

**Quantifying the Functional Morphology of Productidine Brachiopods
through Performance**

by

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Abstract

Functional morphology is an important tool for paleoecology. However, functional interpretations which are based on tenuous logic without a proper test or which rely on circular reasoning can be problematic. Biomechanical tests can help to provide structured and absolute assessments of functionality and performance. But by combining multiple measures of performance, performance spaces/landscapes can be constructed. In the same way a morphospace quantifies overall morphology with multiple measurements, a performance space quantifies overall function through multiple measures of performance. By including more than one measure of performance, it becomes possible to evaluate how changes in morphology affect multiple aspects of function and performance. Thus, we can more easily identify evolutionary trade-offs and evaluate whole organism fitness. Additionally, by combining performance with additional taxonomic or environmental context it is possible to look for cases of adaptation, both as a process and as a product. In this thesis, I examine productidine functional morphology using the framework of a performance space.

The first application of the performance space used in this thesis was to quantify adaptation as a process of evolution. By combining the performance with taxonomic context, performance across lineages can be used to evaluate whether taxonomic, and thus morphological, patterns mirror or correspond to performance patterns. In Chapter 2 I used the performance of the brachiopod superfamily Echinoconchoidea to test for adaptation. Because they are libero sessile suspensions feeders, hydrodynamic performance is expected to exert strong selective pressure on brachiopod morphology. The echinoconchoid performance space I constructed consists of 5 performance axes: 1) stability in mobile substrates, 2) stability of soft substrates, 3) feeding efficiency, 4) respiration/metabolic efficiency 5) defense against predation. This performance space was populated with eight North American genera from two families, one primitive (Sentosiidae) and one derived

(Echinoconchidae). The Echinoconchidae contains two disparate subfamilies the Echinoconchinae with bands of short densely spaced spines, and the Juresaniinae with longer and variably spaced spines. I found two patterns in echinoconchoid performance. The first is a trend driven by size ($r=0.85$, $p=0.006$), in which larger echinoconchoids had increased passive feeding, proportionally smaller lophophores, and lower cost/benefit ratios for potential predators. This coincides with a general increase in echinoconchoid size through time. The second pattern is the relative spacing of genera in the performance space in which genera are distant from each other essentially “filling out” the space. This spacing suggests niche differentiation based, at least in part, on hydrodynamic performance.

The second application of the performance space evaluated adaptation as a product of evolution. In this context, it is expected that the performance of a given organism should be at the very least consistent with environmental conditions. Combining performance and paleoenvironment serves as a test of both the functional hypotheses and as an additional test of paleoenvironmental interpretations. I constructed a performance space using genera with well-described environmental distribution patterns from the late Paleozoic of the North American Mid-continent. I chose three performance variables reflecting environmental variables: 1) stability in high velocity flow over mobile substrates, 2) stability on soft muds in calm water 3) respiration potential using lophophore (the brachiopod feeding and respiration apparatus) size as a proxy. This study included genera from all three productidine superfamilies. For this study, I chose eight genera: two associated with nearshore environments, two associated with offshore well oxygenated settings, two associated with dysoxia, and two rare genera with ambiguous distributions and associations. This study produced two broad results. The first result is that Mid-continent productidine generic performance is consistent with paleoenvironmental interpretations and distributions. Nearshore taxa remain stable in high velocity flows and have proportionally smaller lophophores. Rare and well oxygenated setting taxa perform well on muds and mobile

substrates and have proportionally smaller lophophores. Dysoxic taxa have high resistance to sinking in soft muds and proportionally larger lophophores. The second result is a demonstration that productidine spine length greatly affects overall hydrodynamic stability; longer spines prevent instability in mobile substrates and increase resistance to sinking better than short spines.

Overall, productidine spines and morphology display adaptation to multiple functions and environments. This study tests and supports the hypothesized function of spines as a means of maintaining stability without a pedicle.

Dedication

To my mom,

“You never gave up on me”

Reba McEntire

To God and everyone who has shaped me

“Here I am with you all over me.

Here I am to touch eternity.

All I am I am because of you.”

Jenny Berggren

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Table of Contents

Abstract	ii
Dedication	v
Acknowledgements	vi
Table of Contents	vii
List of Tables	xi
List of Figures	x
Chapter 1	1
1.1 References	4
Chapter 2	6
2.1 Introduction.....	6
2.2 Materials and Methods	11
2.2.1 Mobile/Sandy Substrates.....	12
2.2.2 Soft Substrates.....	12
2.2.3 Ambient Flow.....	13
2.2.4 Respiration.....	14
2.2.5 Predation	15
2.2.6 Analysis of Performance.....	15
2.3 Results.....	16
2.3.1 Transport Experiments.....	16
2.3.2 Settling Times	16
2.3.3 Passive Flow	16
2.3.4 Respiration Proxy	17
2.3.5 Defensive Cost/Benefit Ratio	17
2.3.6 PCA	17
2.4 Discussion	17
2.4.1 General Performance	17

2.4.2 Size and Performance	18
2.4.3 Hydrodynamic Performance	20
2.4.4 Echinoconchoids in Performance Space	21
2.5 References	24
Chapter 3	36
3.1 Introduction.....	36
3.2 Materials and Methods	39
3.2.1 Genera	39
3.2.2 Settling and Environmental Framework.....	40
3.2.3 Physical Model Creation	43
3.2.4 Measures of Performance	43
3.2.4.1 Transport Resistance.....	43
3.2.4.2 Stability on Soft Substrates.....	44
3.2.4.3 Respiration/Metabolic Proxy	45
3.2.5 Analysis of Performance.....	46
3.3 Results.....	46
3.3.1 Stability in Sand and High Velocity Current.....	46
3.3.2 Settling Times	47
3.3.3 Respiration Proxy	48
3.3.4 PCA	48
3.4 Discussion	48
3.4.1 General Findings	48
3.4.2 Nearshore Taxa	49
3.4.3 Offshore Taxa	50
3.4.4 Rare/Other Taxa	52
3.4.5 Macroevolutionary Context	53
3.5 References	56

Chapter 4	68
References	70

List of Tables

Table 2.1	30
Table 2.2	30
Table 3.1	64

List of Figures

Figure 2.1.....	31
Figure 2.2.....	31
Figure 2.3.....	32
Figure 2.4.....	33
Figure 2.5.....	33
Figure 2.6.....	34
Figure 2.7.....	34
Figure 2.8.....	35
Figure 3.1.....	65
Figure 3.2.....	66
Figure 3.3.....	67
Figure 3.4.....	67
Figure 3.5.....	68

Chapter 1

Introduction

Understanding the biomechanics and functional morphology of brachiopods is critical to understanding their paleoecology and to their use as paleoenvironmental indicators. Brachiopods also contribute to a large portion of the fossil record overall (Sepkoski, 1981) and our understanding of brachiopods is important to understanding the history of life on Earth. While the application of the idea/theory of uniformitarianism has been valuable to understanding the lives of extinct brachiopods, it has limitations (Grant, 1981; Alexander, 2001). For example, while aspects of modern brachiopod ecology such as growth, muscle mechanics, or reproduction are more easily applied to fossil brachiopods, there is less consensus on other aspects of fossil brachiopod ecology such as feeding (e.g. Rudwick, 1960 vs. William, 1960; Mancenido, 2008) or life orientation (e.g. Lescinsky, 1995 vs. Leighton, 1998) in completely extinct groups. Disagreement over the functionality of brachiopods is largely the result of the somewhat subjective nature of functional morphology. To untangle the complexities of productidine evolutionary and functional morphology a broader approach comparing multiple functions is required.

To thoroughly test functional morphology hypotheses alternate functions and contributions to overall function and fitness must be quantified and compared. By comparing how well a structure or morphology performs a single function or multiple functions, a more accurate understanding of overall function and fitness can be reached. To fully test an *a priori* functional hypothesis alternate functions should also be evaluated. If a character or trait performs well in a measure of assumed function but less well in tests of other functions the initial hypothesis is strengthened for the initial or assumed function. While this approach initially appears similar to the paradigm model (Rudwick, 1964; Hickman 1988) in which the function of a structure is inferred based on optimality there are two key differences. The first is that here I assume that biomechanical systems may not always be optimized for a single function. The second is that unlike the paradigm method, if a character or trait has average performance in multiple measures of function it could indicate that the trait may be subject to multiple selective pressures or that the character is constrained in some way preventing optimization. An even simpler explanation is that optimization may not always be required to be well adapted. While morphological optimization may enhance functionality and efficiency; overall, the system may lack the selective pressure necessary for an optimal shape to evolve. Thus, it is critical to include

evolutionary and environmental context with performance before adaptation can be invoked.

It is also likely that morphology is the result of multiple selective pressures being applied to create trade-offs. To test for trade offs more thoroughly performance landscapes/spaces can be used as a more direct means of measuring fitness or adaptation (Polly et al., 2016; Stayton, 2019). By combining performance with morphology, a performance based adaptive landscape can be constructed (Polly et al., 2016). One step further, performance spaces consisting purely of functional measures can be constructed. Performance spaces function as an absolute frame of reference in which to compare performance independently from morphology. This independence opens up the possibility that multiple morphotypes may have similar performance despite dissimilarities in morphology. Once the performance space has been populated with individuals or genera additional morphological, environmental, or phylogenetic patterns can be added back to aid in interpreting patterns of performance as evidence of adaptation.

The suborder Productidina useful for examining performance and functional morphology for several reasons. The first reason is that like most brachiopods in the class Strophomenata productidines lacked pedicles (a fleshy appendage which affixes most extant brachiopods to the substrate) throughout most of ontogeny. In extant, and extinct, brachiopods of the class Rhynchonellata the pedicle serves the crucial role of maintaining stability by affixing brachiopods to a hard surface or providing anchorage in soft substrates. Lacking pedicles, productidines instead relied on body morphology and spine geometry to interact with the substrate and maintain stability. As a result, productidine external morphology is expected to reflect environmental conditions and thus be a useful proxy when applied to paleoenvironmental reconstruction. Numerous functions have been proposed for productidine valve shape and spine geometry (see Alexander, [2003] or Chapters 2 and 3 for examples). However relatively few tests of function have been performed (Alexander, 1984, Leighton, 2000; Garcia et al. 2018). Because the laws of physics are constant, accurate models of productidines are expected to behave in the same manner as living productidines would have behaved and direct observation can be used to infer performance and hydrodynamic behavior. Thus, empirical data collected from physical experiments can be used to constrain hypotheses and evaluate productidine functional morphology.

The second reason productidines are useful is that soft tissue reconstruction is relatively straight forward. In general, brachiopod valves are misleading with respect to actual body size (Rudwick, 1970; Peck, 1992). The volume of most brachiopods consisted of

a small proportion of body cavity and a much larger volume of water filling the mantle cavity. Thus, when reconstructing productidines soft tissue is a minor constituent that makes conservative reconstruction relatively straight forward. Productidines are inferred to have possessed simple lophophores in the form of schizolophes. Schizolophes simple lophophore with two dimensional and attached directly to the dorsal valve. In comparison, spirolophes and plectolophes are three dimensional and are suspended in the mantle cavity.

In Chapter 2, to test for evolutionary patterns, I reconstructed 8 North American genera from the superfamily Echinoconchoidea and used a performance space to evaluate hydrodynamic stability, feeding efficiency, respiration efficiency, and cost/benefit for predators. The echinoconchoid genera belonged to two lineages whose performance was compared to test if echinoconchoid performance adapted and improved through time. The hypothesis tested is that echinoconchoid performance will increase through time and there will be differential performance between lineages. If this is true, then subclades within the superfamily will group in performance space. If performance and systematics are inconsistent there are several alternate possibilities: 1) evolution is acting on a function not examined here or 2) there is convergence in function and performance between families.

In Chapter 3, to test for patterns of adaptation as state or product of evolution I compared the performance of 8 Pennsylvanian-Permian productidine genera from the North American Midcontinent. Genera from all three productidine superfamilies were included. The paleoenvironmental distributions of the genera are constrained enough to test for patterns of performance corresponding to distribution. My hypothesis is that productidine performance will be consistent with environmental distribution. I will test if nearshore and offshore taxa perform consistently with their respective hydrodynamic and environmental conditions. If the results are inconsistent with inferred environmental conditions, then environmental interpretation may have to be altered.

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Chapter 2

The Bigger the Better: Patterns of Performance within Echinoconchoidea

2.1 Introduction

Functional morphology is a useful means of studying the ecology of both modern and extinct organisms. However, often functional morphology is applied to a single trait or organism and consequently, the results may be limited in that they are removed from a broader context. Because adaptation is a long term process driven by multiple factors interacting with the organism as a whole, single-case studies and experiments constrain how functional morphology results can be applied. In this study, we use a performance space to quantify productidine brachiopod functional morphology. Performance spaces are a type of adaptive landscape in which fitness is approximated by performance (McGhee, 2006). Performance spaces consist of a set of axes in which each axis measures or quantifies function using performance. Each axis in a performance space, whether derived through experiments (for example, Alexander, 1984; Hagey et al., 2017, etc.) or mathematics (for example, Carlson, 1991; Niklas, 1998), acts as a measure of function under a specific set of environmental conditions. In the same way that a morphospace provides a way to visualize overall morphology better by integrating multiple simpler measures, performance spaces/landscapes provide a means of quantifying and visualizing overall function in relation to fitness (Levins, 1962; Arnold, 1983, 2003; Polly et al., 2016). Performance spaces can be populated with any operational unit of interest, which could be genera in a clade or an anagenetic sequence or individuals in a population or ontogenetic sequence. The overlay of phylogenetic, morphological, or environmental information on the points in the performance space provides the adaptive and evolutionary context to interpret functional morphology. Here we apply a performance space which uses hydrodynamic and ecological measures to the brachiopod Superfamily Echinoconchoidea (Class Strophomenata, Order Productida).

Connecting form, function, and fitness is an important concept in evolutionary biology (Arnold, 1983). It is also integral for studying paleoecology and paleoenvironmental reconstruction, primarily because the ecology of fossil organisms cannot be directly observed. Therefore, reconstructing the autecology or niches of extinct organisms relies on uniformitarian analogs, or proxies such as distribution or shape/functional morphology. Beyond morphology alone, performance can be used as a more direct means of inferring

function and fitness (Arnold, 1983, 2003) and to predict, detect and test features on adaptive landscapes (Stayton, 2019).

Here we employ a highly simplified hypothetical example to illustrate the connection between environment, morphology, and performance/fitness. On the most basic level niches are the set of environmental conditions -both abiotic and biotic- in which an organism can survive (Hutchinson, 1957). Consider two hypothetical species of antelope (A and B) in which the fundamental niches could be influenced by numerous environmental variables or factors. We examine a hypothetical system with two factors: the average speed of the fastest predator of the antelopes and the height of the browse line. Combining the factors on a single graph produces an ecospace which can be used to describe the conditions in which a species can or cannot survive (Fig. 2.1A). In the ecospace, the fundamental niche is represented by a box which represents the boundaries of survival. For any individual living in conditions outside the box, much more time and energy must be invested in simply surviving rather than breeding and passing on genes. In a healthy population we would expect fewer individuals to occupy the fringe areas of the box, and for there to be optimal or more ideal conditions for survival and reproduction nearer to the center of the box. More favorable conditions would naturally result in a greater number of individuals. Thus, abundance within the ecospace can be used as a rough proxy for fitness.

In addition to occupying the ecospace, individuals and species occupy a morphospace. The morphospace describes the morphological range and variation found within a population (Fig. 2.1B). In our example, the two morphological variables are (1) the ratio of the metatarsal to femur length and (2) height at the hip. Metatarsal to femur length serves as a proxy for speed i.e., lower ratios indicate faster individuals (Garland and Janis, 1993). The average speed of predators acts as a selective pressure on antelopes by setting the average minimum speed required to escape predation. Thus, systems with faster predators would have faster average antelope speeds. Limb length would affect the range of feeding heights available to the antelopes. Longer limbs would allow the antelopes to reach higher feeding levels but could also make feeding at ground level more difficult or awkward. Thus, morphological traits can be directly tied to ecological factors as proxies (Arnold, 2003). In this way, the morphospace approximates an adaptive landscape. However, this adaptive landscape does not include time or perturbations/changes to the system. A performance space/surface (Fig. 2.1C) unites the ecospace and morphospace by quantifying how morphology affects functional performance (Arnold, 2003). In the performance space, each axis is a measure of *how* morphology affects fitness in a given environment. In our hypothetical example, one axis of the performance space is successful escape rate in

predation encounters and the other axis is the rate at which an antelope can acquire food. In a performance space defined by cheetah predation and a 2 m browsing height, performance is dictated by how each antelope interacts with each variable. Antelope A performs better at high grazing heights but is vulnerable to cheetah predation. Antelope B performs poorly at high grazing heights but is more likely to escape cheetahs. Thus, antelope A may be better adapted to forested areas with slower predators and taller trees or shrubs and antelope B to more open plains with faster predators and shorter flora.

Unfortunately, biological systems are rarely this simple. Hutchinson's (1957) definition of a niche includes the phrase "multi-dimensional hypervolume". Niches are defined and constrained by numerous variables and factors that are not always independent. Even in the simplified antelope example, height at the hip could influence both maximum speed and the height at which an antelope can feed. Evolution could also act upon a suite of characters to enhance performance (Arnold, 1983), i.e. in our example, neck or snout length could also affect feeding height in antelopes. Although morphology and environment can be variable, performance tends to be absolute. Whether or not an organism is fit is largely dependent on how well it performs in specific environmental conditions (Arnold, 1983). Thus, overall fitness can be inferred or approximated using a performance space constructed using ecologically relevant variables. Additionally, the performance space could reveal multiple different adaptive solutions to environmental constraints not obvious in a morphospace. Two organisms may have similar performance scores and be equally fit yet occupy different regions of a morphospace.

Adaptive landscapes have been used as a means of visualizing the effects of adaptation and evolution on a population (e.g., Janet, 1895; Wright, 1932; McGhee, 2006). Previous performance landscapes have been created and combined to evaluate evolutionary trends (e.g., Hagey et al., 2017) and trade-offs (e.g., Rivera and Stayton, 2011) in several clades. Performance spaces/landscapes can be used like a multidimensional adaptive landscape where performance is used instead of genetic or morphological trait abundance to infer adaptation and fitness (Arnold, 1983, 2003). By comparing the performance of multiple specimens or populations across space or time, we can quantify adaptation as a state (environmental adaptation) or process (adaptation through evolution). Previous performances spaces (composed of multiple performance landscapes) have been used to identify adaptive peaks and adaptive trade-offs in multiple groups of organisms including land plants (Niklas, 1999), fish (Alfarro et al, 2004, 2005; Muñoz, 2019), and turtles (Stayton, 2011, 2019; Polly et al., 2016). Most performance landscapes are constructed by projecting performance onto morphospaces. Our approach places genera in a morphology-

independent performance framework. In other approaches to performance surfaces, evolution is represented by changes in performance that coincide with changes in morphology. While this approach is undeniably useful, we wanted to allow for the possibility of multiple morphological solutions to the same functional problem. In the performance space created for this study, two organisms could occupy different regions of morphospace but still share the same region of performance space, and adaptation could be represented as multi-dimensional trajectories.

When testing for patterns of adaptation and performance within a performance space, hard-shelled, free-living sessile marine invertebrates, such as brachiopods, are excellent study subjects. This is because sessile suspension feeders cannot flee hostile environmental changes constraining these organisms, which should be reflected in morphology and performance. Minimally their morphology and performance must be sufficient to address functional problems related to feeding, defense, respiration, etc. (Alexander 2001), and ideally their performance may be optimized or enhanced for increased efficiency or advantage. Consequently, there should be an especially strong association between shape, function, and performance in a sessile suspension-feeder. For example, brachiopods must maintain a stable position on the substrate that both prevents transport or burial and allows for efficient feeding. A brachiopod living in high energy conditions on a sandy, mobile substrate needs to maintain stability and resist transportation or reorientation because life orientation is frequently critical for efficient feeding in modern brachiopods (LaBarbera, 1977; Alexander, 1999). Therefore, we expect that a brachiopod which lived in high energy and frequently disturbed environments to perform well on axes which simulate high energy environments. If the environment were to change so that the brachiopod could no longer survive, we expect it to either migrate with its environment and relocate, to evolve a morphology that performs better in the new environment, or to become extinct (Darwin, 1859). Thus, by studying an entire clade in performance space, we can gain a better understanding of how that clade has evolved and adapted in response to changes through time.

The issues outlined above were especially relevant for liberosessile (free living and without attachment; in contrast to fixosessile in which the organism is affixed or cemented in place) members of the brachiopod class Strophomenata, which unlike most extant and many extinct brachiopods, lacked a fleshy stalk called a pedicle which is used to maintain a fixed life orientation. Instead, the strophomenate suborder Productidina relied on a concavo-convex morphology and rigid spines to interact with surrounding sediment. In

comparison to most other animals, brachiopods (especially productidines) are ideal for quantifying functional morphology because they are mostly seawater and little tissue in a mantle cavity surrounded by a rigid external skeleton. In turn, this skeleton interacts with its environment in a primarily passive manner. This implies that productidine morphology - especially spine geometry- should directly affect function and performance. Several hypotheses for spine function have been proposed, such as resistance to transport (Alexander, 1981, 1984; Brunton, 1982; Leighton, 2000; Garcia et al. 2018), resistance to sinking in soft muds (Grant, 1966; 1968), sensory structures (Rudwick, 1970), and defense against predation (Signor and Brett, 1984; Alexander, 1990, 2001; Leighton, 1999, 2001; Richards and Leighton, 2012; Johnson et al., 2013). However, few functional tests have been performed on this clade, and most of these tests focus on just one function. Because productidine performance was constrained by a rigid, external skeleton, function can be inferred relatively conservatively without the need for additional assumptions over the role and function of soft tissue.

We use the Superfamily Echinoconchoidea (Figs. 2.2, 2.3) to populate a performance space constructed using hydrodynamic measures of biological performance to test for patterns of adaptation or optimization. The echinoconchoids originated during the Devonian and survived to the end of the Permian and possibly into the Triassic (Muir-Wood and Cooper, 1960; Brunton et al. 2000). Echinoconchoids were cosmopolitan and consisted of over 40 genera (Muir-Wood and Cooper, 1960; Rudwick, 1970; Brunton et al., 2000). As the clade radiated during the Carboniferous, it became more disparate in morphology, suggesting that different subclades were adapting to different environmental factors. *Praewaagenoconcha* is the most primitive Devonian echinoconchoid known from North America (Leighton, 2000) and displays several primitive or basal traits including small size, long spines in proportion to valve size, spines arranged quincuncially (a checkerboard pattern), and a shallow concavo-convex profile (Leighton and Maples, 2000). Continuing the lineage from the Devonian into the Mississippian, the Sentosiinae display an evolutionary grade of morphological features. Sentosiins were larger, less concave, and began to have spines in bands. Finally, the Echinoconchidae family show the full disparity of the echinoconchoid radiation that took place during the Carboniferous. North American echinoconchids can be separated into two subfamilies, the Echinoconchinae and the Juresaninae. The echinoconchins were generally large, plano-convex, lacking trails (narrow extensions of the commissure above the corpus), and were covered with numerous short and narrow spines in distinct bands. Jurasanins were of medium size with proportionally longer spines, with variable banding and convexity. The disparity within the

Echinoconchidae suggests that the family radiated to fill multiple niches. By comparing the performance of lineages within Echinoconchoidea, the drivers of their adaptation and evolution can be better understood. This study seeks to use a performance space to identify adaptation or optimization by detecting trends in performance as a function of body and spine morphology. The hypothesis of this study is that the divergence in echinoconchoid morphology and systematics also reflects divergence in hydrodynamic and ecological performance.

2.2 Materials and Methods

We sampled eight North American genera from two families of Echinoconchoidea to test for adaptation to substrate, predation, or feeding efficiency using a performance space. Genera range from primitive Devonian taxa to derived Carboniferous and Permian members spanning several clades within the superfamily. The first family selected was the Sentosiidae; the genera selected were *Praewaagenoconcha* and *Stegacanthia*. The second family selected was Echinoconchidae. Within this group there are two subfamilies: the Echinoconchinae (*Echinoconchus*, *Echinaria*, and *Calliprotonia*) and the Juresaniinae (*Parajuresania*, *Pulchratia*, and *Waagenoconcha*).

We selected a well preserved (with at least one intact lateral half, free of matrix, with minimal taphonomic alteration) and representative (typical of morphology and size) specimen for each genus. Most of the specimens were borrowed from the United States Natural History Museum (USNM); two of the specimens were from an author's (Leighton) collection (*Praewaagenoconcha* and *Pulchratia*). We acquired a digital 3D model for each genus using a laser scanner. Scan processing and modification was minimal and restricted to mirroring a more intact half of the specimen, filling in small missing areas of the shell or commissure, or removing any matrix still on the specimen. We used extrusion 3D printing to create physical models of each specimen. Protopasta Stainless steel filament was used to print each model because it has a density of 2.4 g mL^{-1} or approximately 90% of the density of calcite, the material with which brachiopods construct their valves. We printed each model in two halves separated along the medial plane. The halves of the model were filled with silicone of near-neutral buoyancy in fresh water (1.014 g mL^{-1}) and joined using glue. We added spines using one of two methods, depending on the taxon and spine geometry. The first method, combined printing, employs a digital reconstruction in which the spines are modeled with CAD software and printed directly attached to the valves, using a bridging method. We used combined printing for the sentosiids and juresaniins because the spines of these groups were large enough and spaced far enough apart to be printable. For the

Echinoconchinae, we manually added spines because the first method was impossible due to technological limitations. Echinoconchinae spines are both too fine and too densely spaced to be 3D printed using a bridging method. Instead, strips of aluminum mesh were glued to the models to add the spines. Conveniently, aluminum is approximately the same density (2.704 g ml^{-1}) as calcite (2.71 g ml^{-1}). This method allowed for rows of fine spines to be attached accurately and relatively easily.

We constructed a performance space with axes tailored to evaluating echinoconchoid functional morphology. Each axis in the performance space represents a single test or measure of performance. For this study, there are 5 performance axes (the first three are experimentally measured, and the latter 2 are morphologically derived): the first is stability in mobile, sandy substrates; the second is stability on soft substrates; the third is feeding efficiency; the fourth is a proxy for respiration; and the fifth axis measures defense as a benefit/cost ratio for predators.

2.2.1 Mobile/Sandy Substrates

We used a recirculating flume (Fig. 2.4) to measure stability on mobile sandy substrates. The primary working area consisted of a 0.3 m by 0.4 m by 0.15 m box filled with a medium-sized (0.25-0.42 mm) carbonate/siliciclastic sand placed within the longer flume chamber. The surface of the sand was made flush with the plexiglass floor up and downstream. We positioned the working area 1.5 m downstream from a flow straightener. Each model was placed in the sand in a quasi-infaunal orientation (with the commissure above the substrate) based on Muir-Wood and Cooper (1960), Grant (1966), Rudwick (1970), and Garcia et al. (2018). We leveled the sand before each trial to make starting conditions as similar as possible. Each model had three trial orientations: hingeline upstream, hingeline downstream, and hingeline parallel to flow direction. We tested each orientation/model combination with 3 trials. During each trial, the flow velocity was slowly increased by 0.05 m/s every 60 seconds to reduce turbulence until the target velocity of 0.65 m/s in the free stream was achieved. Each trial started when the target velocity was reached and ended in one of three possible outcomes: when transport occurred, when the model shifted from its original position, or when 3600 seconds had elapsed. The end time for each trial was recorded in seconds.

2.2.2 Soft Substrates

We used settling time during drop tests as a proxy for stability on soft substrates. The time to sink in a water column measures the combined effects of density and resistance

on sinking velocity. While water is less dense than mud, the relative order of settling velocities between models should be constant. For each trial, the models were submerged completely and held with the spine tips at 0.3 m above the tank base. The model was released and allowed to fall to the tank base for ten trials per model. We recorded each trial on 30 fps video and settling time was measured using video editing software. The results of all ten trials per model were averaged. All trials took place under the same temperature conditions in the same tank within one 30 minute span. Additionally, the settling time trials can be used to measure the ability of each model to land in the convex-down (and assumed life [Muir-Wood and Cooper, 1960; Grant, 1966, Rudwick, 1970; Garcia et al., 2018]) orientation. Although we expect that settling time in water would accurately reflect relative sinking of the models on a soft substrate, it is possible that specimens might rotate or overturn in one medium, but not the other. The models were also placed in a mud of 60% water by volume for 24 hours to observe whether any rotation or reorientation occurred in mud but not in water.

2.2.3 Ambient Flow

To test feeding efficiency, a gaping model of each genus was constructed, and passive water flow (ambient flow through the mantle cavity) was observed and measured. We constructed the gaping models using a less dense PLA because these experiments had no density requirements for the models (no transport involved) and because this PLA produced higher quantity prints. Each model was given a fixed gape of 45°. Carlson (1989) found that in some brachiopods with deltidodont dentition, such as productidines, the maximum opening moment for the musculature involved in opening and maintaining gape could be >90°. Because productidines lacked teeth and sockets and possessed musculature which allowed for wide gapes, productidine gape was likely limited only by the position of the umbo. In preliminary trials, a gape of about 45° allowed the most water to flow over the lophophore. The lophophore of each model was simulated with a band of false eyelashes. Conveniently, the width of a brachiopod tentacle is similar in diameter to a human eyelash and arranged in a similar equidistant pattern (Dievert et al. 2019). A simple schizolophe reconstruction was used based on the assumption that the productide lophophore was limited to the brachial ridge supports (Brunton et al., 2000) (Fig. 2.5) and because complex calcified 3D lophophore supports are only known from one genus (*Falifer* (Grant 1972)) in the entire order. We placed each model quasi-infaunally in the same conditions as the mobile substrate tests. We used the dissolution rate generated by passive flow to approximate efficiency because it has been demonstrated that modern brachiopods utilize passive flow while also pumping to enhance feeding efficiency (LaBarbera, 1977, 1978;

Vogel, 1978) and because it would be energetically inefficient for a brachiopod to pump against passive water flow. To approximate feeding rate as a function of passive flow, we placed a 0.75 g piece of Wint-O-Green Lifesaver® between the arms of each model's schizolophe. Each piece was cut and sanded with a Dremel® to a uniform mass and shape. The pieces were held by a wire loop at the center of the model schizolophe in the approximate position of the mouth. Dissolution trials lasted 5 minutes at a flow velocity of 0.2 m/s. We ran 15 control trials at the same velocity with the piece of Lifesaver® raised to near the free stream boundary at 0.015 m above the substrate using a wire loop. This control was used to determine dissolution rate in unobstructed flow. Models were run in rounds of nine trials (each model was used once per round, plus control), and in a randomized model order each round. After the trials, the piece of Lifesaver was removed from the model, left to dry, and the mass was measured at least 24 hours later, and a second time after 48 hours. In total, we ran 120 trials using models (five trials times three orientations times eight models).

2.2.4 Respiration

The respiration proxy axis is quantified as the ratio of body volume to lophophore length. This ratio serves as a rough proxy for oxygen requirement (volume) versus oxygen uptake capability (lophophore size). Because the lophophore acts as both a feeding and respiratory organ, the size of the lophophore is a constraint on both food particle acquisition and respiration rates. In productidines and other schizolophous brachiopods, the transfer of oxygen (or food particles) from a relatively simple, and effectively two-dimensional, lophophore to a three-dimensional mass of body tissue is an issue because a two-dimensional surface will not scale linearly with tissue volume as the animal grows. We used brachial ridge length as a proxy for lophophore length. In genera that did not possess brachial ridges we measured the outline of the region without endospines on the dorsal valve. We used total volume as a proxy for the volume of tissue based on studies of modern rhynchonelliforms (Peck et al., 1987). By comparing the two values, a rough sense of respiration efficiency and requirements can be inferred. Volumes were measured using the 3D scan files. Because we used intact, articulated specimens to construct our models, it was not possible to measure the length of the brachial ridges directly with our original specimens. Instead, we scaled brachial valve interior images from the *Treatise on Invertebrate Paleontology* (Brunton et al., 2000) and Muir-Wood and Cooper (1960) to have the same width as the specimens that we scanned. The respiration proxy is expressed as overall volume divided by lophophore length. Higher values indicated proportionally smaller lophophores. A proportionally smaller lophophore could be indicative of living in more highly

oxygenated or food-rich habitats, while a proportionally larger lophophore could indicate oxygen or food- poor habitats.

2.2.5 Predation

The predation axis measures defense from predation as a cost/benefit ratio for potential predators. The use of this ratio was developed to describe and predict gastropod predator/prey dynamics (Kitchell et al. 1981; Kelley, 1988, 1991). This ratio was in turn based on earlier theories of optimal foraging and cost/benefit analysis (Schoener, 1971; Pyke et al., 1977; Krebs, 1977, 1978; Pyke 1984) The cost is the amount of energy expended to capture, kill, and consume an organism and can be complex. The cost is a function of multiple factors, e.g., effective size, handling time, or force required to crush the valves. The benefit is simply the nutritional value and energy gained by consuming another organism. In the case of productidine brachiopods, the muscles represent the largest volume of tissue present and are expected to scale proportionally with size with the superfamily and spines can enhance defense by increasing size. Spines can increase the overall size of a productidine to the extent where it may no longer fit into a predator's crushing mechanism (such a mouth or chelae) (Leighton, 2001b, 2003, 2011). Essentially, spines could also allow a productidine to appear larger or become too large to crush, without the prey having to grow larger or uniformly thicken the shell (Leighton, 2001; Johnsen et al., 2013). Additionally, the cost of predation could be increased via handling time (Leighton, 2001). The necessitated removal of spines prior to consumption would increase the time spent, and the amount of energy invested, on one prey organism, serving as a deterrent when easier prey items are available (Leighton, 2001). In this study, the cost/benefit ratio is measured as the ratio of the shortest dimension (length, width, or height) divided by body volume. The shortest length was used because it represents the minimum gape required of a predator. When interpreting the resulting ratio of cm/cm^3 , greater values represent a greater cost to benefit, while lesser values represent a greater benefit to cost.

2.2.6 Analysis of Performance

The performance space was visualized in two ways. The first was a three-dimensional performance space with axes that were absolute performance values. In the second, we converted performance variable data to Z-scores as a way of standardizing performance so each variable could be weighted equally when ordinated. Unlike the raw values which are absolute, Z-scores are standardized and relative. The Z-scores were ordinated in a principal component analysis (PCA) using PAST (Hammer et al., 2001). An

important aspect of a PCA is that it combines multiple trends in the data to produce covariate axes.

We tested for association between three measures of morphology: size (volume), convexity (length/depth), and spine length versus the first and second axis scores from the PCA, as well as versus all five performance variables, using Pearson's correlation coefficient. We also tested for correlations between the order of origination and PCA scores and performance using Spearman's rank correlation coefficient.

2.3 Results

The results of each test and multiple morphological measurements are recorded in Tables 2.1 and 2.2 and Figs. 2.6, 2.7, and 2.8. The results of just the hydrodynamic experiments are summarised in Fig. 2.6.

2.3.1 Transport Experiments

The results of the transport experiments are summarised in Figs. 2.6 and 2.7. Orientation affected resistance to transport. Two of the eight models (*Waagenoconcha*, *Stegacanthia*) remained stable in all trials. In four of the other six models the anterior upstream orientation was indefinitely stable. In five of these six models the anterior downstream orientation was least stable. *Praewaagenoconcha* was the only model that was least stable in the hinge line parallel orientation. The two least stable overall models were *Calliprotonia* and *Echinoconchus*. Stability in sand could not be significantly correlated to size, convexity, or spine length alone.

2.3.2 Settling Times

Settling times for a distance of 0.3 m ranged from as fast as 1.33 s to as slow as 1.88 s. In all trials the models remained convex down while falling and landed in the same orientation, which is the natural life-position. In the experiment in which the specimens were placed on a liquid-rich mud, none of the models reoriented. Settling time could not be significantly correlated to size, convexity, or spine length alone.

2.3.3 Passive Flow

The results of the dissolution trials for all models, except *Echinaria*, differed from the control. At 0.2 m/s the posterior downstream/gape upstream orientation produced higher dissolution rates than other orientations, ranging from 0.34 to 0.43 g/300s (Table 2.1). In this orientation, larger models had higher dissolution rates ($r=0.72$, $p=0.04$). In the hinge

line parallel orientation, all models had similar dissolution rates of 0.36 to 0.37 g/300 s. In the anterior upstream orientation/gape downstream orientation, dissolution rates ranged from 0.29 to 0.32 g/ 300 s. The control average dissolution rate was 0.43 g/300 s.

2.3.4 Respiration Proxy

The respiration proxies had range of values from 0.23 cm³ of body volume/cm of lophophore length to 3.95 cm³/cm. Smaller specimens had lower ratios and larger specimens had higher ratios ($r=0.97$, $p=0.025$; Table 2.2).

2.3.5 Defensive Cost/Benefit Ratio

The cost/benefit ratio of predation as measured by the length of the shortest dimension divided by internal volume has a range of values from 0.60 cm/cm³ to 14.59 cm/cm³. Smaller models had higher values while larger models had lower values ($r=-0.61$, $p=0.05$). This is the result of the spines of smaller models being proportionally larger in relation to body volume.

2.3.6 PCA

The PCA (Fig. 2.8) displays a size gradient along the principal axis ($r=0.85$, $p=0.006$); the axis accounts for 49.79% of variation. The second axis, which accounts for 26.37% of variation, displays a gradient of hydrodynamic performance in the transport and settling experiments ($r=0.86$, $p=0.006$). One end of the second axis corresponds to better hydrodynamic performance overall in both the destabilization and settling time experiments while the other corresponds to weaker performance in these experiments.

2.4 Discussion

2.4.1 General Performance

In the PCA performance space, the first axis approximates a size gradient and the second, hydrodynamic performance. Along the first axis, as the size of genera increases, so too does the flow through the valves and the ratio of body volume to lophophore size. Because echinoconchoid spine length is relatively consistent, smaller echinoconchoids have higher cost/benefit ratios. In general, relative to overall body size, changes in spine length are less drastic. The second axis shows the combined performance of both substrate experiments. On one end of the second axis, *Waagenoconcha* displays strong performance in both the settling and transport experiments while on the other end *Echinoconchus* performs poorly in both experiments. Taxa in the middle of the gradient perform well in just

one experiment or average in both experiments. Further, genera that had longer settling times plotted in the top left quadrant and tended to be smaller, and genera with higher stability in sands plotted in the top right and tended to be larger. Echinoconchoid performance and systematics do not display a consistent pattern. The genera are also scattered in performance space with no significant correlations of performance with convexity or spine length. This scattering suggests that performance of families within the Echinoconchoidea overlap with each other.

2.4.2 Size and Performance

The broadest pattern identified in this study is the effect of size on performance. While it is intuitive that size could affect settling times or transport resistance, this study demonstrates that an increase in size also enhances passive internal flow. The increased passive flow could also explain why larger echinoconchoids had disproportionately small lophophore bases. A caveat to the size correlation is that volume, and thus size, is included in the calculation of two of the performance metrics (cost/benefit and respiration proxy performance). However, the internal flow experiments support the trend independently.

Part of the size related pattern is the decrease of the predation cost/benefit ratio with increasing echinoconchoid size. Essentially the absolute size, spine length, and volume each scale disproportionately resulting in larger echinoconchoids being proportionally “meatier”. *Echinaria*, the largest genus in this study, had the lowest cost/benefit ratio and would have made a tantalizing prey item for durophagous predators. However, because it was so large, *Echinaria* may have reached a size refugia protecting it from predators with limited gapes. In comparison, *Praewaagenoconcha* would have had a high cost of proportionally large spines to crush or remove, with a small benefit due to its small size. Alexander (1981) suggested that durophagous predation may have exerted selective pressure causing an increase in brachiopod size during the Carboniferous. Productidines were frequent victims of crushing predation (Leighton et al., 2013, Geology). Alexander (1981) also suggested an increase in size was favorable for multiple other reasons including increased hydrodynamic stability and feeding efficiency. Our results support both of Alexander’s (1981) alternate hypotheses. Further, while we did not measure valve thickness (disarticulated specimens are rare), it is expected that larger brachiopods will have thicker valves, and thus, that large echinoconchoids could have also been more reinforced against crushing. It is also possible that the echinoconchoids were instead adapted to drilling predation and utilized dense spine coverage to deter or impede drilling in the same manner

as modern mollusks (Stone, 1998; Willman, 2007) or Devonian productidines (Leighton, 2001).

Larger echinoconchoids also induced greater internal flow when oriented with the commissure upstream. Intuitively, assuming a schizolophous lophophore, the maximum volume of water that can be processed is a function of the two-dimensional cross section of the lophophore facing into flow, multiplied by current velocity. Other factors that would have contributed to internal flow velocity in a living brachiopod would have included the resistance generated by the lophophore and the act of suspension feeding and any pumping action generated by cilia on the lophophore. The use of artificial lashes in our study simulates the resistance of an actual lophophore and takes the first factor into account. Considering the second factor, it is unlikely a living brachiopod would pump against passive flow as it would be energetically costly and inefficient, or improbable when compared to the relatively slow exhalent currents produced by extant brachiopods. Our results suggest that the commissure upstream orientation was the most efficient feeding orientation because this orientation produced the greatest dissolution rates (0.34-0.43 g/300s). In the other two orientations the dissolution rates were lower (0.29-0.37 g/300s). Additionally, commissural elevation played a role in dissolution rates and performance. Both *Pulchratia* and *Waagenoconcha* were oriented with the commissure elevated by the geniculation and displayed greater dissolution rates than the similarly sized *Parajuresania* and larger *Echinoconchus*.

The increased dissolution rates may also explain how larger echinoconchoids survived with proportionally small lophophores. Proportionally smaller lophophores could be explained in several ways including greater passive flow, more efficient particle capture/respiration, or a more efficient metabolism with a lower demand for oxygen and food particles. We assume that the act of suspension feeding costs brachiopods energy while actively pumping water across the tentacles. One of the major questions regarding large productidines (e.g., *Echinaria*, *Gigantoproductus*, *Delepinea*) or strophomenides (*Megastrophia*) is how they attained large sizes with simple schizolophes. Schizolophes are relatively simple lophophores and have a much lower length and surface area in comparison to more complex plectolophes or spirolophes. As mentioned previously, scaling is a problem for larger brachiopods because the smaller surface area of a two-dimensional lophophore may constrain respiration and particle capture rates necessary to sustain a three-dimensional organism. One possible solution is to invaginate the schizolophe once or iteratively to produce a ptycholophe. However, the resultant two-dimensional structure is still far more limited in comparison to a small but tightly coiled spirolophe common to many

fossil biconvex brachiopods. For example, in atrypides of similar sizes to the echinoconchoids examined herein, the lophophore coil could reach lengths of well over a meter (Dievert et al. 2019). There is evidence that *Gigantoproductus* possessed photosymbionts (Angiolini et al. 2019), which would have enhanced nutrient acquisition and allowed it to reach greater sizes without relying on efficient ambient flow for feeding. However, *Gigantoproductus* is a single example of photosymbiosis in a productidine in a different superfamily and the same inference cannot automatically be applied to large echinoconchoids.

The evidence presented here suggests that productides and other large deeply-convex strophomenates could have utilized large gapes and large mantle cavities to produce passive vortices which move water across the lophophore with a lessened need for pumping. Increasing selective pressure during the Carboniferous may have resulted in an increased need for efficient passive flow. The runoff from widespread forests and swamps during this interval could have led to increased eutrophication in nearby marine environments on a seasonal basis or resulted in large influxes of nutrients in runoff and drainage regularly (Olszewski and Patzkowsky, 2003). In a eutrophic environment, more efficient extraction of oxygen and nutrients from the water column through the use of passive flow would have benefitted Carboniferous productidines.

2.4.3 Hydrodynamic Performance

Although we could not correlate any morphological measurements, such as convexity or spine length, with hydrodynamic performance, we observed size and spine length differentially affecting stability and scour formation. The recumbent nature of echinoconchin spines does little to retard scour formation or retain sediment. As a result, echinoconchin stability in sands in fast currents increases with size. Because the echinoconchins are very similar overall, the set of models we tested can be used as a rough ontogenetic sequence for *Echinaria*. When fully grown, *Echinaria* would have been more stable than a sub-adult which could be approximated by *Calliprotonia* or *Echinoconchus*. Because of this, interaction with sediment would likely have been a greater problem earlier in ontogeny. *Echinaria* possibly relied on rapid growth to achieve stability in sandy, high energy environments while also benefitting from increased feeding efficiency from passively induced flow across the lophophore as it grew larger.

Counter to this, the dense band of erect spines on *Stegacanthia*, and the spine corona of *Waagenoconcha* better reduced scour in front of the models by physically trapping sand. As a result, these models remained stable at the top of a sand ripple instead of

surrounded by scour. Grant (1966) proposed that the dense spine corona of *Waagenoconcha* served as anchorage and to distribute its mass over a greater area to prevent sinking into soft muds. The results of this study are consistent with this function as the *Waagenoconcha* model had a long settling time. While we cannot directly tie this performance to the spines, the overall result is consistent. It is also notable that the *Waagenoconcha* model was also indefinitely stable in mobile sandy substrates because the dense corona retarded scour. This demonstrates that the spines of *Waagenoconcha* could serve multiple functions well. Because Grant (1966) sampled softer shale units more thoroughly than coarser grained and harder carbonate units, the possibility exists that *Waagenoconcha* was also abundant in higher energy and coarser grained paleoenvironments (Leighton, 2000).

Additionally, spine length appears to enhance hydrodynamic performance overall. This is highlighted by three genera (*Waagenoconcha*, *Pulchratia*, and *Echinoconchus*); although these taxa are of similar size, they performed differently in the sediment interaction experiments. *Waagenoconcha*, having the longest spines, had the best performance in both the transport and settling experiments and plotted high on the second axis, while *Echinoconchus*, having the shortest spines, performed worst in both experiments and plotted low on the second axis.

This study corroborates earlier studies which demonstrated productidine spines could function to provide stability in mobile sandy substrates (Alexander, 1984; Leighton, 2000; Garcia et al. 2018). Our results also corroborate the studies of Alexander (1984, 1986) and Garcia et al. (2018) which indicated that not all orientations to flow are equally stable. In both Garcia et al. (2018) and the present study the posterior upstream was the most stable orientation (Fig. 2.7). In Alexander (1984) differential stability in multiple orientations of the spinose productide studied was not detected. This is likely the result of lower flow velocity (0.26-0.27 m/s) during Alexander's (1984) experiments resulting in indefinite stability in all trials.

2.4.4 *Echinoconchoids in Performance Space*

When the three experimental results are plotted in a performance space composed of absolute performance values (Fig. 2.6), one trend stands out. Later taxa perform better on average in comparison to earlier genera. Excluding *Calliprotonia*, derived genera have on average increased passive flow as evidenced by higher dissolution rates. When *Calliprotonia* is removed the first axis of the PCA has a significant correlation ($r=0.83$, $p=0.01$) with origination. This trend is likely partially driven by the increase in average genus size through

time. *Calliprotonia* stands out from other late Paleozoic echinoconchoids because it is unusually small. Thayer (1975) suggested that small sized organisms are better suited to life on soft substrates. The apparent dwarfism of *Calliprotonia* in comparison to the closely related *Echinaria* may represent one echinoconchoid solution to soft or fluid rich substrates. The high degree of similarity between all echinoconchin spine geometries in this study display size dependant performance as possibly adaptive solutions which are independent of spine geometry. This is in stark contrast to the juresanin *Waagenoconcha* model which possessed a large dense spine corona and performed better in both hydrodynamic stability experiments than the shorter spined but similarly sized *Echinoconchus* and *Pulchratia* models.

By applying an adaptive landscape in the form of a performance space, we gained a greater insight into echinoconchoid overall functional morphology than a single test of performance or function alone could achieve. Taxonomic position does not necessarily correspond with position in performance space. A priori it was expected that taxonomic units would be separated within performance space as a function of morphology. Instead, each group is spread out within the space and there is overlap between groups. For example, all three echinoconchins share essentially the same spine geometry, however, they are separated in performance space. *Calliprotonia* resides close to the earlier but similarly sized *Praewaagenoconcha* in the performance space. Both large echinoconchins, *Echinaria* and *Echinoconchus*, which are similar enough to have once been classified under a single genus, are separated within performance space. This is primarily a result of *Echinoconchus* having lower hydrodynamic stability. Unlike previous performance landscapes which are generated by mapping performance to morphology to identify and test peaks (Stayton, 2011, 2019; Polly et al., 2016), instead in this study we use an absolute performance framework which is divorced from morphology. As a result, morphologically disparate taxa can occupy the same region of performance space. Because brachiopod communities were typically composed of multiple morphologically distinct genera, performance overlap independent of morphology is to be expected. When two or more productidines are found in a single community, the range of possible paleoenvironmental conditions is most broadly the intersection of conditions in which both individual genera can survive.

A caveat to this study is that the performance space used is composed of only five measures of performance. As a result, we may be missing the critical axis or set of axes acting to guide echinoconchoid evolution and consolidate lineages and taxonomic entities in performance space. A second explanation is that performance is more strongly

differentiated across superfamilies rather than within superfamilies. As a result, the Linoproductoidea, Productoidea, Echinoconchoidea may have already separated from the other lineages in performance space. As a result, the observed pattern may reflect echinoconchoids niche differentiating and diffusing within a more constricted region of performance space. In this respect, because the echinoconchoid performance space is constrained by shared descent, what appears to be a wide scattering of performance may in fact be a narrow corner of a greater productidine performance space.

2.5 References

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Table 2.1 A summary of the performance results and morphological measurements.

Genus	Average Time to Destabilization (s)	Settling Time (s)	Anterior Upstream Dissolution Rate (g/300 s)	Respiration Proxy (cm ³ /cm)	Cost/benefit ratio (mm/cm ³)	Volume (cm ³)	Length (mm)	Length Including Spines (mm)
<i>Praewaagenoconcha</i>	1502	1.74	0.37	0.22	14.59	0.88	17.79	25.25
<i>Stegacanthia</i>	1800	1.71	0.35	1.34	2.29	11.01	34.7	45.57
<i>Echinoconchus</i>	1475	1.33	0.37	3.07	1.09	28.39	49.93	53.74
<i>Echinaria</i>	1780	1.63	0.43	3.95	0.6	52.97	74.71	77.68
<i>Calliprotonia</i>	1464	1.73	0.34	0.66	6.36	2.57	22.07	23.91
<i>Parajuresania</i>	1797	1.38	0.36	1.18	3.06	8.6	29.22	48.41
<i>Pulchratia</i>	1649	1.4	0.39	1.75	1.7	17.06	44.88	60.91
<i>Waagenoconcha</i>	1800	1.88	0.41	1.38	2.47	12.23	35.19	69.37

Table 2.2 Summary of statistical analysis to test for significant relationships between performance, morphology and the ordination values. R-values of correlations reported in the text. All correlations are Pearson's Correlations, except rows marked with an asterisk, which reports Spearman's Rho. Bold font indicates significance at 95%.

	PCA Axis 1	PCA Axis 2	Mobile Substrate	Settling Time	Dissolution Rate	Respiration Proxy	Cost/Benefit
Volume	0.85	-0.06	0.27	-0.26	0.72	0.97	-0.61
Convexity	-0.32	0.33	-0.08	0.45	-0.07	-0.50	0.12
Spine Length	0.55	0.47	0.62	0.19	0.59	0.23	0.52
Origination*	0.50	0.32	0.04	0.16	0.31	0.33	-0.21
Origination without <i>Calliprotonia</i> *	0.83	0.34	0.38	0.02	0.73	0.62	-0.47
Combined* Transport and Settling Performance	-0.08	0.86	0.77	0.78	0.20	-0.21	0.25

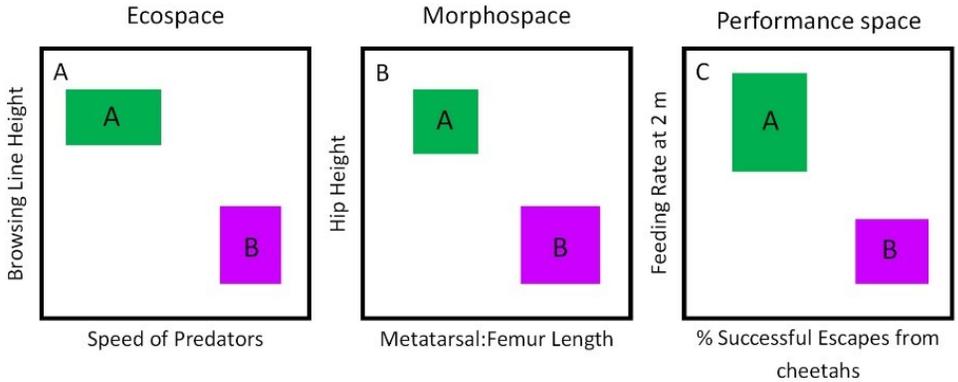


Figure 2.1 A comparison of a hypothetical gazelle ecospace, morphospace, and performance space. Two antelope species are plotted (A and B). The ecospace is defined by the speed of local predators and the height of the browse line. Within the morphospace, hip height and the femur to tibia ratio are used as proxies for ecological performance. In the performance space, antelope A plots as better at grazing at higher levels but less likely to escape cheetah predation. Antelope B feeds poorly at 2m heights but can escape cheetahs more often. The performance of both antelopes is consistent with habitat and morphology. Antelope A is better adapted to denser forests with slower predators while antelope B is better adapted to open settings with fast predators.

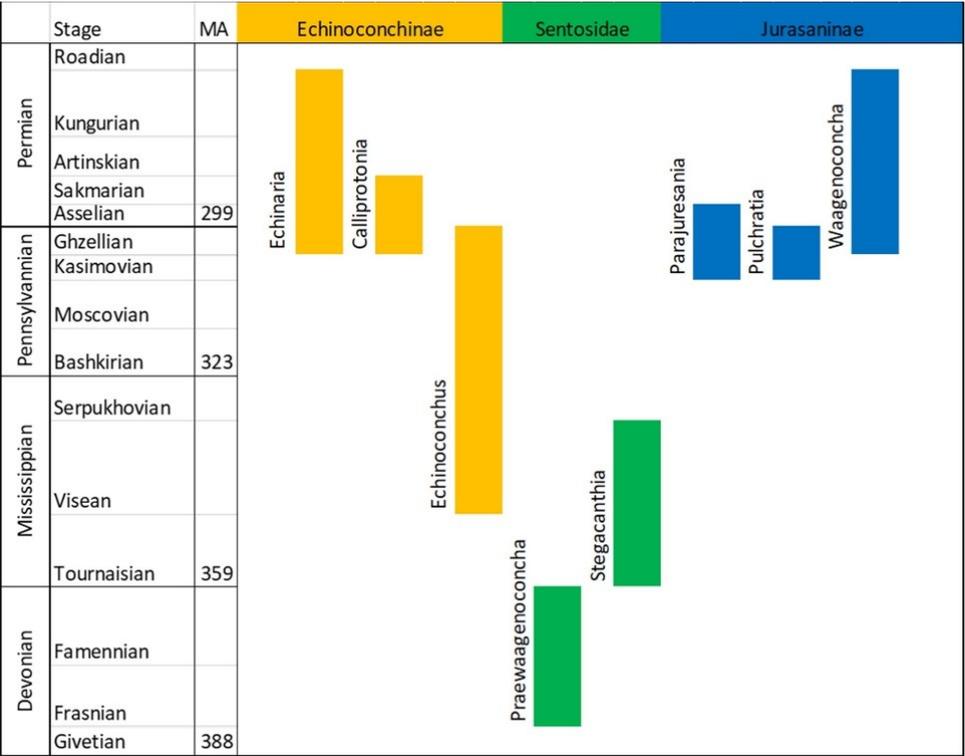


Figure 2.2 Biostratigraphy of North American Echinoconchoid genera. Echinoconchidae is represented by two subfamilies Echinoconchinae (Yellow) (*Calliprotonia*, *Echinaria*, and *Echinoconchus*) and Jurasaninae (Blue) (*Parajuresania*, *Pulchratia*, and *Waagenoconcha*).

The Sentosiidae (Green) is represented by two genera (*Praewaagenoconcha*, and *Stegacanthia*).

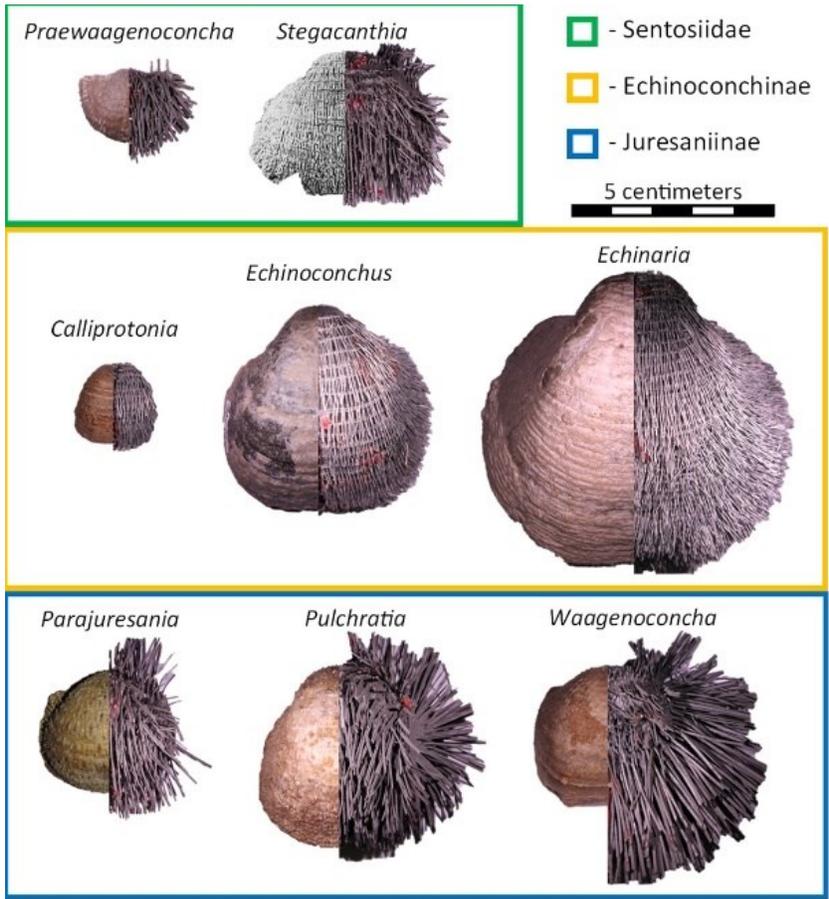


Figure 2.3 Side by side comparisons of fossils and 3D printed models. Note, the *Stegacanthia* image is modified from Brunton et al. (2000) as our model was reconstructed by modifying a scan of *Echinoconchus*. All fossils and models are on the same scale.



Figure 2.4 A photograph of the recirculating flume set up for the transport and feeding experiments. The flow straightener (FS) is situated on the left. The blue arrow indicates flow direction when in operation. A green PLA brachiopod model in the sand is circled in red. The impeller which generates flow is situated on the right. Return flow passes underneath the working chamber.

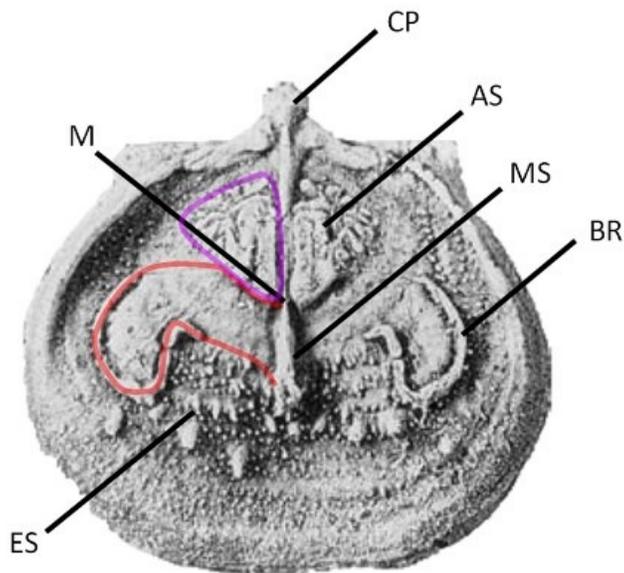


Figure 2.5 An example of echinoconchoid internal morphology (*Calliprotonia*). Lophophore length (bilaterally symmetrical, highlighted only on one side in red) was measured along the red line and doubled. This measurement includes the length of the brachial ridge, distance from brachial ridge to mouth, and distance from the brachial ridge to the medial septum. Labels are as follows: (AS) adductor muscle scars (bilaterally symmetrical, circled in purple on the anatomical right), (CP) cardinal process, (BR) brachial ridges, (MS) medial septum, (ES) endospines, (M) inferred mouth location. Modified from Brunton et al. 2000.

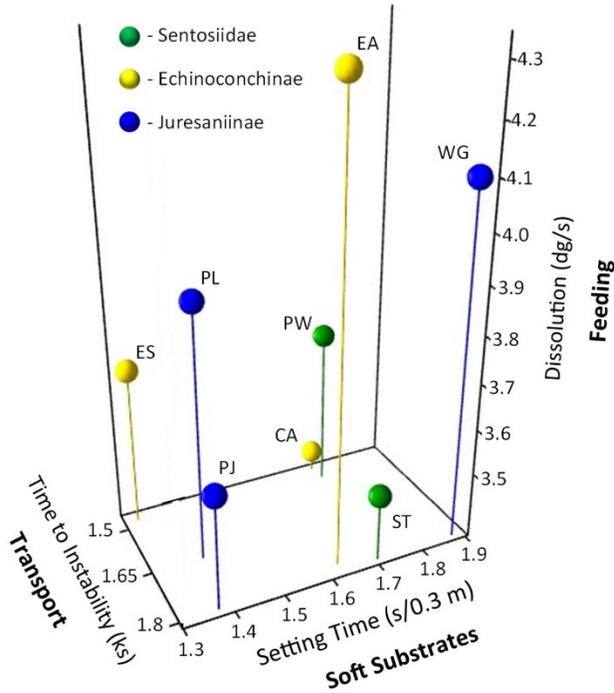


Figure 2.6 The echinoconchoid performance space plotted on three absolute axes. Genera plotted: *Praewaagenoconcha* (PW), *Stegacanthia* (ST), *Parajuresania* (PJ), *Pulchratia* (PL), *Waagenoconcha* (WG), *Echinoconchus* (ES), *Echinaria* (EA), *Calliprotonia* (CA). Units were chosen to scale the axes for easier visualization.

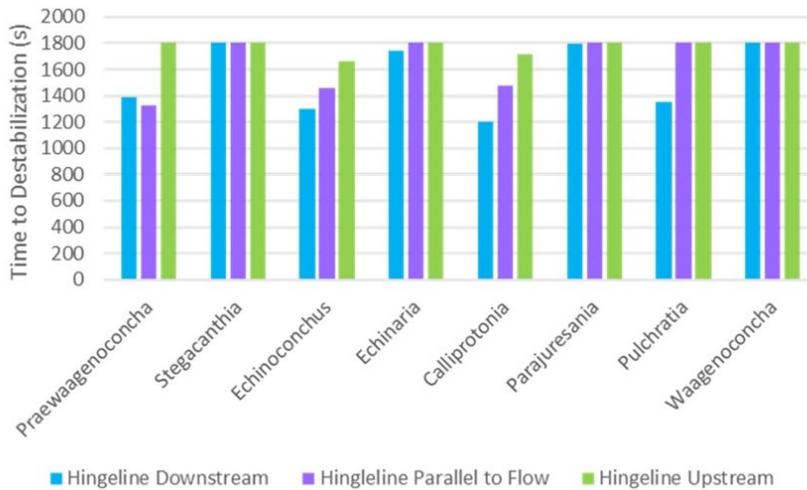


Figure 2.7 Transport resistance data. All models were most stable in the hingeline upstream orientation. On average the least stable orientation was hingeline downstream orientation. All trials ended after 1800 seconds and each bar is an average of three trials. The velocity during all trials was 0.65 m/s.

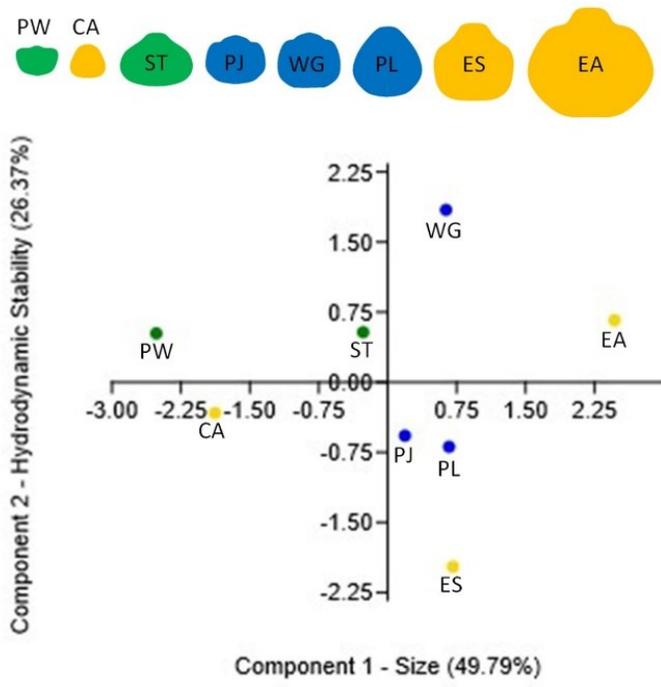


Figure 2.8 The echinoconchoid performance space plotted in a PCA. The first axis accounts for 49.79% of the variation and correlates with a size gradient (larger genera have greater values). The second axis accounts for 26.37% of the variation and corresponds with hydrodynamic performance (transport resistance and settling time). Greater values indicate greater resistance to transport and/or longer settling times. Silhouettes above the ordination are to scale relative to each other. The colours correspond to family/subfamily using the same legend as Figures 2.2, 2.3, and 2.6.

Chapter 3

The Functional Performance of Productidine Brachiopods in Relation to Environmental Variables

3.1 Introduction

The use of fossils as paleoenvironmental and biofacies indicators is a common practice, but the reasoning behind this approach can often be problematic or circular. Issues arise when a taxon is used to indicate environment but this interpretation is predicated on previous sources in which environmental conditions were used to infer the taxon's environmental limits. Additionally, functional interpretations are often "just so" stories (Gould and Lewontin, 1979) based on little evidence. A means of evaluating functional performance independently, such as biomechanical tests of organismal performance under different environmental conditions, is beneficial for paleoenvironmental interpretation. Using a set of biomechanical tests can increase the accuracy of using fossils as indicators by empirically approximating and bounding the environmental range of a given taxon. Just as a given grain size or sedimentary structure might occur within a range of environmental conditions, the behaviour of a free-lying sessile organism as a sedimentary clast limits the range of hydrodynamic conditions in which it could survive. Similar to how ichnology enhances the interpretation of environmental gradients (Pemberton *et al.*, 1992; Gingras *et al.* 2011), the distribution of easily recognizable fossils can be used as an additional diagnostic tool. Here we use the brachiopod suborder Productidina (Figure 1) to compare quantitative measures of hydrodynamic performance explicitly to biofacies gradients. Productidines were concavo-convex brachiopods that possessed spines and lacked a pedicle, the fleshy stalk by which most brachiopods attach to the substrate. With no fixed hold to the substrate, productidines were 'liberosessile' and would have behaved as large sedimentary particles (Menard and Boucot, 1951). In light of this, understanding the function of spines and body shape becomes critical to understanding productidine autecology, and potentially to paleoenvironmental reconstruction.

During the late Paleozoic, productidines were among the most taxonomically diverse and abundant clades and could be found across numerous marine settings (Muir-Wood and Cooper, 1960; Rudwick, 1970; Brunton *et al.*, 2000). The three lineages/superfamilies within the suborder are separated by marked differences in spine geometry, valve convexity and outline profile which potentially may be associated with specific environmental conditions or adaptations. Multiple hypotheses exist for the function of productide spines

which include: support on soft substrates (Grant, 1966; 1968), resistance to transport in high velocity currents (Alexander, 1981, 1984; Brunton, 1982; Leighton, 2000; Garcia *et al.* 2018), or defence against predation (Brett and Signor, 1984; Alexander, 1990, 2001; Leighton, 1999, 2001a; Richards and Leighton, 2012; Johnsen *et al.* 2013). Variations in valve morphology have also been used as evidence for physiological adaptations, such as to enhance respiration, feeding, reproduction, or hinge mechanics (Alexander, 2001). Previous work has attempted to test productidine functional hypotheses using environmental distributions and/or biomechanical tests (Grant, 1966, 1968; Alexander, 1984; Leighton, 2000, Garcia *et al.* 2018) but were typically limited to testing one spine function or geometry or valve morphology.

Because spine geometry is integral to both productidine taxonomy and autecology, it has garnered a great deal of attention. While the three productidine superfamilies are formally defined on the basis of both internal and external characters (Brunton *et al.*, 2000; Leighton and Maples, 2002), each is also distinct and typically distinguishable on the basis of body outline and spine position and morphology. For example, a synapomorphy of Echinoconchoidea is a dense covering of short spines that are often banded and prostrate on both valves whereas Productoidea and Linoproductoidea possessed fewer, sparser and longer spines, typically restricted to just the ventral valve. Linoproductoids are separated from productoids by the hinge-spine morphology and body outlines. During the late Paleozoic, the order Productida (including productidines) underwent a radiation, becoming one of the dominant brachiopod groups (Rudwick, 1970; Brunton *et al.*, 2000). This was possibly linked to the utility of spines that could function like a pedicle and provide stability for productides (Muir-Wood and Cooper, 1960; Rudwick, 1970). The initial paradigm for productidine spine function was that spines served as a means of supporting the brachiopod on a soft substrate by distributing its weight across a greater surface area (Grant, 1966, 1968; Rudwick 1970). This function has been invoked for *Waagenoconcha* (Grant, 1966), and *Marginifera* and *Echinauris* (Grant, 1968), and popularised by Rudwick (1970). While the inferred functional morphology of these three genera is consistent with environmental distribution and the lithology in which they were found, many productidines have been found in sandy lithologies or high energy environments (Brunton, 1982; Leighton, 2000). Alexander (1984) used flume experiments to test the function of spines in a sandy mobile substrate using *Inflatia* specimens with artificial spines formed from aluminium and found that spines were capable of retarding scour formation and enhancing stability. Leighton (2000) further tested the mobile substrate hypothesis using environmental distribution data for the Devonian productidine *Praewaagenoconcha* and found its preferred environment to

be in coarser sediments and higher energy settings on platform margins. Garcia *et al.* (2018) corroborated this conclusion through an experiment in which 3D printed spinose and aspinose *Praewaagenoconcha* models were placed in a recirculating flume to determine relative stability. Garcia *et al.* (2018) found that the spinose models were more resistant to scour, reorientation and transport than the aspinose models. More recently, Dievert *et al.* (2020) utilised a performance space to quantify the functional/evolutionary morphology of echinoconchoids and demonstrated that a single morphology can adequately serve multiple functions

In a community paleoecology study focused on brachiopods, including several productidines and bivalves, Olszewski and Patzkowsky (2001) used successive cyclic marine rock packages formed during the Pennsylvanian-Permian in Kansas to detect and assess biotic gradients across environmental gradients and test for generic and community recurrence. They identified two marine faunal composition gradients, one onshore/offshore, the other oxygenated/dysoxic (Olszewski and Patzkowsky, 2001 Figs. 7, 8, and 11). The first gradient ran from shallow, intertidal to subtidal nearshore facies, to offshore open marine facies. The second axis separated the marine facies further into a gradient between well oxygenated and dysoxic settings (Olszewski and Patzkowsky, 2001, 2003). Because the facies associations in Kansas are well constrained, the inclusion of brachiopod performance and morphological data within this paleoenvironmental framework could enhance the interpretation of productidine-bearing, late Paleozoic rocks where environmental patterns are less clear. Beyond the Kansas cyclothems, productidines are cosmopolitan and common throughout the late Paleozoic. A better understanding of the connection between productidine functional morphology and paleoenvironment has wide utility.

Using the Kansas framework, our study uses biomechanical experiments to test if taxon performance matches taxon distribution and inferred paleoenvironment. Essentially, multiple biomechanical experiments test the plausibility of environmental hypotheses (Fisher, 1985; Savarese, 1995). The results of these experiments are plotted on a performance space/landscape (*sensu* Arnold, 1983), a multi-dimensional space in which each axis represents performance of a different function; taxa are plotted within the space for comparison with each other. Performance spaces provide a means to visualise and compare the results of multiple experiments simultaneously. In the same way that a morphospace evaluates and quantifies morphology (Raup, 1966), the performance space quantifies functional performance. Just as morphologically similar species would plot in the same region of a morphospace, functionally similar species would plot close together in the performance space. Furthermore, the performance space allows researchers to compare

absolute and relative performance simultaneously, through and between lineages to test evolutionary hypotheses using performance and inferred fitness through time. Recently performance landscapes have been used to analyse aspects of morphology and function simultaneously (e.g. Polly *et al.* 2016) and used to predict and test adaptive landscapes (e.g. Stayton, 2019). This study uses a performance space to evaluate the functional morphology of extinct productidine genera using performance relevant to three environmental conditions: 1) stability in coarse/mobile substrates, 2) performance on soft substrates, and 3) performance in dysoxia. Stability on mobile substrates is used as a proxy for ability to handle high velocity currents and mobile substrates, whether regularly or as uncommon events, such as storms, associated with near shore environments. Performance on soft substrates is used to evaluate performance in low energy, muddy environments. Performance on a morphology-based axis of metabolic/respiratory efficiency is used to evaluate adaptation to dysoxic environments. Our hypothesis is that taxa performance will be consistent with environmental distribution and previous paleoenvironmental interpretations. We hypothesise that 1) near shore taxa will perform better in mobile substrate experiments; 2) offshore taxa will perform better in soft substrate experiments; 3) dysoxic taxa will be more metabolically efficient. If performance results are consistent with previous paleoenvironmental interpretations (Olszewski and Patzkowsky 2001, 2003), then the performance space serves as additional independent support. If the results do not match, then either the paleoenvironmental interpretations need to be re-evaluated or productidine morphology is more independent from physical environmental conditions than previously thought.

3.2 Materials and Methods

3.2.1 Genera

Eight common productidine genera, observed across the environmental gradients of Olszewski and Patzkowsky (2001), were selected to test our hypotheses. The genera are spread across the three superfamilies of the suborder Productidina. Our descriptions are generalizations for the superfamilies and are not formal definitions. The first superfamily, Productoidea, is represented by three genera (*Hystriculina*, *Kutorginella* [= *Retaria* of Olszewski and Patzkowsky 2001], and *Reticulatia*). Productoids (Fig 1A) were small to medium sized, with long, curved spines scattered sparsely across the ventral valve, and a deeply concave and geniculate dorsal valve, which lacked spines. Productoids also had wide hinge-lines with large ears and were commonly sulcate. The second, Echinoconchoidea (Fig 1B, 1D), is represented by three genera (*Parajuresania* [= *Juresania* of Olszewski and

Patzkowsky 2001], *Pulchratia* [absent from Olszewski and Patzkowsky 2001 but present in the region during the Pennsylvanian], and *Echinaria*). Echinoconchoids were commonly medium to large in size, had planar to weakly concave dorsal valves, and were covered on both valves in a dense mat of banded sub-erect to recumbent short spines. Echinoconchoids had narrow hingelines, lacked lateral extensions of the commissure (ears), and were weakly sulcate. The third, Linoproductoidea (Fig 1C), was represented by two genera (*Linoproductus* and *Canocrinella*). Linoproductoids were small to large, ventrally spined with sparse, medium-length, comparatively straight spines; dorsal valves were commonly geniculate and deeply concave and variably spined. Linoproductoids were subcircular in outline with wide and commonly spined hingelines.

For each genus, one species was selected to be reconstructed using a well-preserved individual, representative in terms of size, shape, and typical features. By using a single species, we assume that intergeneric disparity is greater than interspecific disparity. Seven of the eight species present in the study region were recognised by Olszewski and Patzkowsky (2001); the exception is the species *Pulchratia symmetrica* McChesney, 1960. The species reconstructed herein are *Canocrinella boonensis* Swallow, 1958; *Echinaria semipunctata* Shepard, 1838; *Hystriculina hystricula* Dunbar and Condra, 1932; *Kutorginella lasallensis* Worthen, 1873; *Linoproductus prattenianus* Norwood and Pratten, 1855; *Parajuresania nebraskensis* Owen, 1852; *Pulchratia symmetrica*, and *Reticulatia huecoensis* King, 1931.

3.2.2 Setting and Environmental Framework

The genera used in our study come from the Late Pennsylvanian and Early Permian of the North American Midcontinent. The Late Paleozoic was notable as an “icehouse” period (Fischer, 1984) which resulted in complete glaciation of the south pole (Zeigler *et al.* 1997). Episodic periods of glacial growth and retreat as well as cycles between arid and humid climates (West *et al.* 1997) resulted in recognisable cyclic rock packages on a global scale (Veevers and Powell, 1987). During this time, much of North America was submerged under a shallow epeiric sea (Olszewski and Patzkowsky, 2001; Algeo *et al.* 2008), which allowed repeated transgression and regressions to be recorded as multi-metre-scale sequences. Olszewski and Patzkowsky (2003) adapted earlier models (Heckel, 1977, 1984) to incorporate smaller, metre-scale carbonate-siliciclastic couplets described by other researchers (Miller and West, 1993, 1998; Boardman *et al.*, 1995; Miller *et al.*, 1996; Mazzullo *et al.*, 1997; Mazzullo, 1998). The carbonate component of each couplet is interpreted by Olszewski and Patzkowsky (2001) to have formed during arid climactic

conditions while the siliciclastic component is interpreted to have formed as a result of a more humid climate producing a greater influx of terrigenous material. This synthesis of multiple scales allowed for the overall structure and sequence of paleoenvironments in the Midcontinent to be recognised and described at a finer resolution. Olszewski and Patzkowsky (2003) identified two end-member metre-scale couplet types: onshore and offshore. They described transitional couplets combining nearshore and offshore facies recording briefer environmental shifts within sequences. In the nearshore, each couplet begins with a limestone overlain by a siliciclastic mudstone and can be capped by structures and lithologies indicating subaerial exposure. In the offshore, each couplet consists of a marine limestone overlain by a black or grey mudstone. Offshore couplets lack evidence for subaerial exposure and both the carbonate and siliciclastic packages may be condensed. Olszewski and Patzkowsky (2001) interpreted offshore couplets as being dominant during the transgressive portion of the sequence when accommodation space was increased, while the nearshore couplets formed during the regressive part of the sequence when accommodation space was limited. Complicating cyclothem interpretation in Kansas, the cyclic packages do not occur uniformly across North America and the same environmental and taxonomic gradients are less apparent in earlier Kansas rocks or in the contemporaneous rocks of Texas or Ohio (Heckel *et al.* 1994; Forcino *et al.*, 2010; Perera and Stigall, 2018). This discrepancy has been hypothesised to be the result of the Midcontinent couplets forming in more sediment starved systems, with the cycles being masked by a higher detrital influence in other regions such as Texas or the Appalachian basin (Heckel, 1994).

The five larger sequences and ~50 thinner (i.e. metre scale) cycles/couplets recorded recurring facies over several million years in both the nearshore and offshore. Olszewski and Patzkowsky (2001, 2003) used this recurrence to propose a framework for interpreting facies and cyclothems and to test for community recurrence and faunal associations; we describe their interpretation below. The inferred nearshore facies encompass several lithologies and are interpreted as having been well oxygenated, photic, and ranging from intertidal to below fair-weather wave base (Fig. 2). The nearshore paleoenvironments that occurred during humid periods ranged from shallow micritic lagoons and tidal flats to coarser grained high energy environments located more distally to the shoreline. These environments are recorded as interbedded micritic limestones and mudrocks, and packstones and grainstones. During siliciclastic dominated high stands, nearshore environments were primarily muddy tidal flats with intermittent sand bodies associated with deltas, tidal channels and bars, and incised valley fills. These environments

are recorded as mudrocks and sandstones, respectively. *Parajuresania* and *Linoproductus* were common in near-shore facies during both periods of carbonate and siliciclastic dominance. *Parajuresania* displays a preference for siliciclastic environments, while *Linoproductus* displays no preference for substrate with similar abundances in both siliciclastics and carbonates (Leighton and Schneider, 2008). Additionally, *Linoproductus* was also abundant in offshore facies whereas *Parajuresania* was not.

Offshore facies also display a range of environments. In earlier sequences the offshore environments were broad shallow platforms with seafloors composed of micritic mud. In later sequences, carbonate dominant offshore environments were composed of a mosaic of shallow, well oxygenated, high energy bioherms rising out of oxygenated and photic micrite mud in epeiric “lagoons” or shallow platforms. The bioherms were largely composed of fusulinids (Sequence III) and phylloid algae (Sequences IV and V). In one example a richthofenioid brachiopod bioherm dominated by *Teguliferina* occurred (Sequence IV). These environments are recorded in packstone and micritic limestone lithologies. Siliciclastic offshore environments were dominated by muds with dysoxia/anoxia occurring near deltas grading laterally and distally into well oxygenated mud banks. Dysoxic and anoxic conditions in the Mid-continent produced characteristic dark grey to black shales, while better oxygenated conditions formed grey fossiliferous and calcareous mudrocks. *Hystriculina* is commonly found in dysoxic shales. *Linoproductus*, *Reticulatia*, and *Kutorginella* were distributed among more oxygenated offshore muds. Both *Linoproductus* and *Reticulatia* display little preference between siliciclastics and carbonates and had wide ranges of environmental tolerance (Leighton and Schneider, 2008). *Kutorginella* displays a narrower range of environmental tolerance and a preference for siliciclastics. Rare taxa, *Echinaria* and *Canocrinella*, were weakly associated with more offshore oxygenated facies. *Echinaria* is also strongly associated with carbonate environments. Both *Canocrinella* and *Pulchratia* are difficult to place on the environmental gradient because *Canocrinella* is rare in the collections studied and *Pulchratia*, despite being present during the interval and in the region, was left out of the Olszewski and Patzkowsky (2001) recurrence study. *Pulchratia* may have instead been treated as a variant morphotype of *Parajuresania* in Olszewski and Patzkowsky (2001). Leighton and Maples (2000) described evidence consistent with this treatment and described the distribution of *Pulchratia* as more common in interbedded micritic limestones and mudrocks.

3.2.3 Physical Model Creation

Each specimen was imaged with a laser scanner to produce a digital 3D model. The digital model was “split” in half along the medial plane. Spines were added digitally using CAD software to all models except for *Echinaria*. The methods used were adapted from Garcia *et al.* (2018) and Dievert *et al.* (2019). For most of the models, spines were placed horizontally on the models and attached to a surrounding support wall. Using a printing technique called “bridging”, the thin individual spines could be physically suspended during printing. After the models cooled, the support wall was cut off and the spines were posed and shaped using a heat gun set on low. The spines of *Echinaria* were added as strips of aluminium mesh after the spineless valves were printed. *Echinaria* possessed spines too fine, densely spaced, and prostrate to be printable via the bridging method. All models were printed using a PLA plastic with a density of 2.4 g ml⁻¹ (88% of the density of calcite (2.7 g ml⁻¹)). This density closely approximates live density, considering living brachiopod valves would have also contained organic compounds (Curry *et al.* 1989) which would likely lower the valve density slightly. The models were filled with a silicone rubber with a density of 1.05 g ml⁻¹, which is nominally equal to the density of both soft tissue and seawater.

3.2.4 Measures of Performance

3.2.4.1 Transport Resistance

The first experiment evaluated transport resistance and stability on mobile sand substrates. The models were placed ventral-valve down, quasi-infaunally, which is the likely life position (Muir-Wood and Cooper, 1960; Grant, 1966, Rudwick, 1970; Garcia *et al.*, 2018). Stanley (2020) suggested that productidines lived fully infaunally. However, as Stanley’s (2020) proposed burrowing mechanism remains untested we used a quasi-infaunal orientation. The models were placed in a medium grained, moderately sorted (0.25-0.42 mm), arenaceous and carbonate sand mix in a recirculating flume. The grain size and sorting used in our experiments is consistent with the sandstone lens lithologies described by Olszewski and Patzkowsky (2003). The sand filled a 0.3 m x 0.4 m x 0.15 m volume box, the top of which was flush with a plexiglass substrate in the working chamber, located 1.5 m downstream from a flow straightener at the upstream end of the flume. The chamber was filled to 0.3 m with water. Each model underwent three replicate trials in three orientations: (1) anterior upstream, (2) anterior downstream, (3) and hinge-line parallel to flow. The free stream target velocity of the trials was 0.65 m/s. During each trial, the velocity was slowly increased from 0 m/s to 0.65 m/s to reduce turbulence and maintain laminar flow. Turbulence can introduce variability and inconsistency to experimental conditions and therefore must be minimised. The experimental velocity falls within the lower

range of tidal currents (Ludwick 1970; Knebel, 1981) and storm velocities (Knebel, 1981; Meyer *et al.* 1981). When the target velocity was reached, the trial began and continued until transport/instability or until 30 minutes had elapsed. Time to transport/destabilization was recorded for each trial. Destabilization is defined as any change in position from initial position, for example, a model separating from the surrounding sediment, reorienting and falling into surrounding scour. Alexander (1984) demonstrated that orientation of brachiopods can influence overall stability. Reorientation may precede transport because the new orientation may increase drag and/or lift. In a natural setting, a brachiopod no longer anchored but resting in its scour would have been more vulnerable to transport if turbulence or increased wave action occurred (Menard and Boucot, 1951). Trials were assessed as stable if no transportation or reorientation occurred.

3.2.4.2 Stability on Soft Substrates

In a second experiment, we dropped the models in water and recorded (a) whether they landed in life-position, and (b) their settling time. The ability to land in life position represents another high energy environment performance variable; entrainment into the water column could occur as the result of high velocity flows and/or turbulence. After entrainment, a productidine needs to land in the correct life-orientation as orientation could have a major effect on subsequent stability (Alexander 1984) and feeding (Vogel, 1978; Alexander, 2001).

Settling velocity serves as a proxy for performance on soft substrates, specifically how well the taxon resists sinking, whether this is in water or in fluid-rich muds. Settling in water is a function of multiple factors, notably density and drag (Vogel, 1994). Both density and drag are influenced by shape; for example, a more convex brachiopod would have a lower ratio of shell volume to mantle cavity volume and thus be less dense. A more convex brachiopod would also have greater surface area resulting in greater drag. Spines could achieve the same increase in surface area without increasing mass at the same rate that enlarging the valves would. We performed 10 trials per model, dropping each model a vertical distance of 0.3 m. Each model was held completely submersed, ventral (convex) valve down and released. When a concavo-convex or hemispherical object, such as a strophomenate without spines, is entrained, the normal landing orientation is convex down, as this is a more streamlined orientation that reduces drag when settling through water. Spineless specimens dropped in a convex up orientation will invariably flip over to a convex down orientation within a few seconds after being dropped. Thus, if any deviation from the starting orientation occurs, it is the result of the spines or body shape interacting with flow

while settling. Time in the water column was observed using 33fps video recording of the drops. We assert that the rank order of taxa in terms of resistance to sinking remains the same in both water and denser fluids such as liquid muds, however, whether the specimens reoriented during sinking could differ with respect to the fluid medium. Flow of the water around the valve may induce rotation or changes in orientation during sinking and so, reorientation in water is not necessarily a demonstration of equilibrium orientation when stationary in a mud. A previous pilot experiment, in which the models were placed on a carbonate mud of 60% water by volume, assessed whether any rotation which occurred during the drop tests could occur while sinking into a denser mud. We observed no rotation of the models in the mud, which suggests rotation of the models while settling is induced by drag forces at a relatively higher velocity.

3.2.4.3 Respiration/Metabolic Proxy

We assessed respiration potential, specifically how well taxa may have handled low-oxygen conditions, by calculating the ratio of lophophore length (oxygen uptake) divided by volume of an adult specimen (oxygen requirement). Brachiopods respire (and feed) through a ciliated ribbon of tissue, the lophophore, within their mantle cavity. The ability of a roughly two-dimensional surface (the lophophore) to respire and capture food sufficient for a three-dimensional volume of body tissue is a fundamental constraint on productidine physiology. Brachial ridge length is a proxy for lophophore base length, and total volume a proxy for the volume of tissue (Peck *et al.*, 1987). By comparing the two values, a rough sense of respiration efficiency and requirements can be inferred. It is important to note that unlike the lophophore of most biconvex brachiopods (including most extant genera), the base of the productidine lophophore has been assumed to be two dimensional: either in the form of a simple schizolophe or a slightly more complex multi-lobed ptycholophe (Alexander, 2001). The ratio of lophophore area to body volume may therefore scale disproportionately during growth and could potentially have constrained respiration in a dysoxic or food-poor environment. This type of “scaling problem”, in which oxygen passing across a two-dimensional surface must be sufficient to support a three-dimensional organism, is an issue for most animals (Peters, 1986). Other studies (Thayer, 1981; Alexander, 1994; Twitchett, 2007; He *et al.* 2010) have suggested that dysoxia can result in a predominance of smaller and flatter brachiopods.

Because our specimens were articulated and intact, it was impossible to take direct internal measurements from these specimens. The total volume was measured from the aforementioned 3D scans using RHINO. Lophophore length was measured using images

from the Treatise of Invertebrate Paleontology Part H Volume 3 Productida (Brunton *et al.* 2000) and Muir-Wood and Cooper (1960) and scaled to match the size of the specimens used in this study. Lophophore length was measured as the length of brachial ridges and an extension of the lophophore to form a lobe along the medial septum. In specimens with no brachial ridges, the termination point of the lophophore was inferred to be positioned where endospines begin anteriorly.

3.2.5 Analysis of Performance

The first performance space visualization used raw performance data and was composed of three axes: time to instability, settling time, and the metabolic proxy. The values on each axis are absolute, but the scales have been cropped and transformed to fit together in one volume. This performance space is Euclidean.

The second performance space visualization was plotted as an ordination. The performance of each genus on each of the 4 axes was converted to a Z-score relative to the performance of all models for that axis. This standardised the performance so that each axis could be weighted equally despite different units. For example, the transport axis measures stability on the scale of hundreds of seconds, while the settling times were measured in *hundredths* of a few seconds. The Z-scores were ordinated in a Principal Component Analysis using PAST (Hammer *et al.*, 2001). A PCA allows for all axes to be plotted orthogonally and visualised simultaneously. It also ranks and correlates the line of best fit for all data points on the primary axis so that the overall performances can be reduced to fewer axes and gradients.

3.3 Results

The results of the experiments and measurements are recorded in Table 1 and Figures 3, 4, and 5.

3.3.1 Stability in Sand and High Velocity Current

In order of importance, the factors affecting stability in sand were spine length, profile, and orientation to flow. The most stable brachiopods during the sandy substrate experiments were the three long-spined productoids (*Reticulatia*, *Kutorginella*, and *Hystriaculina*) and the linoproductoid *Canocrinella*. All three productoids remained anchored in the sand regardless of orientation to current, despite experiencing heavy scouring and complete undermining, as the tips of the spines remained embedded in the sand even with the body of the models elevated out of the substrate (Fig. 4). The short-spined taxa were

less stable because they could not handle the same depth of scour. Larger and less streamlined models were also less stable (*Pulchratia*, *Linoproductus*) than smaller models with planar dorsal valves (*Parajuresania*, *Cancrinella*). Orientation also affected stability; for all five of the more unstable models, the anterior upstream orientation was the least stable, as this orientation resulted in a supporting ramp of sediment downstream of the brachiopod, similar to those observed by Alexander (1984). The three largest models (*Echinaria*, *Linoproductus*, *Pulchratia*) were not transported after destabilizing instead rotating in relation to the substrate falling into the upstream scour. Smaller shorter-spined models (*Pulchratia*, *Parajuresania*) however were overturned and transported after destabilization. In all models, except for *Linoproductus*, the anterior downstream and hinge-line parallel to flow orientations were indefinitely stable for the entire trial duration. During preliminary trials, all models were indefinitely stable at velocities less than 0.25 m/s, producing scour less than 0.01 m deep.

While the flow was raised to target velocity, saltation of sediment began at 0.25 m/s and scour formation at 0.3 m/s. Ripples between 0.01-0.02 m tall and 0.1-0.2 m long formed at the target velocity of 0.65 m/s. These bedforms are predicted from empirically derived transitional and critical velocities for sediment transport (Paphitis, 2001). The greatest amplitude in bedform occurred at the leading edge of the sediment box and had an amplitude of over 0.05 m.

3.3.2 Settling Times

All of the echinoconchoid models landed convex down (life-orientation) in 10/10 trials. The other models landed convex up (*Cancrinella*, *Kutorginella*, and *Reticulatia*) in all trials or on the umbo (*Hystriculina*) in 9/10 trials. The four models which landed convex up were also the same taxa that were the most hydrodynamically stable in the moving sediment experiments.

The settling rates of the models were affected by model size, shape, and spine geometry. The smallest models with the longest spines sank the slowest (< 0.15 m/s). The fastest settling times were those of sub-hemispherical, short-spined, medium sized models (> 0.2 m/s). The larger models sank at velocities between these extremes.

3.3.3 Respiration Proxy

The respiration ratio ranged from 0.25 cm of lophophore per cubic centimetre of volume (cm/cm³) to 5.07 cm/cm³. Larger brachiopods had lower ratios of lophophore length to total volume.

3.3.4 PCA

The results of the PCA are plotted in Figure 5. The first axis separates the taxa based on overall performance. Genera on the left (*Pulchratia*, *Linoproductus*, *Parajuresania*, and *Echinaria*) have poorer hydrodynamic stability and proportionally smaller lophophores. Genera on the right (*Reticulatia*, *Canocrinella*, *Kutorginella*, and *Hystriculina*) have better hydrodynamic stability and proportionally larger lophophores. We define better hydrodynamic stability as longer settling and destabilization times. The driver of the second axis could not be resolved.

3.4 Discussion

3.4.1 General Findings

When placed in a paleoenvironmental context, the performance of physical models is consistent with the distribution of the fossil taxa. Nearshore taxa could withstand short periods of high velocity currents and had proportionally small lophophores, consistent with a more oxygenated, moderately high energy environment. Offshore-oxygenated taxa performed in a manner consistent with living on firmer muds in well oxygenated environments, with slightly faster settling times and proportionally smaller lophophores. Dysoxic taxa had proportionally larger lophophores and displayed resistance to sinking in soft substrates, consistent with a soft substrate and low dissolved oxygen environment, as suggested by the black shale lithology in which they were typically found.

Spine length and size plays a major role in productidine hydrodynamic performance (Fig. 3, 5). Longer spined models remained stable for longer durations. However, all productidines remained stable for over 20 minutes in high velocity (0.65 m/s) currents, demonstrating competency in short duration, high velocity flows. When settling, longer spine geometries inhibit landing in the correct orientation, which would be an issue if these taxa were entrained, but these same geometries also had increased settling times, consistent with increased resistance to sinking on soft substrates. In models with shorter spines, smaller models were transported when scour became deep enough to render the model essentially epifaunal. The observed transport supports previous evidence (Garcia *et al.*, 2018) and assertions (Stanley, 2020) that productidines living epifaunally would be less stable. Stanley (2020) speculated that productides actively burrowed into the sediment by expelling water from the mantle cavity. However, the observed rotation of larger shorter spined models as they fall into upstream scour demonstrates a simpler and passive “burrowing” mechanism for maintaining life orientation through ontogeny.

3.4.2 Nearshore Taxa

The models representing those taxa which are thought to have occurred in the nearshore environments, *Parajuresania* and *Linoproductus*, while not as stable as the long spined productoid models, were still generally stable under high velocity flow on sandy mobile substrates. *Parajuresania* remained stable for the entire 30 minutes of trials in 2 of 3 orientations and on average remained stable for just under 30 minutes in the third orientation. In the performance space (Fig. 3), *Parajuresania* plots in the high stability on mobile substrates and fast settling time region of the sediment interaction plane. *Linoproductus* remained stable for over 25 minutes, on average, in its weakest performing orientation. While this duration is shorter than that of a storm, it is far more likely that daily tidal forces would have had greater selective pressure. Observation in a study of modern tidal flats found a short (3 minute) window in which flood velocity surged at 0.5 m/s suspending the greatest amount of sediment (Zhang *et al.* 2016). The same study also found the maximum ebb velocities to be less than half the maximum flood velocity (Zhang *et al.* 2016). Given the results of our experiments, it is reasonably likely our models could have remained stable in tidal flat conditions inferred from the nearshore fine sands and red and green mudstones. Our experimental design also represents a worst-case scenario, in which there is limited sediment available to fill or reduce scour and undermining. Despite nearshore environments often being associated with regular high energy and fast currents, the epeiric nature of the midcontinent coastline allows for the possibility that daily tidal variation was constrained, and the long, shallow ramp allowed for water depth to increase slowly with greatly attenuated waves. This would have decreased turbulence and sediment transport under normal conditions. While the frequency of storms is unknown, it is almost certain that rare, non-periodic weather-induced high velocity flow did occur. Essentially, the North American Midcontinent would have functioned as a large-scale Super-Estuary with micro-scale tides (Algeo and Heckel, 2008). The presence of ooid sands in the foreshore facies as described by Olszewski and Patzkowsky (2003) also suggests that at least in general, persistently high energy settings were located more distally from the shoreline.

The landing orientation results from the settling trials are also an important component of the nearshore taxa model performance. Both *Parajuresania* and *Linoproductus* landed in the correct convex down orientation in all ten trials. It is expected that if these genera were swept into the water column by a turbulent current, they would have been more likely to land in an optimal position. *Parajuresania* had the fastest settling time of any model, indicating that it would have had the least resistance to sinking into a soft mud. This is consistent with the near shore distribution in which it lived; *i.e.* in coarser grained

carbonate substrates, tidal sand bodies or firmer muds. *Linoproductus*, with an above average settling time, would have performed better on soft substrates than *Parajuresania*. This is consistent with the distribution of *Linoproductus* as it was not limited to nearshore environments but has been collected from across a wide range of lithological and paleoenvironmental settings. A central placement in the ordination of Olszewski and Patzkowsky (2001) is also consistent with an averaging of a range of distributions between oxygenated and dysoxic environments. Leighton and Schneider (2008) described a similar pattern of broad distribution and environmental tolerance. The weaker performance of *Linoproductus* on the transport axis would have restricted it to lower energy muddy substrates when it occurred in the nearshore (Fig. 3). Both *Linoproductus* and *Parajuresania* also have lower ratios of lophophore length to body volume consistent with well oxygenated environments.

3.4.3 Offshore Taxa

The offshore taxa were distributed across a range of open marine conditions (Olszewski and Patzkowsky, 2003). In general, the environments consisted of a muddy substrate at a subtidal depth below fair-weather wave base with patches of elevated bioherms (Olszewski and Patzkowsky, 2003). Within the marine environments, genera were distributed along an oxygenation gradient. The presence of algae indicates a shallower, photic, and well oxygenated environment as one end member, while darker and finer shales and limestones suggest that the other end member was lower energy and dysoxic (Olszewski and Patzkowsky, 2001, 2003). Along this gradient, *Linoproductus* and *Reticulatia* were associated with the oxygenated environments, *Kutorginella* with less oxygenated settings, and *Hystriculina* with dysoxic environments (Olszewski and Patzkowsky, 2001). The performance of *Hystriculina* is consistent with living on a soft, fine, fluid rich substrate, in a low energy, dysoxic environment. The long settling time of *Hystriculina* demonstrates greater resistant to sinking. The small size, and high ratio of lophophore length to volume, are consistent with a dysoxic environment where oxygen is a limiting factor, requiring proportionally larger lophophores and limiting overall size. *Kutorginella* performed similarly, exhibiting a slow settling time and a large lophophore length to body volume ratio.

The performance of these last three taxa in the transport experiments is somewhat inconsistent with paleoenvironmental distribution. The long spine length of *Hystriculina*, *Kutorginella*, and also *Reticulatia*, would have prevented transport at high velocity currents over sandy substrates while also increasing drag/resistance and settling times (Fig. 3). In these productoid models, the long spines were able to withstand deep scour so well that all

three models remained stable when the top 2-3 cm of sediment were eroded, and the body of each model was suspended completely in the water column held up by the spines. Although these calm-water taxa handle high velocities better, they did not land in a convex/spine down orientation in the settling trials. This is in contrast to the taxa which were less resistant to transport but consistently landed convex down in settling trials. The long spine morphology is effective at resisting sinking and transport; however, when entrained, this morphology was unlikely to land in an optimal or even survivable orientation.

Alternatively, Olszewski and Patzkowsky (2003) allowed for the possibility that the dysoxic environments were not necessarily in deep water or the result of upwelling as suggested by Heckel (1977). Olszewski and Patzkowsky (2003) speculated that the dysoxia was the product of algal blooms in eutrophic water fed by the nutrient rich runoff from nearby inland and coastal coal swamps and that dysoxia would have formed in proximal open marine conditions with oxygenation increasing distally from the shore and laterally away from deltas. Additionally, lowered rates of dissolution have been experimentally observed in warmer and less agitated water (Downing and Truesdale, 1955). Given the parameters of the Super-Estuary model (Algeo and Heckel, 2008), it is possible the weak tidal action and mild climate produced periodic dysoxia in shallow settings. In both of these latter scenarios, dysoxia could occur in relatively shallow water which may have been at risk of periodic or rare disturbance. Alternatively, in the upwelling hypothesis explaining the origin of the black shales, the dysoxia is the result of upwelling drawing up water from more distal deeper water (Heckel, 1977), possibly generating stronger currents. However, the fine sediment constrains flow velocity to below 0.2 m/s, above which sediment would be prone to transport. In both the shallow and deep-water dysoxia scenarios, the ability to handle deep scour would have benefitted productoids living in fine, easily disturbed sediment.

On the well oxygenated end of the gradient, *Linoproductus* and *Reticulatia* demonstrated low lophophore length to body volume ratios as expected. As well, both taxa have average settling times, suggesting proficient resistance to sinking on firmer muds. Furthermore, living below the fair-weather wave base, both genera would have been relatively sheltered from high velocity disturbances found in the onshore facies. The average performance of *Linoproductus* is consistent with a multi-environment distribution ranging from nearshore to offshore. This is consistent with the results of Leighton and Schneider (2008), in which both *Reticulatia* and *Linoproductus* were found to be approximately evenly distributed between carbonate and siliciclastic environments with a wide range of substrate and environmental tolerances.

3.4.4 Rare/Other Taxa

On the Olszewski and Patzkowsky (2001) ordination, both *Echinaria* and *Canocrinella* plot on the well oxygenated end of the gradient, close to *Parajuresania*. Similarly, all three genera plot close together (along with *Reticulatia*) in our performance spaces (Figs. 3, 5). All three taxa are also relatively similar in morphology and performance, although very different in size. *Echinaria* was slightly less stable in the transport experiments but had a longer settling time, and a much lower lophophore length to body volume ratio. This is consistent with *Echinaria* being restricted to well oxygenated environments, and corroborated by the results of Leighton and Schneider (2008) who found *Echinaria* to have a narrow environmental range and a strong preference for carbonate substrates. The dense, medium-length spines and low profile of *Canocrinella* are morphologically similar to *Parajuresania*. Both models had similar performance in the transport experiments, producing delayed scour formation. Both genera also have dorsal spines; *Canocrinella* is unusual in this regard compared to other linoproductoids. It has been hypothesised (Grant, 1966; Rudwick, 1970) that dorsal spines functioned to hold a mass of sediment in place on the dorsal valve in a current. In our experiments and those of Garcia *et al.* (2018), the observation of sediment retention on the dorsally spined models supports this hypothesis. The sediment may have served to disguise or camouflage concavo-convex brachiopods as suggested by Garcia *et al.* (2018). In a low energy setting, sediment would be less likely to erode; in a higher energy environment, spines may have been necessary to hold the sediment. Although the precise paleoenvironment of *Canocrinella* is difficult to determine, the results of our study suggest that it could have lived under a wide range of environments and that hydrodynamic stability was not the limiting factor in its distribution.

The *Pulchratia* model was the least stable of all models in the transport experiments. When placed with the geniculation elevated in the anterior upstream orientation, a deep scour was produced, reducing stability. This orientation, while more unstable, has been observed in productidines preserved in life orientation (Grant, 1966) and would have provided benefits regarding feeding and processing water. The elevated commissure would have reached higher into the water column, facilitating waste removal, providing access to more food particles as a function of available water volume, or by allowing the organism access to a different part of the water column from that of competitors in a form of niche partitioning (Walker, 1972; Tyler and Leighton, 2011) or tiering on a small scale (Ausich, 1980). Assuming, all other things being equal, that the quantity of food particles available to a sessile suspension feeder is a function of current velocity, efficiency is more important in lesser currents and low energy settings. In comparison to *Parajuresania*, it is likely that

Pulchratia was adapted to lower energy and softer substrate settings. *Pulchratia* was more common in 'marly' limestones overlaying shales containing *Parajuresania* (Leighton and Maples, 2000) with *Echinaria* living in strictly carbonate mud environments. The driver of this pattern may have been energy, turbidity, productivity or even substrate preference. The instability of *Pulchratia* in comparison to *Parajuresania* observed in our study may indicate that energy may have influenced echinoconchoid distribution.

3.4.5 Macroevolutionary Context

During the Devonian, strophomenate evolution displays a double-wedge (*sensu* Benton, 1987; Sepkoski, 1996) shift between aspinose strophomenides to spinose productides. Both orders were concavo-convex and liberosessile and likely filled similar ecological roles. This pattern of replacement is apparent on multiple scales within each order: chonetidines replace plectambonitoids (Mills and Leighton, 2008), and productidines replace the strophomenoids (Leighton, 2001b). Strophomenides and productides shared a similar general morphology but the strophomenide version lacked spines. It has been suggested that spines were the key innovation that facilitated the radiation of chonetidines into higher energy settings and thus into new niches in which plectambonitoids would be less well adapted (Rachebouef, 1990; Mills and Leighton, 2008). The same pattern may also hold true for strophomenoids and productidines. Experiments by Garcia *et al.* (2018) using standardised physical models demonstrated that spinose ornament increases stability over aspinose ornament in high velocity conditions. An expansion of range into new niches is also demonstrated by the late Paleozoic productidines *Parajuresania* and *Linoproductus* living alongside bivalves such as oysters and mytilids in nearshore settings (Olszewski and Patzkowsky, 2001). This is further corroborated by the results of our study in which all models display, to varying degrees, competency on mobile substrate in high velocity currents.

It is of further note that the taxa in this study represent a wide range of productidine morphological forms and that the results of this study, while limited to eight taxa, have broader implications for the clade. Our taxa represent three superfamilies and display a diversity of solutions to similar ecological problems such as sediment interaction. During the Lower Carboniferous, the Productidina radiated beyond the small and relatively homogeneous Devonian forms. This radiation coincides with a global reduction of reef area after the late Devonian Mass extinctions (Copper, 2002; Kiessling, 2002) and an increase in muddy Waulsortian-type banks (Kiessling, 2002). The decrease in hard reef rocks may have facilitated the radiation of productidines by increasing the niche space available on both

soft, muddy and mobile, sandy substrates. Unlike the sister clade Stropholosiidina, which were fixosessile and cemented themselves to hard substrates, reef environments would have been unsuitable for liberosessile productidines, but the spines of productidines would have facilitated anchorage in any sediment, whether mobile, firm, or soft. Kammer *et al.* (1998) suggested the success of advanced cladid crinoids during the late Paleozoic was partially the result of specialization for siliciclastic environments in response to a shift towards more siliciclastic dominated environments. Thus, increased siliciclastic input during the late Paleozoic may have exerted selective pressure on both crinoids and brachiopods. Productidines have been noted as common constituents of European Lower Carboniferous Waulsortian mud facies (Lees and Miller, 1995) but obviously were also common constituents of the broad range of habitats observed in Kansas.

During the Lower Carboniferous, all three productidine superfamilies also became more morphologically disparate. Our results suggest that the strong performance of the long-spined productoid morphology may have facilitated their radiation by allowing them to survive in a wider range of environments. Acid etched limestones have demonstrated that long spines allow productidines to be entangled in bryozoan colonies (Muir-Wood and Cooper 1960) or in “thickets” of conspecifics. The echinoconchoid spine morphology, however, was less capable of resisting transport. On average, echinoconchoids were also large. Recent experiments (Dievert *et al.*, 2020), have demonstrated that much of echinoconchoid performance was driven by size, and less by spine morphology, and that larger sizes were beneficial to both feeding and stability in mobile substrates as speculated by Alexander (1981). While growing larger would have been beneficial to echinoconchoids, a maximum size may have also had drawbacks. Forces generated by wave acceleration, but not velocity, scale disproportionately with organism size and thus in high energy environments may act as a constraint on size (Denny *et al.* 1985). In this regard, the distribution of *Parajuresania*, the smallest and flattest echinoconchoid in this study, is consistent with a higher energy nearshore environment. The linoproductoid spine morphology fell between the productoids and echinoconchoids and allowed for a more generalist strategy. Species and even populations within *Linoproductus* display morphological variability ranging from aspinose to moderately-spined, with variable convexity, concavity and trail formation. As demonstrated by this study, the addition of spines or a change in profile could drastically change hydrodynamic performance, suggesting that either the genus *Linoproductus* was highly plastic or that its constituent species were highly adapted to very specific conditions. The relatively average performance of *Linoproductus* on all three axes supports a generalist niche explanation; strong,

specialised performance would likely be associated with adaptation or strong selective pressure.

In addition to interacting with substrate, both short and long spines may also be defensive adaptations to increased rates of durophagy during the Carboniferous (Signor and Brett, 1984), a hypothesis that we were not able to test. Spines resist predation by making spinose taxa too large for crushing apparatuses (mouth, chelae, etc.) by increasing effective size (Palmer, 1979; Miller and LaBarbera, 1995; Johnsen *et al.*, 2013). Spines could also increase predator handling time (Willman, 2007; Johnsen *et al.*, 2013), or behave like the crumple zones of cars by buffering crushing force or in extreme cases necessitating a second crushing action, a function demonstrated by Miller and LaBarbera (1995) with modern gastropods. Additionally, denser spine arrangements could have served to resist drilling predation by making the productidines more difficult to grapple or a dense recumbent mat of spines could serve to make the valves effectively thicker, thus increasing drill times or making boring more difficult (Stone, 1998; Willman, 2007). The function of spines for defence has been empirically demonstrated to lower drilling success rate in spinose vs. aspinose Devonian strophomenates (Leighton, 2001a). It has also been suggested (Garcia *et al.* 2018) that dorsal spines may have functioned to attract epibionts for the purpose of camouflage in a manner similar to modern thorny oysters (Feifarek, 1987). Future studies could incorporate additional tests and axes to evaluate the performance of spines as defensive or camouflaging structures.

Overall, the performance of the productidine models within performance space was consistent with the distribution of productidine genera across paleoenvironmental gradients of the Pennsylvanian and Permian Midcontinent. Additionally, this study has shed light on the effects of valve morphology and spine geometry on productidine functional morphology. Long spines increase stability in mobile substrates and increase resistance when sinking, but also interfere with settling orientation if entrainment were to occur. Size also affects performance with larger productidines being more stable in mobile substrates but less resistant to sinking. Separation of taxa within the performance space is consistent with a radiation of productidines filling that space and niche differentiating based on hydrodynamic performance.

3.5 References

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Table 3.1 A summary of performance results and raw morphological measurements. Each orientation in the transport resistance trials is an average of three trial times. Settling times are an average of 10 trials. *The *Hystriculina* model landed on its umbo in 9 out of 10 trials.

Genus	Mobile Substrates/ Time to Destabilization (seconds)				Soft Substrates/ Entrainment		Respiration Proxy		
	Hingeline Down-stream	Hingeline Parallel	Hingeline Up Stream	Average of All Orientations	Settling Time (s)	Correct Settling Orientation	Lophophore Length (cm)	Volume (cm ³)	Lophophore Length/ Volume
<i>Linoproductus</i>	1535	1716	1800	1684	1.74	10	12.25	21.34	0.57
<i>Canocrinella</i>	1800	1800	1800	1800	1.60	0	6.10	2.43	2.51
<i>Hystriculina</i>	1800	1800	1800	1800	2.57	9*	2.45	0.48	5.07
<i>Retaria</i>	1800	1800	1800	1800	2.13	0	4.53	1.39	3.25
<i>Reticulatia</i>	1800	1800	1800	1800	1.51	0	9.13	10.85	0.84
<i>Pulchratia</i>	1348	1800	1800	1650	1.40	10	9.77	17.06	0.57
<i>Parajuresania</i>	1792	1800	1800	1797	1.38	10	7.30	8.60	0.85
<i>Echinaria</i>	1740	1800	1800	1780	1.63	10	13.40	52.97	0.25

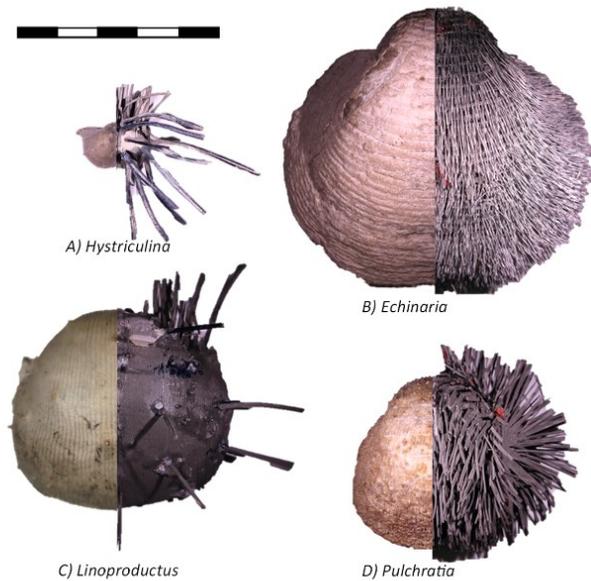


Figure 3.1 Representative fossils and models for the three subfamilies tested. (A) Productoidea: generally small, possessing large ears (as visible on the top left of the *Hystriculina* fossil) and a few scattered long-spines (B, D) Echinoconchoidea: generally large possessing hundred to thousands of short dense spines commonly arranged in bands. Specimen B is USNM PAL 706489. (D) Linoproductoidea: generally medium to large with scattered medium-length straight spines. The *Linoproductus* specimen has been enlarged by a factor 1.5 to match typical adult size ranges. Each image is a composite of a photograph of the original specimen and the 3D printed model showing the ventral valve, with the posterior at the top.

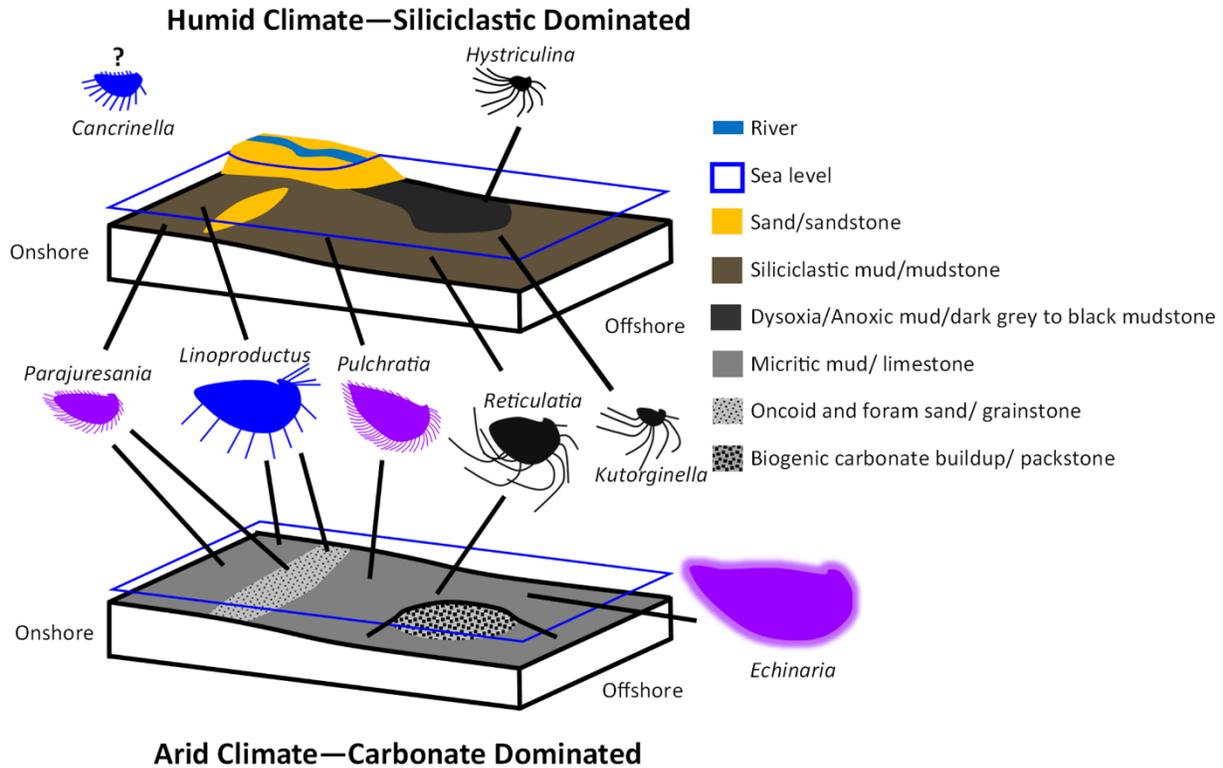


Figure 3.2 Paleoenvironmental distribution of the eight genera used in this study. Vertical depth is exaggerated with water depth ranging in 10s of metres and lateral axes in the 100s or 1000s of m. Productoidea (*Reticulatia*, *Kutorginella*, and *Hystriculina*) are marked in black; Echinoconchoidea (*Parajuresania*, *Pulchratia*, *Echinaria*) in purple; Linoproductoidea (*Canocrinella*, *Linoproductus*) are marked in blue. All silhouettes are to scale. The scale bar is 5 cm. Substrates and environments correspond to facies and environments described by Olszewski and Patzkowsky (2003).

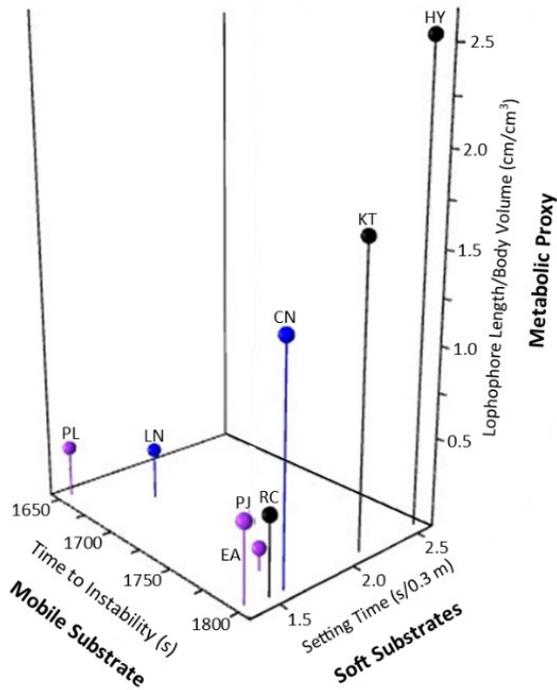


Figure 3.3 A performance space displayed on three axes: mobile substrate performance, soft substrate performance, metabolic proxy. Plotted genera: *Hystri culina* (HY), *Kutorginella* (KT), *Can crinella* (CN), *Pulchratia* (PL), *Linoproductus* (LN), *Parajuresania* (PJ), *Reticulatia* (RC), and *Echinaria* (EA). The colours are the same as in Figure 3.2.

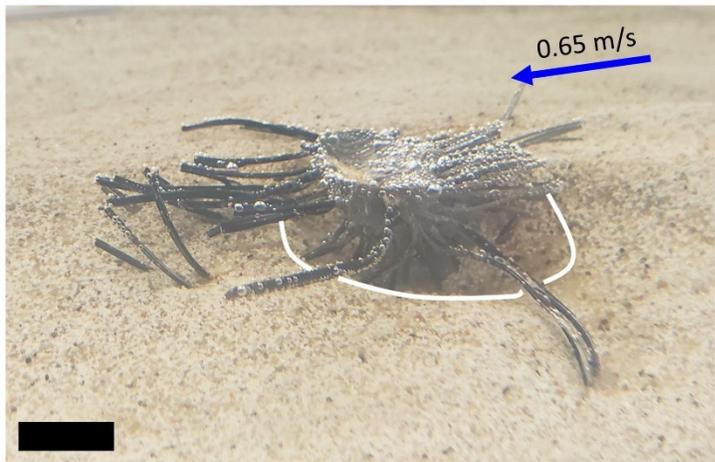


Figure 3.4 A *Kutorginella* model in sand during a mobile substrate experiment. Image taken at 1500 seconds elapsed. Note that the scour completely surrounds the model and is highlighted in white. Flow direction and velocity are noted. The scale bar is 1cm.

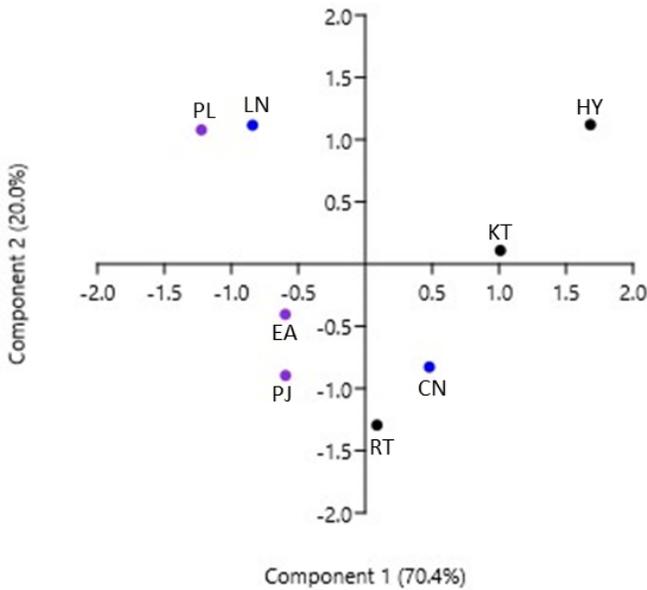


Figure 3.5 Performance Z-Scores plotted using in a PCA. Component 1 represents hydrodynamic performance with positive values corresponding to greater transport resistance and longer settling times and negative values corresponding to lesser transport resistance and shorter settling times. Component 2 could not be further resolved. Plotted genera: Hystriculina (HY), Retaria (RR), Cancrinella (CN), Pulchratia (PL), Linoproductus (LN), Parajuresania (PJ), Reticulatia (RC), and Echinaria (EA). The colors are same as those used in Figures 3.2 and 3.3.

Chapter 4

Conclusions

Inferred and measured performance is a useful proxy for evaluating the functional morphology and ecology of extinct organisms. By applying a performance space framework to whole organisms, a greater understanding of function and fitness can be gained. By constructing physical models of productidines and measuring performance I was able to test hypotheses of productidine functional morphology. By combining productidine performance with evolutionary data I identified cases of adaptation through evolution. By comparing productidine performance to environmental distribution I was able to identify cases of adaptation as state. This research reached several conclusions which furthered the greater understanding of productidine paleoecology and demonstrated a use for performance spaces:

- 1) Echinoconchoid performance is driven by size. Larger echinoconchoids have increased hydrodynamic stability, greater feeding efficiency, and proportionally smaller lophophores.
- 2) Within the Echinoconchoidea, spacing of genera within performance space indicates possible niche partitioning in which genera are separating on hydrodynamic performance.
- 3) The performance of productidines from the Pennsylvanian-Permian Mid-continent of North America are consistent. Dysoxic taxa having greater stability on soft substrates and proportionally larger lophophores while near shore/ well oxygenated taxa can handle high velocity currents and have proportionally smaller lophophores.
- 4) Resistance to transport and sinking in soft substrates are both increased with productidine spine length. Longer spines also interfere with self-righting when settling.

Because productidines were major contributors to brachiopod diversity during the late Paleozoic understanding their ecology provide greater insight to our understanding of that time interval. Further, performance spaces provide a framework in which to compare the functionality and performance of multiple taxa simultaneously and objectively. By using multiple measures of performance multiple functions can be evaluated and by including environmental and taxonomic data adaptation can be identified.

In future studies performances space can be applied to other clades of brachiopods or organisms to quantify adaptation and evolution. Additionally, due to the constraints in feasibility this study was limited in scope to 14 genera. Future studies could expand the sample size in several ways. The first way would be the inclusion of additional genera. Alternatively, the sample size and scope could be increased by including additional models of hypothetical morphology. By constructing hypothetical models or multiple models with greater variability a better understanding of how morphological variation and subtleties impact performance. Because the number of axes included in performance spaces are virtually unlimited, new measures of hydrodynamic performance such as susceptibility to burial, behavior in multidirectional currents, or behavior across multiple grain sizes or velocities could be developed further. Additional axes may reveal alternative selective pressures or morphological functions.

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