, and it is quite possible that the true cause is a combination of both differences in attack and success rates.

The result of greater LOR at lower convexities is inconsistent with current knowledge of the effect of Convexity on predator success (Alexander, 1989). Modern durophagous arthropods, as well as some fish, execute an attack by first selecting a prey individual and then point-loading pressure on the shell in an attempt to fracture it (Boulding and LaBarbera, 1986; Vermeij, 1987 and references therein) – on brachiopods, the location of point loading was usually near the commissure (Alexander, 1989). Propagation of this initial damage would determine whether the shell would be crushed completely. Greater general convexity, as well as geniculations, have been shown to reduce the propagation of fractures to brachiopod shells (Alexander, 1989), suggesting that flatter shells are easier to crush completely and should have a lower LOR. What we see here is in fact the opposite: there are more repairs on flatter shells. We tentatively suggest that rather than a difference in success, our result is due to a difference in attacks; specifically, that flatter brachiopods were attacked more often than convex ones. From a benefit:cost ratio perspective, this may initially seem counter-intuitive since less convex taxa frequently have smaller body cavities and less muscle tissue for predators to consume. However, an additional characteristic of the shell may help to explain this interpretation: ornament. Spinose individuals belong to the Order Productida and a defining characteristic of productides is that they are convex – at least relative to other strophomenates. In our dataset, spinose individuals are much more convex than non-spinose individuals (Figure 3.5). Not only might less convex individuals be easier to break into because of the ease of propagating damage, they might also be less ornamented – appearing smaller to predators and having thinner, more fragile shells. Even though ornament did not appear in our selected model, it was included in each alternative model (Table 3.5), and it is possible that the relationship between ornament and convexity was influential in the outcome of more convex individuals having a lower LOR. It would be prudent to examine the effect of ornament, as well as its relationship with convexity, in future work focused on other time intervals and taxa.

The inclusion of Paleolatitude in the selected model follows work by Leighton (1999), Dietl and Kelley (2001) and modern workers (Vermeij, 1987; Schemske et al., 2009; Roslin et al., 2017; Reynolds et al., 2018) demonstrating a latitudinal predation gradient. The possible explanations for the Paleolatitude result are either: 1) predators are less successful nearer the equator, or 2) predators are more abundant and thus there are more attacks at lower latitudes. In modern oceans, predators are stronger and more abundant in tropical seas (Vermeij, 1987; Harper and Peck, 2016). Devonian North America likely followed this trend, as more evolved predators were first introduced to the WCSB and later migrated to the more temperate basins (Boucot et al., 1969; Young, 2010). A greater abundance of predators would logically be related to an increased number of attacks nearer to the equator. Additionally, predators make more frequent attack attempts at higher temperatures (Leighton and Tyler, 2021) which typify tropical environments at low latitudes. A difference in temperature corresponding to latitude would then also support an increased attack frequency and LOR for individuals nearer to the equator. A caveat to this is that the Devonian was a greenhouse environment and the gradient of temperature across latitudes may have been substantially less than it is today. As for the hypothesis of differences in success rates, it is conceivable that predator success was lower in tropical regions if the brachiopod prey were well-adapted to their more capable predators. However, this would imply that the adaptive gap – the relative difference in abilities between predators and prey (Vermeij, 1987) – was smaller at lower latitudes, and that brachiopod prey had managed to advance beyond the improvements in abilities of their predators. While not impossible, we view it as more reasonable that prey were adapted merely sufficiently to maintain the adaptive gap with their predators, resulting in a constant success rate across latitude. We suggest that an increased frequency of attacks is the most likely explanation for the latitudinal trend in LOR.

3.4.2 Strophodonta-only Analysis

The results for the analysis of Strophodonta are generally consistent with the model for all taxa so we will focus on the differences between models here. The inclusion of Individual as a random effect in this model was considered non-trivial based on having a standard deviation > 1. As Individual allows for a range of intercept values depending on the specimen, this gives the intercept a 95% confidence interval of -6.959 to -1.815 in logit units. Converted to probabilities, the intercept ranges from 0.00 to 0.14 (with a mean value of 0.01) depending on the individual measured, which is considered a negligible effect relative to the effects of size, convexity, and lithology.

While both models showed an increase of LOR from bins 1-4 before reaching a size refuge in bin 5, the interactive effect of Convexity is slightly different for the Strophodonta model, specifically in bin 1. In the analysis of all taxa, individuals belonging to size bin 1 are more likely to be repaired if they are strongly convex; this relationship is reversed when only Strophodonta is examined. This difference may be due to the presence of highly convex spinose taxa in the all-taxa analysis. Johnsen et al. (2013) found that the size refuge for a spinose brachiopod (Devonoproductus walcotti) began at a smaller size than the refuge for a similar brachiopod without spines (Douvillina arcuata), indicating an anti-predatory effect of spines and that predators were less successful against the spinose species. Spinose brachiopods in our dataset were small (none grew larger than bin 3), but spinose families still possess higher rates of repairs than most other taxa (Figure 3.6) and the rate of repair of spinose individuals in size bin 1 is almost double the rate of non-spinose individuals (Figure 3.7). Small prey in particular are more likely to be successfully crushed and are often removed from the fossil record (Pruden et al., 2018). That we find such high rates of repairs in productides supports the idea that these spinose taxa are better defended against predation and attacks on them are less successful.

The other major difference between analyses is that the selected Strophodonta model included Lithology while the selected model for all taxa included Paleolatitude. As previously mentioned, there was a latitudinal gradient of lithology in North America during the Devonian owing to the Appalachian orogeny in the area of New York. This resulted in the more southern basins (Appalachian and Michigan) having a greater siliciclastic content while basins further from the orogeny were mostly carbonate-dominated. While Lithology alone may be responsible for the difference in LOR between carbonate- and siliciclastic-dominated settings, no direct or indirect relationship between lithology and predation has been definitively demonstrated in the modern or fossil record. Paleolatitude (and temperature) may instead be the cause for the relationship between lithology and LOR, and the ΔAIC between our selected model (for Strophodonta) and a model that includes Paleolatitude rather than Lithology is only 3.4 – quite close to our cutoff of $\Delta\text{AIC} \leq 2$ in determining whether models are equally good at explaining the response in LOR. Lithology appearing in the Strophodonta model over Paleolatitude may be a mathematical, rather than biological, difference in explanatory power. An alternative hypothesis to Lithology being explained by Paleolatitude is that lithology is associated with water depth. In subtidal settings, predation pressure decreases with depth (Vermeij, 1987; Oji, 1996; Harper and Peck, 2016). If siliciclastic-dominated samples in our dataset were consistently from further-offshore settings than carbonate-dominated samples, the relationship with depth would be a reasonable explanation. Unfortunately, facies analyses of water depth have not been conducted for each sample or basin included in our dataset, so this hypothesis cannot presently be confirmed.

Interestingly, there was no effect of Stage on LOR in either model. As predators and prey evolved from the Givetian through the Frasnian, it is expected that predation pressure would increase, however this is clearly not reflected in repairs. This result does not refute the hypothesis of increasing predation pressure through time, rather it suggests that there may have been a shift in both the attack and success frequency through time. If predators were more abundant during the Frasnian, we would expect more repairs than in the Givetian unless Frasnian predators were also more successful. An additional factor to note is that each stage was not evenly recorded in all sampling areas. Due to the nature of changing suitable habitats for brachiopods over time, as well as differences in preservation, there are more samples from temperate latitudes earlier in the time interval while most Frasnian samples were collected from lower paleolatitudes. This artefact of the data may mean that either Stage, Paleolatitude, or both had an effect on LOR, and we recommend further examination of these variables in earlier and/or later time intervals.

3.4.3 Variables not tested

The result of the Family Leptostrophiidae having significantly more repairs than several other families is not surprising as members of the Leptostrophiidae are especially flat and specimens in our dataset frequently grew to a large size, making this result consistent with our modelled trends. The Illinois basin having more scars than the Iowa, Michigan, and Appalachian basins, however, appears contradictory to the latitudinal trend found in our selected model of all taxa. The resolution to this issue comes from the sample sizes of the basins: the Illinois basin consists of just one sample of 43 individuals whereas other basins have between four and twenty samples with 229 to 1642 individuals. It is clear with this context that the high repair frequency in the Illinois basin is insufficient to eliminate the latitudinal trend when the individual level is analysed. Additionally, over 95 % of the specimens from the Illinois basin belong to the family Leptostrophiidae – the most frequently scarred taxon. When evaluated in the context of our model, then, the high LOR in the Illinois basin is likely owing to a strong effect of Size and Convexity and a weaker effect of Paleolatitude.

In addition to Basin and Taxon, there are several variables we excluded from analysis for practical reasons. Temperature is one environmental parameter that is strongly associated with predation (Sanford, 1999; Allan et al., 2017; Romero et al., 2018; Leighton and Tyler, 2021) and would ideally have been included in our dataset. Unfortunately, no isotope analyses have been conducted on material from the Michigan or Illinois basins at the time of our study, precluding us from analysing temperature for these regions. As we did find a latitudinal trend in LOR, we strongly suspect that temperature did vary from equator to temperate regions, at least enough to produce differences in metabolic rates and attack frequencies.

We also excluded shell thickness from our analysis. Thickness can vary strongly as material is accreted along the commissure during the brachiopod lifespan. Measurements of thickness are typically performed on sectioned shells, making it a destructive and time-consuming process. And even when sectioning is feasible, it can be difficult to determine where on the shell to measure: does one take the thickest measurement regardless of position, or should there be a standardized position that is measured for each shell? This problem is compounded when individuals are split into size bins, as multiple measurements would be required for each individual that could be considered representative of each range of size. Additionally, shell thickness is often inconsistent after a predatory attack: the shell is thinned in the immediate damage area and the material that is accreted to repair it is commonly thicker than the surrounding undamaged shell. In the case of repaired individuals, measurements of thickness at the size of attack may be influenced by the repair and not representative of the actual thickness while the individual was attacked. Due to these numerous complications, we elected not to measure and include shell thickness in our analysis. Thickness is, however, a predictor of predator success (Vermeij, 1982; Johannesson, 1986; Alexander, 1990; Stafford et al., 2015) and is worthy of examination under more feasible conditions.

Despite the regional and taxonomic differences in LOR, we were still able to identify broad trends in Size, Convexity, and Paleolatitude that were associated with the LOR of Devonian strophomenates. Size had the strongest effect on LOR, while the effect of Convexity was strongly dependent on both the size bin examined and the taxonomic composition of the sample (see Figures 3.3 and 3.4), and the effect of Paleolatitude was relatively minor. This is not surprising as the size of the prey is directly related to the amount of nutrients a predator stands to gain from attacking a prey individual. The specific effect of each of these variables is most likely associated with a difference in the attack frequency: there were more predatory attacks on larger, less convex brachiopods living at lower latitudes, until these prey grew large enough to enter a size refuge. We cannot, however, rule out the possibility of an additive effect of differences in success, particularly that predators may be less successful when attempting to take larger prey.

These results do not preclude the possibility that LOR is driven by the number of predators in a system (as in Stafford et al., 2015), rather that in cases where predators and their abundances are unknown, prey size and convexity, as well as paleolatitude are useful in explaining and predicting the LOR on any one individual.

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Sample	**Source**	**Basin**	**Formation**	**Age**	**Lithology**	**Sample size**
AB-W-C1	Field	WCSB	Waterways	Frasnian	Carbonate	30
AB-W-C3	Field	WCSB	Waterways	Frasnian	Carbonate	41
AB-W-C5	Field	WCSB	Waterways	Frasnian	Carbonate	46
AB-W-M7	Field	WCSB	Waterways	Frasnian	Carbonate	55
NWT-TF	Field	WCSB	Twin Falls	Frasnian	Carbonate	57
IA-LC-N8	Field	Iowa	Lime Creek	Frasnian	Carbonate	81
IA-LC-NE10	Field	Iowa	Lime Creek	Frasnian	Carbonate	107
IA-LC-NE11	Field	Iowa	Lime Creek	Frasnian	Carbonate	63
IA-LC-NE13	Field	Iowa	Lime Creek	Frasnian	Carbonate	128
IA-LC-E13	Field	Iowa	Lime Creek	Frasnian	Carbonate	40
IA-LC-E14	Field	Iowa	Lime Creek	Frasnian	Carbonate	45
IA-LC-N13	Field	Iowa	Lime Creek	Frasnian	Carbonate	107
IA-LC-N14	Field	Iowa	Lime Creek	Frasnian	Carbonate	212
IA-LC-BH16	Field	Iowa	Lime Creek	Frasnian	Carbonate	34
IA-LC-BH17	Field	Iowa	Lime Creek	Frasnian	Carbonate	140
IA-LC-BH18	Field	Iowa	Lime Creek	Frasnian	Carbonate	198
IA-LC-BH19	Field	Iowa	Lime Creek	Frasnian	Carbonate	38
IA-SR-MC-UIR	UIR	Iowa	Shell Rock	Frasnian	Carbonate	58
IA-LGC-BQ-UIR	UIR	Iowa	Lithograph City	Givetian	Carbonate	135
IN-NV-SQ	Field	Illinois	North Vernon	Givetian	Carbonate	43
MO-CR-CC-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	37
MO-SN-SC-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	60
MO-SN-SC5-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	59
MO-SN-SC10-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	40
MO-SN-SC1-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	19
MO-SN-SC2-YPM	YPM	Iowa	Snyder Creek	Frasnian	Siliciclastic	41
OH-SS-U7	Field	App.	Silica Shale	Givetian	Siliciclastic	51
OH-SS-U7B	Field	App.	Silica Shale	Givetian	Siliciclastic	84
OH-SS-U9	Field	App.	Silica Shale	Givetian	Siliciclastic	31
MI-GUP-UMMP	UMMP	Michigan	Genshaw	Givetian	Carbonate	79
MI-GLO-UMMP	UMMP	Michigan	Genshaw	Givetian	Carbonate	37
MI-FPUP-UMMP	UMMP	Michigan	Ferron Point	Givetian	Siliciclastic	95
MI-FPLO-UMMP	UMMP	Michigan	Ferron Point	Givetian	Siliciclastic	45
MI-PF-UMMP	UMMP	Michigan	Potter Farm	Givetian	Carbonate	93
MI-GPU-UMMP	UMMP	Michigan	Gravel Point	Givetian	Siliciclastic	50
MI-GPL-UMMP	UMMP	Michigan	Gravel Point	Givetian	Siliciclastic	94
MI-PT-UMMP	UMMP	Michigan	Petoskey	Givetian	Carbonate	68
MI-GPL-YPM	YPM	Michigan	Gravel Point	Givetian	Siliciclastic	45
MI-GUP-YPM	YPM	Michigan	Genshaw	Givetian	Carbonate	158
MI-FP-YPM	YPM	Michigan	Ferron Point	Givetian	Siliciclastic	112
MI-PF-YPM	YPM	Michigan	Potter Farm	Givetian	Carbonate	116
NY-LVW-PRI	PRI	App.	Ludlowville	Givetian	Siliciclastic	34
NY-LVC-PRI	PRI	App.	Ludlowville	Givetian	Carbonate	35
NY-MSK-PRI	PRI	App.	Moscow	Givetian	Siliciclastic	40
NY-LVW-YPM	YPM	App.	Ludlowville	Givetian	Siliciclastic	68
ON-HH-YPM	YPM	App.	Widder	Givetian	Carbonate	61

Table 3.1

(above) General information for the 46 samples that analyzed individuals belong to. Sample names are broken into multiple parts: 1) general region (province or state), 2) Formation, 3) sample, 4) museum. Field = collected by the Leighton Lab using a standard procedure; UIR = University of Iowa Repository; YPM = Yale Peabody Museum; UMMP = University of Michigan Museum of Paleontology; PRI – Paleontological Research Institution; App = Appalachian basin.

Table 3.2

(below) Fixed and random effect variables included in analysis. All variables included in both the all-taxa and *Strophodonta*-only analyses except for ornament as *Strophodonta* is never spinose.

Variable	Measurement/Value	Variable Type
Fixed Effect Variables		
Size	Length perpendicular to hinge from umbo to commissure (mm); split into size bins 4 mm or 7 mm in width	Categorical; for 7 mm bins, categories 1-5 representing individuals 2-37 mm in length
Convexity	Ratio of height (mm) to length (mm)	Continuous; values range from 0.07 to 0.63
Ornament	Spinose or not	Categorical
Stage	Givetian or Frasnian	Categorical
Latitude	Output of paleolatitude calculator from input coordinates of sampled localities	Continuous; values range from -43 to -10
Lithology	Carbonate- or siliciclastic-dominated	Categorical
Random Effect Variables		
Individual	Specimen that an observation represents; one level for each specimen	Categorical
Sample	Sample to which an individual belongs	Categorical
Collection Source	Field-collected or the museum sourced from	Categorical

Sample	**Stage Source**	**Lithology Source**
AB-W-C1	Mendonca et al., 2018	Mendonca et al., 2018
AB-W-C3	Mendonca et al., 2018	Mendonca et al., 2018
AB-W-C5	Mendonca et al., 2018	Mendonca et al., 2018
AB-W-M7	Mendonca et al., 2018	Mendonca et al., 2018
NWT-TF	Barclay et al., 2013	Barclay et al., 2013
IA-LC-N8	Day and Witzke. 2017	Identified in the field
IA-LC-NE10	Day and Witzke. 2017	Identified in the field
IA-LC-NE11	Day and Witzke. 2017	Identified in the field
IA-LC-NE13	Day and Witzke. 2017	Identified in the field
IA-LC-E13	Day and Witzke. 2017	Identified in the field
IA-LC-E14	Day and Witzke. 2017	Identified in the field
IA-LC-N13	Day and Witzke. 2017	Identified in the field
IA-LC-N14	Day and Witzke. 2017	Identified in the field
IA-LC-BH16	Day and Witzke. 2017	Identified in the field
IA-LC-BH17	Day and Witzke. 2017	Identified in the field
IA-LC-BH18	Day and Witzke. 2017	Identified in the field
IA-LC-BH19	Day and Witzke. 2017	Identified in the field
IA-SR-MC-UIR	Day et al., 2008	Day et al., 2008
IA-LGC-BQ-UIR	Day et al., 2008	Day et al., 2008
IN-NV-SQ	Brett et al., 2011	Identified in the field
MO-CR-CC-YPM	Branson, 1944	Day et al., 1996
MO-SN-SC-YPM	Branson, 1944	Day et al., 1996
MO-SN-SC5-YPM	Branson, 1944	Day et al., 1996
MO-SN-SC10-YPM	Branson, 1944	Day et al., 1996
MO-SN-SC1-YPM	Branson, 1944	Day et al., 1996
MO-SN-SC2-YPM	Branson, 1944	Day et al., 1996
OH-SS-U7	Leighton, 2003	Leighton, 2003
OH-SS-U7B	Leighton, 2003	Leighton, 2003
OH-SS-U9	Leighton, 2003	Leighton, 2003
MI-GUP-UMMP	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-GLO-UMMP	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-FPUP-UMMP	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-FPLO-UMMP	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-PF-UMMP	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-GPU-UMMP	Kesling, 1974	Kesling, 1974
MI-GPL-UMMP	Kesling, 1974	Kesling, 1974
MI-PT-UMMP	Kesling, 1974	Kesling, 1974
MI-GPL-YPM	Kesling, 1974	Kesling, 1974
MI-GUP-YPM	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-FP-YPM	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
MI-PF-YPM	Ehlers and Kesling, 1970	Ehlers and Kesling, 1970
NY-LVW-PRI	Brett et al., 2011	Brett et al., 2011
NY-LVC-PRI	Brett et al., 2011	Brett et al., 2011
NY-MSK-PRI	Brett et al., 2011	Brett et al., 2011
NY-LVW-YPM	Brett et al., 2011	Brett et al., 2011
ON-HH-YPM	Brett et al., 2011	Brett et al., 2011

Table 3.3

(above) Summary of literary sources for Stage and Lithology of samples. The lithology of all field-collected samples was noted during fieldwork.

Table 3.4

(below) Interaction effects tested in analysis. Any interaction involving ornament was not included in the *Strophotonta*-only analysis.

Interacting Variables			Reason for Inclusion
Size	x	Ornament	Spinose taxa can have a size refuge at smaller size than non-spinose taxa (Johnsen et al., 2013) and can cause predators to be less successful when attacking smaller prey. This could influence the LOR of spinose prey by increasing the LOR of small individuals and decreasing the LOR of individuals that have reached the size refuge.
Size	x	Convexity	More convex individuals are expected to have a higher LOR at all sizes due to a lower predator success rate, but this protective effect should be especially apparent at smaller sizes.
Size	x	Stage	As predators evolve to become more specialized from Givetian to Frasnian, we expect the size refuge to change. The direction of this change depends on how the prey adapted: if they adapted poorly, the size refuge would increase, if they adapted well, the size refuge could decrease.
Size	x	Latitude	If predators were stronger and more abundant at lower latitudes, we would expect a greater LOR in tropical regions and potentially a difference in the size refuge across latitudes.
Convexity	x	Ornament	Convexity and ornament are associated in our dataset (Kruskal-Wallis test $p < 0.001$) so we expect their individual effects to be strengthened.
Ornament	x	Stage	If brachiopod prey adapted to their improving predators over time, we might expect more spinose individuals during the Frasnian with greater LOR.
Ornament	x	Latitude	We expect that while all lower latitude individuals might experience more attacks, spinose individuals would experience fewer successful attacks than their non-spinose relatives, resulting in a greater LOR.

Table 3.5

GLMMs for whether individuals of all strophomenate taxa are scarred. Only models within $\Delta AIC \leq 2$ of the lowest AIC model, as well as a null model with no fixed effects, are presented. The summary output of a selected model containing variables limited to those found in all displayed candidate models ($\Delta AIC \leq 2$) is shown below. Z values are Wald-Z test scores used to calculate p-values; significant p-values shown in bold. Units of random and fixed effects are logits.View Figure 3.3 for effects of Size, Convexity, and Paleolatitude on the probability scale. S = Size; C = Convexity; O = Ornament; La = Paleolatitude; St = Stage; Li = Lithology.

Scarred/unscarred models of all taxa (family = binomial [link = logit])

Model	**AIC**	**BIC**	**logLik**	**Resid.dev**	**Resid.df**
SxC + SxO + La	5079.2	5190.4	-2523.6	5047.2	7677
SxC + O + La	5080.8	5178.1	-2526.4	5052.8	7679
SxC + La	**5080.8**	**5171.1**	**-2527.4**	**5054.8**	**7680**
SxC + SxO + OxC + La	5080.9	5199.0	-2523.4	5046.9	7676
SxC + SxO + La + St	5081.1	5199.2	-2523.5	5047.1	7676
SxC + SxO + La + Li	5081.2	5199.3	-2523.6	5047.2	7676
Null	5296.9	5317.8	-2645.5	5290.0	7690

Selected Model **S x C + La**

Random effects	**Name**	**Variance**	**Std. Dev.**
Individual	(Intercept)	0.6861	0.8283
Sample	(Intercept)	0.1929	0.4392

Fixed effects	**Estimate**	**Std. Error**	**z value**	**Pr (>|z|)**
Intercept	-3.1972	0.1210	-26.429	**< 0.0001**
Sizebin 2	0.9887	0.0977	10.122	**< 0.0001**
Sizebin 3	1.3662	0.1307	10.453	**< 0.0001**
Sizebin 4	1.7902	0.1670	10.718	**< 0.0001**
Sizebin 5	0.5568	0.4266	1.305	0.1918
Convexity	0.2807	0.0848	3.310	**0.0009**
Paleolatitude	0.1861	0.0756	2.462	**0.0138**
Sizebin 2 : Convexity	-0.4167	0.0978	-4.262	**< 0.0001**
Sizebin 3 : Convexity	-0.5538	0.1238	-4.472	**< 0.0001**
Sizebin 4 : Convexity	-0.3813	0.1454	-2.623	**0.0087**
Sizebin 5 : Convexity	-0.8110	0.3100	-2.616	**0.0089**

Table 3.6

Results of log-likelihood tests to determine whether random effects are needed in the models. Significant values have been bolded.

All-taxa Analysis	
Random effect	**Log-Likelihood p-value**
Individual	**< 0.0001**
Sample	**< 0.0001**
Collection Source	0.5000
***Strophodonta*-only Analysis**	
Random effect	**Log-Likelihood p-value**
Individual	**< 0.0001**
Sample	0.2011
Collection Source	0.4998

Table 3.7

Results of pairwise Chi-Square and Fisher’s exact tests for repair rates of basins and taxa, respectively. Significant pairwise comparisons are shown in bold. WCSB = Western Canadian Sedimentary Basin; Mich = Michigan basin; App = Appalachian basin; Stro.d = Strophodontiidae; Lept = Leptostrophiidae; Douv = Douvillinidae; Areo = Areostrophiidae; Chon = Chonetidae; Sent = Sentosiidae; Mont = Monticuliferidae; Arak = Araksalosiidae; Prod = Productellidae; Stro.l = Strophalosiidae; Trop = Tropidoleptidae.

Chi-Square p-values for Basin repair rates

	Iowa	**Illinois**	**Mich.**	**App.**
WCSB	0.083	0.182	**0.008**	0.163
Iowa		**0.002**	0.345	0.730
Illinois			**< 0.001**	**0.007**
Michigan				0.199

Fisher’s Exact p-values for Family repair rates

	Lept.	**Douv.**	**Areo.**	**Chon.**	**Sent.**	**Mont.**	**Arak.**	**Prod.**	**Stro.l.**	**Trop.**
Stro.d.	**0.037**	1	1	1	0.667	1	1	1	0.490	0.490
Lept.		0.095	**0.037**	**0.011**	0.196	0.095	**0.019**	0.095	**0.002**	**0.002**
Douv.			1	0.609	1	1	0.668	1	0.235	0.235
Areo.				1	0.667	1	1	1	0.490	0.490
Chon.					0.349	0.609	1	0.609	1	1
Sent.						1	0.419	1	0.110	0.110
Mont.							0.668	1	0.235	0.235
Arak.								0.668	0.490	0.490
Prod.									0.235	0.235
Stro.l.										1

Table 3.8

GLMMs for whether individuals of the Genus *Strophodonta* are scarred. Table structure as in Table 3.5. View Figure 3.4 for effects of Size, Convexity, and Lithology on the probability scale. Abbreviations of fixed effects shown in Table 3.4.

Scarred/unscarred models of Strophodonta (family = binomial [link = logit])					
Model	**AIC**	**BIC**	**logLik**	**Resid.dev**	**Resid.df**
SxC + Li	**2154.5**	**2229.8**	**-1065.2**	**2130.5**	**3939**
SxC + Li + La	2155.5	2237.2	-1064.8	2129.5	3938
SxC + Li + St + La	2155.8	2243.8	-1063.9	2127.8	3937
SxC + Li + St	2156.2	2237.8	-1065.1	2130.2	3938
Null	2343.1	2355.7	-1169.6	2339.1	3949
Selected Model				**S x C + Li**	
Random effects	**Name**	**Variance**	**Std. Dev.**		
Individual	(Intercept)	1.654	1.286		
Fixed effects	**Estimate**	**Std. Error**	**z value**	**Pr (>|z|)**	
Intercept	-4.3866	0.2811	-15.605	**< 0.0001**	
Sizebin 2	1.8886	0.2426	7.785	**< 0.0001**	
Sizebin 3	2.3559	0.2520	9.350	**< 0.0001**	
Sizebin 4	2.8611	0.2832	10.102	**< 0.0001**	
Sizebin 5	1.5675	0.6068	2.575	**0.0100**	
Convexity	-0.6869	0.2790	-2.462	**0.0138**	
Li – Siliciclastic	-0.4868	0.1654	-2.944	**0.0032**	
Sizebin 2 : Convexity	0.4365	0.3014	1.448	0.1476	
Sizebin 3 : Convexity	0.6781	0.3084	2.199	**0.0279**	
Sizebin 4 : Convexity	0.6413	0.3295	1.946	0.0516	
Sizebin 5 : Convexity	-1.8582	0.9725	-1.911	0.0560	

Figure 3.1

Examples of repair scars on A) *Strophodonta fissicosta* (Petoskey Formation, Michigan, UMMP collections), B) *Douvillina arcuata* (Lime Creek Formation, Iowa), and C) *Praewaagenoconcha sp.* (Waterways Formation, Alberta). A) repair scar traced in red; growth line distorted by the scar traced in white; size at attack (SAA) is measured perpendicular to the hingeline from the umbo to the growth line distorted by the scar (intersection of white lines in figure). Arrows in B and C highlight scars. Scale bar = 1 cm.

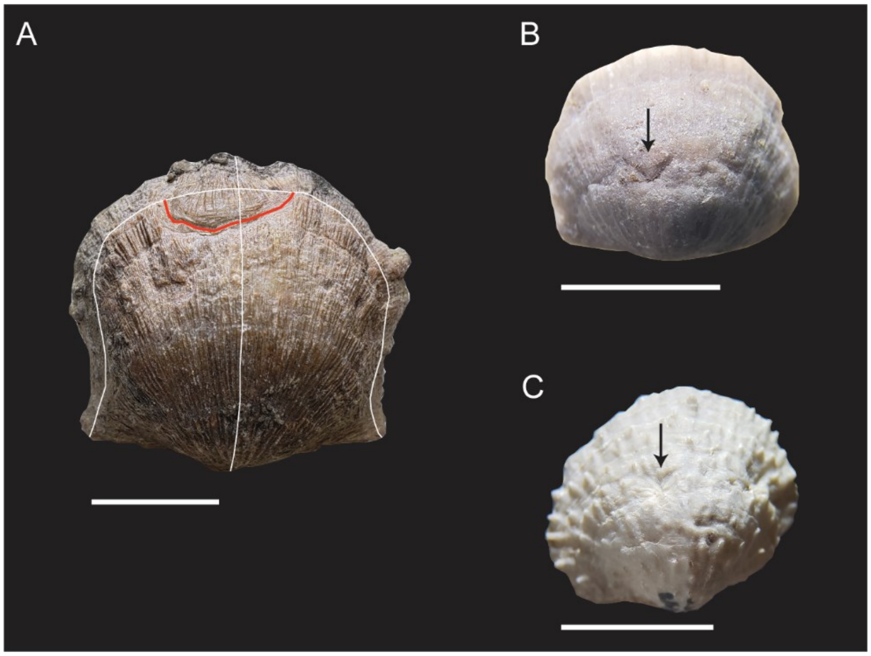


Figure 3.2

Map of North America during the Givetian. Grey areas are land and white areas are marine. Black line across the top left is the approximate location of the equator. Approximate sample localities are shown in red dots. WCSB = Western Canadian Sedimentary Basin. Figure modified from Brett et al., 2011.

Figure 3.3

Predicted LOR and EMMs of variables included in the model of all taxa. LOR on the probability scale (0-1). A) Predicted LOR across convexity with separate slopes for each size bin; raw value scale for convexity. B) Predicted LOR across latitude; only latitudes within the range of values sampled are shown. C) EMM LOR for each size bin at a constant mean value of convexity; red arrows represent confidence intervals for each bin, a significant pairwise difference in LOR exists where arrows do not overlap.

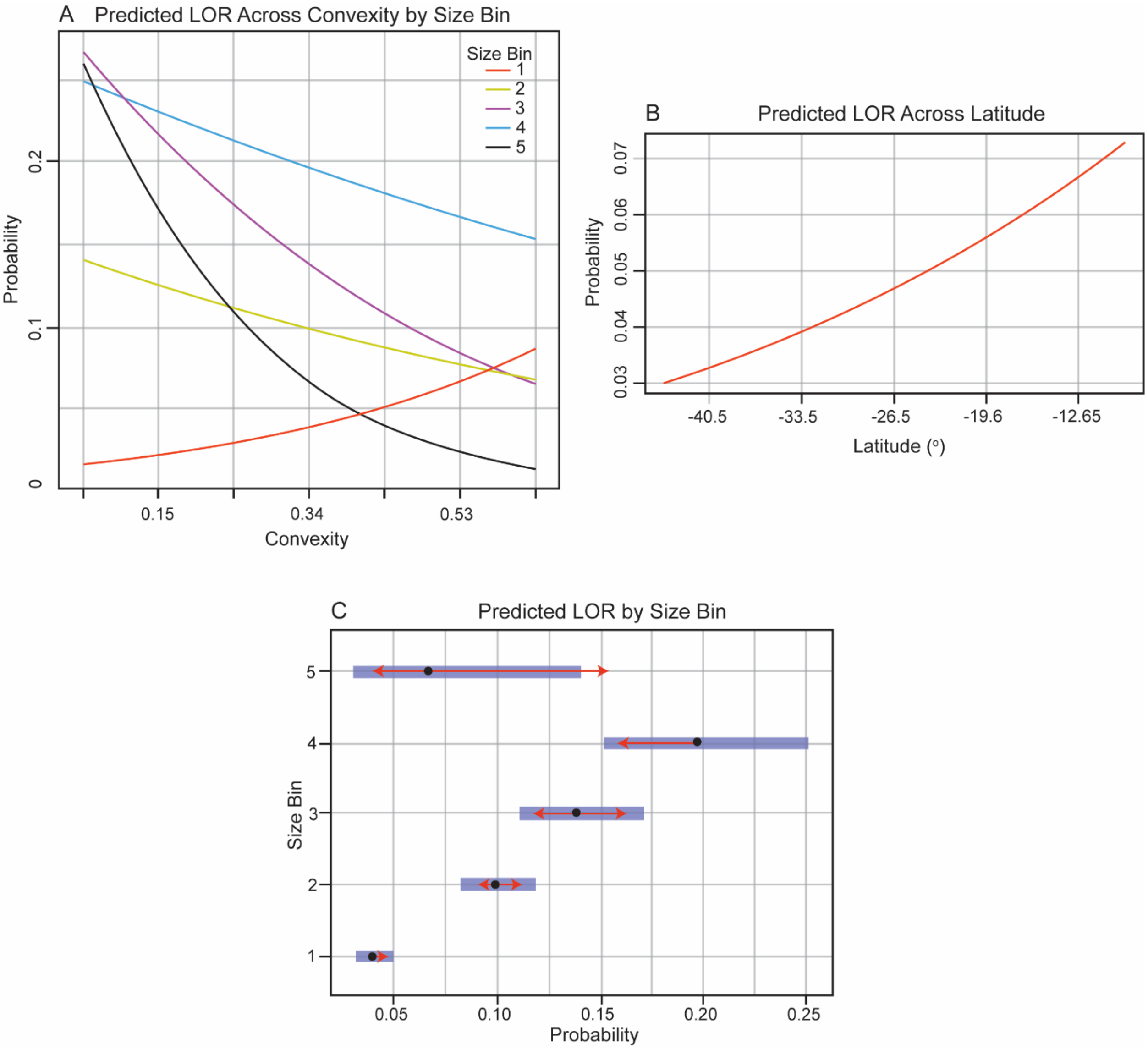


Figure 3.4

Predicted LOR and EMMs of variables included in the model of *Strophodonta*. LOR on the probability scale (0-1). A) Predicted LOR across convexity with separate slopes for each size bin; raw value scale for convexity. B) EMM LOR for lithology types. C) EMM LOR for each size bin at a constant mean value of convexity; red arrows represent confidence intervals for each bin, a significant pairwise difference in LOR exists where arrows do not overlap.

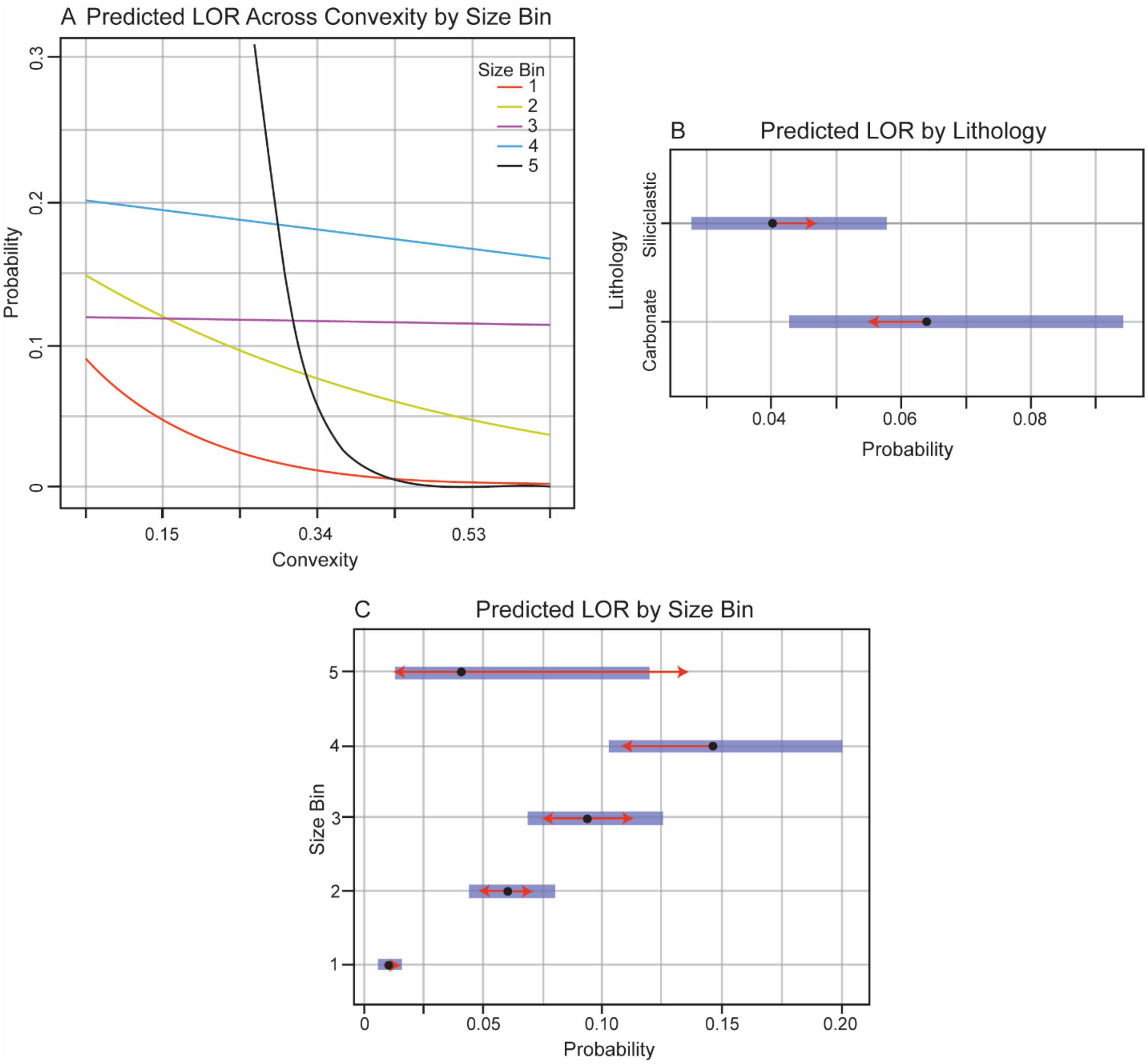


Figure 3.5

Boxplot of differences in convexity by ornament (spinose/not spinose). Boxes give range of values between upper and lower quartiles; central lines represent median values; whiskers show the minimum and maximum values of the data; outliers represented by circles.

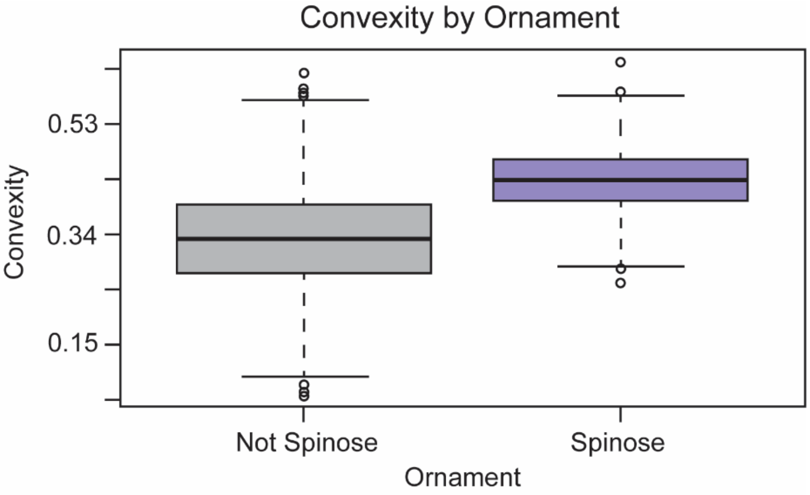


Figure 3.6

Bar charts displaying the proportion of repairs in A) basins, and B) Families. Spinose taxa highlighted in purple. WCSB = Western Canadian Sedimentary Basin, App = Appalachian Basin, Stro.d = Strophodontiidae, Lept = Leptostrophiidae, Douv = Douvillinidae, Areo = Areostrophiidae, Chon = Chonetidae, Sent = Sentosiidae, Mont = Monticuliferidae, Arak = Araksalosiidae, Prod = Productellidae, Stro.l = Strophalosiidae, Trop = Tropidoleptidae.

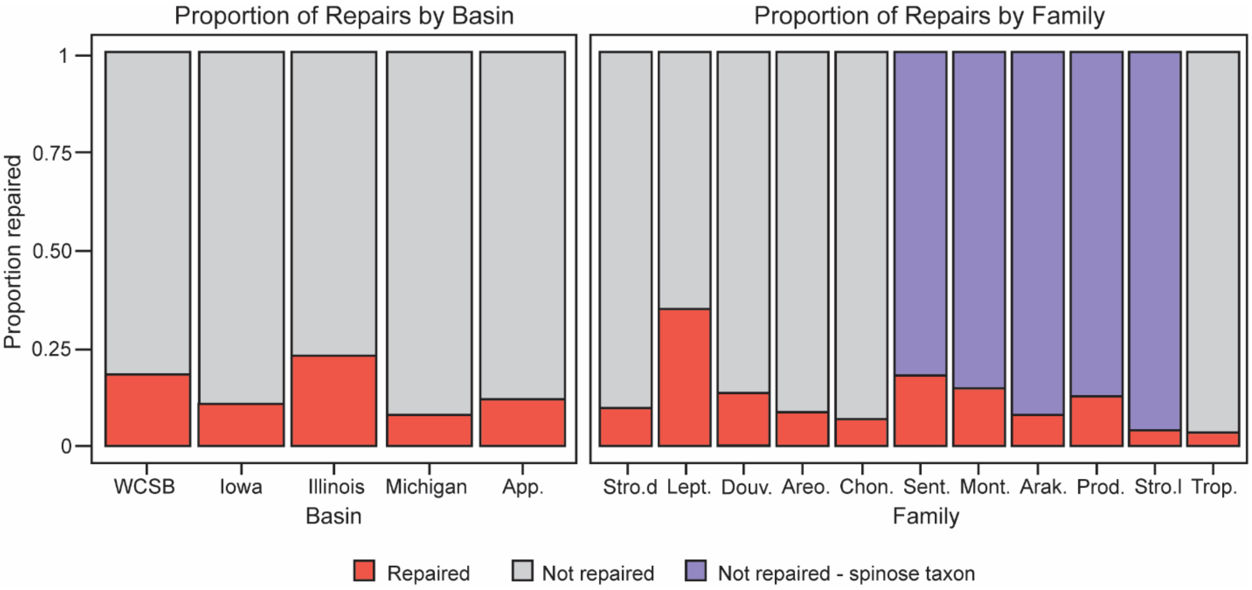
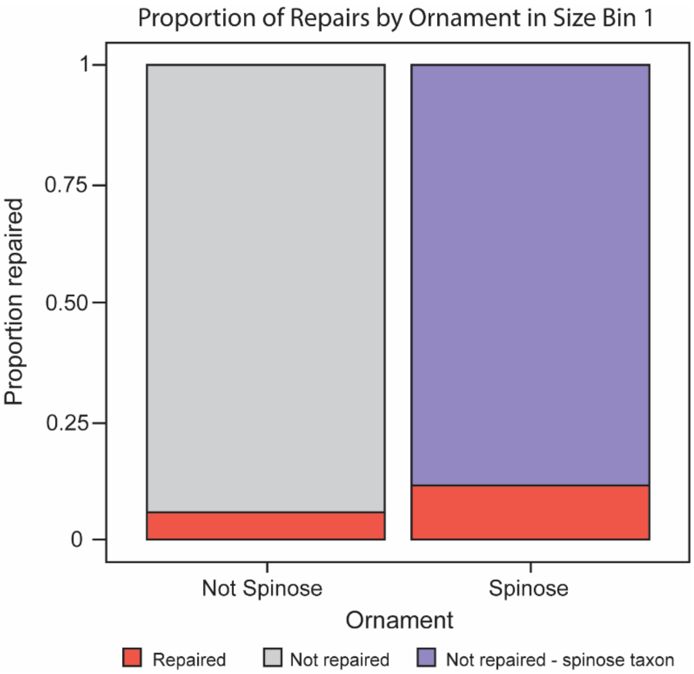


Figure 3.7

Bar chart showing the proportion of repairs for spinose vs. not spinose taxa in size bin 1.



Chapter 4

Conclusions

Predation is an essential process to ecosystem function that both controls species behaviour and distribution and is influenced by the environmental conditions and adaptations of prey taxa to their predators. Though repair scars are an incomplete proxy in that they measure failed attacks, they are useful in detecting differences in predation between communities and individuals. The results of this thesis support the idea that predation has a role in shaping communities, even in the fossil record, and that prey and environment have an influence on predation – both attack and success rates. Considering the goals of this research, there are several important conclusions to be drawn:

1. Predation is detectable as a driver of species distribution and community structure in the fossil record. This refutes the idea that environmental processes will always overprint ecological ones at the sampling scales of fossil studies and enforces the concept that paleocommunities can be fully understood only when both environmental and ecological processes are examined – although we recognize logistical challenges of doing so in many cases.
2. The detection of ecological processes may not be possible at all scales. This study was performed at a relatively fine-scale compared to most paleocommunity studies, so it is possible that a process like predation would be overprinted if an onshore-offshore gradient were sampled.
3. When all brachiopods are considered, size, convexity, and latitude are the strongest predictors of likelihood of repair (LOR) of an individual. The relationship between each variable and LOR is best explained by differences in attack rates: larger, flatter

brachiopods living at lower latitudes are more likely to be attacked. This result holds true for all North American concavo-convex brachiopods from the Mid to Late Devonian, however, the trends in size and latitude have been found for other time intervals, suggesting a robust effect on predation.

4. When only *Strophodonta* is considered, size, convexity, and lithology are the strongest predictors of LOR. The difference between this analysis and the one of all taxa may be an artefact of the data, as lithology and latitude are strongly correlated. Examination of latitude and lithology in other time intervals or regions may help to disentangle their effects on predation.
5. The effect of size is the strongest, with convexity having a similar effect depending on prey size. Latitude has a much weaker effect on LOR.
6. We cannot eliminate the possibility of an effect of predator success on LOR in the case of prey size. In reality, it is likely that predators both attempt to take more large prey and are less successful against these individuals, so this result is not undesirable.
7. Convexity and ornamentation together may reduce predator success in the smallest individuals. Very young brachiopods are likely to be successfully crushed in every predatory encounter, so the greater LOR on convex, spinose individuals suggests that they are more likely to survive than their flatter, non-ornamented relatives.

Study of predation in the fossil record is challenging but rewarding in that we can broaden our understanding of predation as a process beyond the ecosystems that are alive today. I identified predation as a driver of Devonian brachiopod paleocommunity structure and found that size, convexity, and latitude are the most important morphological and environmental predictors of LOR.

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