

NEW QUANTITATIVE METHODS FOR ANALYZING BRACHIOPOD SHELL SHAPE:
AN EXPLORATORY STUDY OF THE MORPHOLOGY OF CINCINNATIAN
RHYNCHONELLIFORMEA DURING THE LATE ORDOVICIAN RICHMONDIAN
INVASION

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Abstract

The external valve morphology of Brachiopoda is a common focus within the field of invertebrate paleontology and previous studies have been largely focused on the morphological features that are indicators of functional adaptations, but there is a need for comprehensive descriptions of the entire external morphology of brachiopods to fill the gaps in systematic descriptions and studies of morphology. This study established a Multilevel Morphological Index composed of 18 characters each with 5 character states structured that allows for coding and analysis in multi-dimensional space where the relative relationship of each brachiopod's morphology can be observed. To test the validity of the Multilevel Morphological Index, this approach was applied to species from Stigall (2010)'s study on the paleobiogeographic distribution of Cincinnati-type brachiopods from the Cincinnati-Arch. Species were analyzed for morphological variability with and without a priori groups based on niche tolerance and bio-stratigraphic occurrence across the Richmondian Invasion during the late Ordovician. Results support the new approach as a viable and effective mode of morphological analysis, providing insight into patterns in distribution based on changing environmental conditions and habitat tolerance including support of delayed niche occupation revealed by morphological consistencies between locally extinct species and invasive species in the Richmondian.

Introduction

Brachiopoda is one of the most extensively studied fossil invertebrate phyla and are abundant in varied marine environments from the early Cambrian to present (Chen et al., 2003; Carlson, 2016). Many studies have focused on the external and internal morphology of fossilized brachiopods due to their high diversity, variable shell form, and stable shell mineralogy (Tyler and Leighton, 2001; Ciampaglio, 2004; Berrocal-Casero et al., 2017), yet no studies have successfully described the external morphology in a systematic, comprehensive, concise, and comparable manner regardless of temporal and geospatial constraints. Previous approaches to morphological analyses are often dependent on the geological context, are temporally or geographically restricted, or lack a comprehensive and systematic application that is accessible for readers (e.g. “Permian brachiopods from Southern Thailand” Grant, 1976). The new methods developed in the study aim to fully describe and quantify the morphological characteristics of shell shape in a way that is broadly applicable, independent, and directly comparable. This will be achieved by creating a system of characters with a fixed number of character states and without the need for geologic, environmental, or ecological context.

Systematic descriptions include terms that require a detailed foreknowledge of brachiopod anatomy and often have insufficient information to fully characterize external shell morphology descriptions. The systematic description in the Treatise Part H (Ager et al., 1965) do not provide a complete picture of the external morphology suitable for consistent comparison of taxa across the phylum and often require heavy reliance on independent

interpretation from associated figures in the text (Williams and Rowell, 1965). The current and traditionally used system of morphological terms has been adequate for general descriptions of morphology but lacks the ability for direct applications of detailed morphological comparisons within and across groups. A new approach to external brachiopod morphology is explored in this study through the creation of methods structured using an ordered numerical index that can be readily used in multivariate statistical applications. These new methods aim to analyze the entirety of external valve morphology through individual characters that, similar to a puzzle, come together to create a full summary without needed visual and geological context. The goal of this new approach is to establish methods that can be applied to a range of morphology-based studies of both modern and fossil brachiopods (i.e. ontogenetic shifts, intraspecific variation, taxonomic classification, phylogenetics, environmental and ecological niche shifts).

Within the phylum Brachiopoda are three subphyla, Craniiformea, Linguiliformea and Rhynchonelliformea, defined by the presence or absence of dentition along the hinge line (Williams and Rowell, 1965; Carlson, 2016; Harper et al., 2017). Due to the differences between the subphyla in shell composition, life mode, and abundance, the approach of this study focuses on describing the external shell morphology of the 18 classes of brachiopods that fall within the rhynchonelliform subphylum. A slightly modified approach to external morphology of subphyla Craniiformea and Linguiliformea should be viable and function in the same way. Rhynchonelliformea are well studied and defined as having interlocking dentition along the hinge line and calcitic shells which have a higher preservation rate than the shell material that composes the other two subphyla (Ager et al., 1965; Harper et al., 2017).

To explore the applicability and viability of the results of this new approach to characterization of brachiopod external morphology, methods will be applied to a robust dataset of rhynchonelliform brachiopods from Stigall (2010) using the a priori groups described therein in an attempt to observe morphological variation and similarity within and between taxa from different biogeographic regimes, niche tolerance, and taxonomic classification in relation to the geographic, stratigraphic, and environmental parameters in the Cincinnati Arch. Stigall (2010) focuses on brachiopod paleobiogeography and stratigraphy in the Cincinnati region during the late Ordovician Richmondian Invasion, a well-documented event. The abundance of research on the Richmondian Invasion provides important stratigraphic, paleobiogeographic, paleoecological and paleoenvironmental context making this time period ideal for testing a new approach to quantifying and describing brachiopod morphology within geologic context.

Background

Other quantitative methods for analyzing brachiopod morphology

Beyond traditional, descriptive methods there have been numerous studies that use the external shell morphology of rhynchonelliform brachiopods to investigate other wide-ranging of research including morphospace, functional morphology, environmental effects on growth, ontogeny, and taphonomy (Alexander 1977; Brunton, 1981; Brunton, 1995; Logan et al., 1997; Alexander, 2001; Haney, 2001; Tyler and Leighton, 2001; Ciampaglio, 2004; Berrocal-Casero et al., 2017). The approach to quantifying morphological

variation has, in the past, been tailored to investigate only the morphological features that are relevant to the secondary topic of the study, such as sulcus depth and filter feeding efficiency (Shiino and Kuwazuru, 2010), patterns in shape change of Ordovician *Sowerbyella* (Haney, 2001), growth increment width on the surface of the valve in relation to size through life (Alexander, 1977).

Previous studies that aim to quantify the external morphology of brachiopods have successfully discussed the functional features through landmark analysis (Carlson, 1989; Haney, 2001; Bose, 2012; Tyler and Leighton, 2011; Berrocal-Casero et al., 2017) and using the principal of uniformity and geologic context (Alexander, 2001; Ager, 1967; Richards, 1972). The only study that has aimed to comprehensively and systematically describe external brachiopod morphology using a coding system is Ciampaglio (2004). Ciampaglio (2004) uses a combination of continuous, discrete, and a combination of both discrete and continuous variables to define character and character states which are coded and placed into multivariate space. What lacks in the methods outlined in Ciampaglio (2004) is the capacity for expansion and elaboration. Ciampaglio (2004) accounts for a significant portion of external morphology through space and time across 600 genera, but the system with which the brachiopods have been coded is based on a limited number of traditional morphological terms. Each character has an inconsistent number of character states: presence-absence, continuous, and discrete features which ranged in the number of character states from two to eight (Ciampaglio, 2004). This makes it difficult to maintain comparable individual characters and may lead to weighting bias into the dataset when plotting the coded genera and the greatly limits the ability to investigate variability within character states. The methods outlined in previous studies, while appropriate internally within the study, do not

address the need for a system of morphological analysis with quantitative methods that produce clear, simplified, comparable, and evenly distributed character and character states that incorporates as much of the traditionally used morphological terms as possible. There is a need to fill in the gaps in morphological variability not accounted for in studies of only functional morphological characters.

While the methods described in the present study do not apply landmarks to address morphological variation, the difficulties in maintaining uniformity of landmark positions with the morphological disparity within Brachiopoda makes it nearly impossible to collect comprehensive meaningful landmark data for all brachiopods. Landmark data may prove more effective when investigating specific functional features or for quantifying intraspecific variation where the parameters of study are more constrained and Procrustes can be applied without modification to the dataset, a nearly impossible feat when comparing all morphological variation across the diversity of the phylum. These issues associated with landmark application in the context of this study makes a coding system ideal for encompassing a greater amount of disparity of shell shape.

Richmondian invasion of brachiopods

To test the viability and efficiency of the new method to characterize external brachiopod morphology, the new methods, termed Multilevel Morphology Index, was applied to 49 Cincinnati brachiopod species described in Stigall (2010)'s study on the niche tolerance as interpreted from the paleobiogeographic distribution and range of Cincinnati Rhynchonelliformea Brachiopoda to observe potential morphological patterns between and among species through space and time (Figures 1-2). These 49 species range a total of ten families (Plectorthidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Sowerbyellidae,

Anazygidae, Glyptorthidae, Rhynchotrematidae, Plaesiomyidae, and Rafinesquinidae) and 19 genera (*Austinella*, *Sowerbyella*, *Leptaena*, *Strophomena*, *Holtedohlina*, *Rafinesquina*, *Tetraphalerella*, *Thaerodonta*, *Glyptothyris*, *Catazyga*, *Retrosirostra*, *Zygospira*, *Plectorthis*, *Dalmanella* (*Cincinnatiina*), *Hebertella*, *Vinlandostrophia* (*Platystrophia*), *Hiscobeccus*, *Leipodocylus*, and *Rhynchotrema*). The Richmondian Invasion was chosen for analysis here because of the abundance of information on the taxonomy, geology, ecology, and environment in the literature which allows for the direct comparison of morphological variation and multiple factors that may explain any patterns in shell shape. Stigall (2010) was chosen because of the high-resolution locality information and well-constrained groups that make direct analysis of morphological variation in multiple contexts and thus a robust exploration of the viability of the Multilevel Morphology Index.

The Cincinnati series is composed of four stages defined by midcontinent conodont zones subdivided into sequences C1-C6 from 451 Ma to 443 Ma (Figure 2) (Sweet, 1984). The Maysvillian and Richmondian stages are the focus of Stigall (2010) and this study which contain sequences C2-C6 (Sweet, 1984). The underlying Edenian stage is entirely composed of sequence C1 is considered a stage that contains residual species that continued into the Cincinnati from older sequence M6 from the Mowhawkian series and Franklinian stage (Holland and Patzkowsky, 1996). The early Gamachian Stage is placed just within the Cincinnati series, sharing only half of the C6 sequence with the Richmondian and is also included in the definition of regimes (Figure 2). The Richmondian Invasion is a shift in community structure driven by orogenic events during the Late Ordovician which drove changes in environment across the Maysvillian and equivalent stages to the Richmondian stage (Holland and Patzkowsky, 1996). Multiple extirpations occurred in Appalachian region

prior to the Cincinnati and during the transition from Maysvillian to Richmondian. For example, tabulate and colonial patch corals appeared prior C1 and reappeared in the C4-C6 sequences (Holland and Patzkowsky, 1996). The invasive species that appear in the Richmondian are the same taxa endemic to the Midcontinent regions (*Glyptorthis insculpta*) (Wright and Stigall, 2013). It has been theorized that the differences in community structure are attributable to shifts in local environment as indicated by changes in carbonate lithologies across the Maysvillian - Richmondian boundary marked by a large transgressive event which deposited large quantities of sediment likely attributable to the Taconic orogeny or a short Late Ordovician warming event and led to warmer tropical-like conditions (Holland and Patzkowsky, 1996; Fortey and Cocks, 2005). High dispersal rates and the tropical-like conditions in the Cincinnati region have been linked to the invasion of fauna into the arch region (Wright and Stigall, 2013). Further studies have suggested that the Richmondian Invasion was not caused by extinction but rather continuous environmental degradation with taxa in C2 gradually dropping in diversity and invasion taxa first appearing in the C4 sequence but not becoming a well-established group until C5 (Figure 2) (Patzkowsky and Holland 2007). The C3 sequence is marked by a reduction in species diversity and the C4 sequence is also marked by high turnover which is largely attributable to a small extinction pulse followed by an influx of new species into the region (Patzkowsky and Holland, 1997).

Stigall (2010) outlined four groups, referred to as regimes in this study, defined by the local first appearance datum (FAD) and last appearance datum (LAD) of type – Cincinnati Rhynchonelliformea in Late Ordovician Cincinnati Arch C1-C6 sequences in Ohio. The four regimes are defined as Maysvillian Restricted (C1-C3), Carryover, (C1-C6), Descendant of Native (C1-C6), and Extrabasinal Invader (C4-C6) (Figure 2) (Stigall, 2010). According to

Kidwell and Flessa (1996) the fauna are preserved in a storm deposit but have not been laterally transported significantly far from source and thus the physical surroundings of the deposits can be interpreted as if the fauna were preserved in situ. The conclusions of Stigall (2010) determined that persistence across the Maysvillian – Richmondian boundary, extirpation, and the paleobiogeographic range of each group were indicators of niche tolerance and concluded that Carryover and Extrabasinal Invaders were generalist fauna and Maysvillian Restricted and Descendant of Native taxa were specialists and these levels of niche tolerance are incorporated into this study alongside the regimes to investigate patterns in morphology at different scales across the communities. Stigall (2010) provides a well-established data set for the application of new methods for testing morphological variation. The patterns have the potential to reveal patterns in morphology that are related to biogeographic distribution, adaptation across migrational events, and changes to ecological niche of the brachiopod taxa listed in Stigall (2010) Table 1.

I hypothesize the new approach to external valve morphology of Rhynchonelliformea Brachiopoda will address morphological variation within the given dataset that, when plotted in multidimensional space, will reveal patterns that are associated with the a priori regimes, ecological niche tolerance, paleobiogeographic distribution, taxonomic classification, and environmental conditions during life.

Methods

Development of new methods for characterization and comparison of Rhynchonelliformea shell shape

The goal of this new approach for documenting, communicating, and analyzing the external morphology of rhynchonelliform brachiopod is achieved through the development of standardized, comprehensive, and concise methods with comprehensive and concise across all characters and forms. In addition, selected characters and their defined character states should, whenever possible, be based on traditional morphological terms and features as described in the Treatise (Williams and Rowell, 1965) (Tables 2-3; Appendix 1; Figure 3). Dividing brachiopod shell morphology in this way allows for easy and direct analysis of independent geometric aspects of shell shape without requiring knowledge of their anatomical details. However, the new scheme must allow for differentiation of closely similar forms using the traditional morphological terms that are directly associated with the character and states. Characters and character states should be structured for analysis of brachiopods widely varied brachiopod shell shapes through space and time and therefore cannot be dependent on size, volume, or other scaled metrics. Observable and measurable features should be organized into discrete, continuous, and a combination of continuous and discrete character types to account for variability in size within the character structure. The character states should also allow for the possibility of distributions that approximate for normality in the number and distribution of influence each character state has. For the methods to have any quantitative applications, a coding system must be integrated in the character/ character state system. This structure will allow for multivariate data analysis including principal component analysis (PCA), principal coordinate analysis (PCoA),

canonical variance analysis (CVA), cluster analyses (CA), and multi-dimensional scaling (MDS).

The methods developed for this study were established using both morphologically disparate brachiopod hand specimens from teaching collections and hundreds of images in the Treatise of Invertebrate Paleontology Part H (Ager et al., 1965) ranging in age from Early Ordovician to Recent. Character and character states were continuously tested, modified, organized, and expanded to obtain the most comprehensive and separate characters with a uniform number of states (discrete and defined options) for each character. The processes of defining and determining characters was largely based on how well traditional morphological terms are organized within the defined character states and how well these characters combine to describe the three-dimensional morphology of brachiopod shell shape. Due to the limitation of available of two-dimensional plate images of individual specimens, characters were determined largely from the dorsal (brachial) valve and sagittal (lateral) views of brachiopod genera with the assumption that that brachiopod left-right symmetry is adequately maintained across all specimens to allow for characterization of the general shell shape. The methods do not aim to replace current and traditionally used morphological terms, but rather create characters and character states with quantitative applications that describe features of external morphology within which some traditional morphological terms are organized for further analysis and detail if necessary. The viability of the Multilevel Morphology Index coding system was tested using several multivariate analyses PAleontological STatistics Software (PAST) 3.26b (Hammer et al., 2001) on a dataset of fifteen morphologically disparate genera (*Orthida*, *Strophomenida*, *Spiriferida*, *Terebratulida*, *Atrypida*, *Pentamerida*, *Rhynchonellida*, *Hesperorthis*, *Vellamo*, *Plaeosmys*,

Austinella, *Atrypa*, *Eospirifer*, *Brachythyris*, *Cyrtospirifer*), including nine hand specimens and five sets of dorsal and sagittal images from the Treatise Part H (Ager et al., 1965) assuming that the morphology of each specimen was representative of the entire genus. The Multilevel Morphology Index was structured to ensure ease of coding for character states using only one dorsal view and one sagittal view image while still describing the total three-dimensional shell shape.

Application of the Multilevel Morphology Index using Cincinnati dataset

Standardized dorsal and sagittal digital images were taken from one representative specimen per Cincinnati-type brachiopods listed in Stigall (2010) at the Cincinnati Museum Geier Collections and Research Center using a photography copy stand and a Nikon D7000 digital camera with Nikon DX AF-S NIKKOR 35mm 1:1.8 G lens (Supplemental Image Files). Two species from Stigall (2010), *Austinella scovellei* and *Leptaena gibbosa*, were excluded from this study due to a lack of well-preserved specimens. Forty-seven of the 49 species were used in the Multilevel Morphology Index detailed in Table 2 and Appendices 1-2. This study was conducted with the assumption that the selected specimen is a suitable representation of the species morphology.

This study uses PAST 3.26b on all default settings (Hammer et al., 2001). Principal component analysis (PCA) performs ordination analyses on multivariate datasets containing variables (morphological characters) and items (species) within multidimensional space to determine which variables have the greatest influence on the dataset (Wold, 1978; Wold et al., 1987). PCA results included principal component (PC) axes which is a linear combination of all variables plotted along its length from the most positive value to the most negative value based on a loading coefficients. PC Axis one accounts for the most variance in

the dataset, PC Axis two accounts for the second most variance in the dataset, and so on. The most and least positive loading coefficients along an axis are associated with the variables that account for the most variance in the total dataset out of all the variables (positive values high on the axis, negative values low, and values near zero at the center). Principal coordinate analysis (PCoA) functions similarly and is often a more reliable analysis for non-normalized categorical data such as the data in this study (Mohammadi and Prasanna, 2003). Canonical Variance Analysis (CVA), referred to as Linear Discriminant Analysis (LDA) in PAST 3.26b, has a similar ordination and dimension reduction process as PCA but incorporates a priori groups (stratigraphic regimes and niche tolerance) and compares the dataset within and between the groups and produces post-hoc groups which may be different from the a priori groups by organizing the dataset to reduce variation within a priori groups (Larimore, 1987).

PCA, PCoA, and CVA plots were created using PAST 3.26b with the default settings to observe distribution of taxa (items) in a multidimensional space defined by the variability of exterior valve morphology (variables). Shell shape variability was analyzed with and without a priori groups defined in Stigall (2010): Regime 1) Descendant of Native (13 species), Regime 2) Maysvillian Restricted (15 species), Regime 3) Carryover (8 species), and Regime 4) Extrabasinal Invaders (11 species), Generalists (3. Carryover and 4. Extrabasinal Invader), and Specialists (1. Descendant of Native and 2. Maysvillian Restricted). To reduce confusion, this study will refer to the a priori groups as Regime 1 (Descendent of Native), Regime 2 (Maysvillian Restricted), Regimes 3 (Carryover), and Regime 4 (Extrabasinal Invader). Preliminary analyses found no difference between PCA and PCoA plots despite using a non-normalized dataset, thus PCA plots were used in this

study because PCA loading coefficients, scores, and summary outputs provide more information for analyses than PCoA outputs. PCA plots with a priori groups were analyzed with all four regimes, both niche tolerances, between informative pairs of regimes and the two levels of niche tolerance, and as individual regimes/ types of niche tolerance. These analyses are conducted with the intent to observe morphological variation in association with the ability of a (group of) species to adapt to shifts in community structure and environmental factors including documented changes in ecological and environmental parameters, changing niches, and geologic events that effect temperature and depth in the Cincinnati Arch. All PCA and CVA graphs are listed in Table 4.

Results

Brachiopod shape characterization

The new approach, termed the Multilevel Morphology Index, is composed of 18 distinct and well-constrained characters, each with five character states. This approach comprehensively and concisely describes the external morphology of rhynchonelliform brachiopods. Characters are defined as broadly encompassing aspects of external brachiopod morphology that can be analyzed as both as singular characters and as an entire descriptive summary of shell shape. Each of the 18 characters have five indexed (predefined) character states numbered 0-4. The five predefined character states, which are different expressions of the greater character, are defined by morphological features which are often analogous to traditional morphological terms (Figures 4-6; Appendix 1). Features are a combination,

separation, or individual expression of a traditional morphological term as seen in Williams and Rowell (1965) which are used in the definition of character states. Features are either measurements (Maximum Body Length and Maximum Body Width in Character 2 – Length : Width (DV); character state: 2 – Equal (Eq); Features: Maximum Body Length (MBL) = Maximum Body Width (MBW)) or discrete physical features (Zig-Zag Commissure in Character – 18 Shell Texture (O); Character State: 2 – Plications or Ridges; Feature: Zig-Zag Commissure) and are the smallest division of the multilevel index (Table 3) (Williams and Rowell, 1965). The boundaries of each character state are determined by the type of feature(s) being used. Features not included in this study include volume, size, shell thickness because this approach is only concerned with the external valve morphology and size is too variable to be organized with any significance in these methods. Pedicle aperture associated features are also not included because of the difficulty of collecting morphological data from only a DV and SV image with any confidence. Characters that can be used as a proxy for pedicle aperture size include Beak Size Dorsal Valve, Beak Size Ventral Valve, and Ventral Valve Extension (Tables 1-2, Appendix 1).

The characters are determined by a combination of (1) measured, (2) observed, and (2) scaled characters. Measured and scaled characters exist on a continuous scale with the possible values ranging from negative to positive infinity, so in order to maintain the same number of character states across all characters, an adjusted weighting ratio was applied to all character states that broke the continuous variables into discrete categories. (1) Measured characters are defined as characters that require the direct measurement of features and the calculation of the relative relationship between said features with a center value at character state 2 and degree of difference from the center such as the length : width of the dorsal valve

(Characters 1-3, 5, 8-9, 14-15). (2) Observed characters are characters that are based on discrete, observable physical features with no center, intermediate values, or order (Characters 4, 6-7, 17-18). (3) Scaled characters are characters that are discrete but have an order in which they are organized based on the presence and degree of the expression of a feature such as the concavity or convexity of a valve (Characters 10-13, 16).

Quantitative methods for capturing morphological variation in a dataset

The Multilevel Morphology Index is subdivided into three orientations, or “views”, of data collection: Dorsal View (DV) (Figure 4), Sagittal View (SV) (Figure 5), and Other (O) (Figure 6). The specimen orientation is important for maintaining consistent data collection using the 18-character system. This study uses two standardized images, one for DV and one for SV. Characters that fall into the O orientation group are interpreted from a combination of the DV and SV images. The coding structure of the Multilevel Morphology Index produces a comprehensive, comparable, and idealized three-dimensional summary of a specimen’s shell shape using two-dimensional DV and SV images in multidimensional space. Each of the 18 characters are a single dimension with five possible positions in morphospace making the Multilevel Morphology Index ideal for investigating variability in shell shape in an 18-dimensions with a total of 90 (= 18 x 5) possible positions using multivariate statistics. In this study, the term code or coding refers to the concatenate of the associated numbers of each character state within the greater character from 1-18.

The same number of character states are maintained to ensure equal spacing and weight on each coded value such that when the final code is placed into multivariate space,

each character, and thus character states, is weighted equally. To further refine and ensure equally weighted and spaced character states, the relative relationship of each character state was adjusted for the naturally introduced bias of more or less common expression of features for (1) measured characters (Characters 1-3, 5, 8-9, 14-15). Character states 0 and 4 account for 10% each, character states 1 and 3 account for 30% each, and character state 2, the middle value, accounts for 20% (Table 5). Character states 0 and 4 often include a wider variety and range of character expression because they extend into positive and negative infinity respectively so the expression of these characters is theoretically larger. Character 2 is the middle value and encompasses 10% of the values that fall on either side of true equal. Characters 1 and 3 then account for all intermediate expressions of a character. Equations and conceptual models of the relative relationship of the discrete character states for (1) measured characters can be found in Appendix 1 and Table 5.

Directions for collecting and analyzing rhynchonelliform brachiopod external valve morphology for descriptive and multivariate data analyses purposes:

An example of a fully coded specimen is *Vinlandostrophia (Platystrophia) cypha* formatted ((#) - character (shorthand), # - character state (shorthand)) (Figure 7). Complete code for *Vinlandostrophia (Platystrophia) cypha* is (3-1-1-4-0-2-4-3-1-0-0-0-1-1-1-3-2-2):

1. Use images of an articulated brachiopod with minimal to no taphonomic or preservation issues with at least 1 high quality dorsal (DV) and 1 high quality external lateral/ sagittal (SV) photo (~150 ppi) (Supplemental Image Files).
2. Orient dorsal (brachial) images with distal-bottom, proximal top, dorsal valve up, line of symmetry vertical (0° - 180° N-S). Orient sagittal images with distal-left, proximal

right, dorsal (brachial) upper, ventral (pedicle lower), commissural plane horizontal (90° - 270° E-W) (Figure 3).

3. Begin with Category 1 and code sequentially, assigning a single character state number (0-4) that best describes the morphological feature(s).
 - a. Reference Appendix 1 for coding system, Figures 4-6 for visualization of each character state within the 18 categories, Figure 7 for an example specimen, and Appendix 2 for data table structure.
 - b. NOTE: These categories were created to reduce the amount of measuring needed, but formulas are provided in Appendix 1 and Table 5 if there is a specimen that does not clearly fall into one of the character states. For categories 1-3, 5-6, and 9-10, the termination of the range of relative values within the 5 character states is definite, while the beginning value is any decimal that increases the value above the previous terminated value (e.g. For category 1, a Proximal : Distal (DV) relationship = 0.20 codes as character state 1 (Proximal Narrow), while a Proximal : Distal (DV) relationship = 0.200000001 codes as character state 2 (Equal)) (Appendix 1).
4. Once all the morphological features have been coded, create a clean dataset appropriate for multivariate data analysis. The clean dataset should contain a total of 18 numbers per specimen.
 - a. Once clean, the dataset can be uploaded to various statistical software and run through numerous multivariate statistical analyses such as principal component analysis (PCA), principal coordinate analysis (PCoA), multi-

dimensional scaling (MDS), cluster analysis (CA), and canonical variance analysis (CVA).

b. PCA and CVA outputs are found in Figures 8- 13.

Dorsal View characters code: (3-1-1-4-0-2-4). (1) Proximal : Distal (P : D), 3 – Distal Narrow (Dst Nw); (2) Length : Width (L : W), 1 – Wide (W); (3) Mid Max Width (M : Mw), 1 – Short (Sh); (4) Lateral Shape (LS), 4 – Compound 2 (Cmp2); (5) Ventral Valve Extensions (VVe), 0 – Very Narrow or Absent (v. Nw o Ab); (6) Proximal Shape (PS), 2 – Convex (Cvx); (7) Distal Shape (DS), 4 – Compound (Cmp).

Sagittal View characters code: (3-1-0-0-0-1-1-1-3). (8) Asymmetric Dorsal Valve (AsDV), 3 – Distal High (Dst H); (9) Asymmetric Ventral Valve (AsVV), 1 – Proximal High (Pr H); (10) Median Sagittal Section Dorsal Valve (MSsDV), 0 – High Above (H Abv); (11) Median Sagittal Section Ventral Valve (MSsVV), 0 – High Above; (12) Shape of Dorsal Valve (SDV), 0 – Highly Convex (H Cvx); (13) Shape of Ventral Valve (SVV), 1 – Convex (Cvx); (14) Beak Size Dorsal Valve, 1 – Narrow (Nw); (15) Beak Size Ventral Valve (BSVV), 1 – Narrow (Nw); (16) Commissure Shape (CommS), 3 – Highly Asymmetrical (H Asym).

Other characters code: (2-2). (17) Number of Folds (Folds), 2 – One Fold (One); (18) Surface Texture (STxt), 2 – Plications or Ridges (Plc o Rdg).

The uniformly indexed structure of this new approach has been constructed such that the Multilevel Morphology Index, developed to accommodate that breadth of brachiopod shell variation, could be expanded upon with the expansion of character states to investigate further variability. An example would be if numerous specimens in a dataset all coded as the

character state 3- Costae (Cost) for the character (18) STxt and there was a need for differentiation in the type of costae which effectively creates sub-characters. It is important to note that PCA and other multivariate statistical analyses do not accommodate for hierarchal or nesting so these sub-characters must be treated on their own or alongside another set of sub-characters to maintain the scale of analyses. In this example, the sub-characters, or different expressions of the character state Cost, would only be able to plot in multivariate space with only the Cost sub-characters and not alongside the other character states: Smooth (Smth), Cost, Plc o Rdg, Sp, and Cmp).

Application of the Multilevel Morphology Index onto Cincinnati Brachiopoda across the Richmondian Invasion

Multivariate data analyses conducted on the Cincinnati species listed in Stigall (2010) resulted in numerous plots that display the relative relationship of the morphological characters within the dataset.

PCA 1.1, PCA 1.2 (Figure 8a-b) display the first two PCA Axes for all 47 species. The initial spread of all species in PCA 1.1 and 1.2 is evenly distributed along PC Axis one (Figure 8a-b). Two groups are divided along PC Axis two with a majority of species plotting in the negative with little vertical spread. Figure 8a displays groups by taxonomic classification divided along PC Axis two. Members of the Platystrophiae and Plectrothidae families plot to the positive of PC Axis one in quadrants one and two and the remaining eight families, Strophomenidae, Dalmanellidae, Sowerbyellidae, Anazygidae, Glyptothidae, Rhynchotremitidae, Plaesiomyidae, and Rafinesquinidae, plot to the negative of PC Axis

one. Figure 8b includes 95% confidence internal ellipses which displays the relative relationship of four regimes in this multidimensional space. Regime 4 (Extrabasinal Invader) is nested within Regimes 3 (Carryover) and 2 (Maysvillian Restricted), and Regimes 2-4 are all nested within Regime 1 (Descendant of Native). Only two of the 18 genera included in this analysis plot to the positive of PC Axis one. The most positive and negative loading coefficients for PC Axis one (31.3% variance) are Proximal Shape & Distal Shape and Median Sagittal Shape of the Dorsal Valve & Shape of Dorsal Valve & Median Sagittal Shape of the Ventral Valve respectively (Appendix 1). The most positive and negative loading coefficients of PC Axis two (21.9% variance) are Commissure Shape & Lateral Shape and Middle Maximum Width respectively. Regime 1 (Descendant of Native) extends the furthest in the positive direction of PC Axis one and has the most variability of the four regimes. Regime 4 (Extrabasinal Invaders) is the most condensed and falls almost entirely to the negative of PC Axis one and mostly within quadrant four. *Sowerbyella rugosa* is the only species to not fall within the 95% confidence internal ellipse for their regime, Regime 2 (Maysvillian Restricted). All other species fall well within the boundaries of their respective regimes (Figure 8b).

PCA 1.3, and PCA 1.4 (Figure 8c-d) display the third and fourth PC Axes for all 47 species. The initial spread of all species in PCA 2.1 is well mixed in one large cloud (Figure 8c-d). The distribution of families and regimes using 95% confidence internal ellipses has no pattern (Figure 8c-d). Neither genera nor species display a pattern of distribution and the regimes all appear to be majority overlapping. The most positive and negative loading coefficients of PC Axis three (9.4% variance) are Proximal Shape and Commissure Shape respectively. The most positive and negative loading coefficients for PC Axis four (8.2%

variance) are Shape of Dorsal Valve and Lateral Shape respectively. Regime 4 (Extrabasal Invader) displays the most variance, followed by Regime 3 (Carryover), in PCA 1.3 and 1.4 and all confidence internal ellipses on all four regimes have a much closer fit to the data than in PCA 1.2 (Figures 8b, d).

PCA 2.0 (Regimes 1-4; 4 modal values) (Figure 9) analyzes the modes of each of the four regimes using all 18 characters that act as a representative morphology, or morphotype, of the regime. Regime 1 (Descendant of Native) plots on its own, opposite to the other three regimes. Regimes 2 (Maysvillian Restricted) and 4 (Extrabasal Invader) plot in nearly the same exact point on the PCA and Regime 3 (Carryover) plots just above 2 (Maysvillian Restricted) and 4 (Extrabasal Invaders). The most positive and negative loading coefficients for PC Axis one (64.3% variance) is Lateral Shape and Median Sagittal Shape of the Ventral Valve & Median Sagittal Shape of the Dorsal Valve respectively. The most positive and negative loading coefficients for PC Axis two (31.3% variance) are Proximal Shape and Lateral Shape respectively. Regime 1 (Descendant of Analysis) plots at the most positive point along PC Axis one. Regimes 2 (Maysvillian Restricted) and 4 (Extrabasal Invader) plot opposite of Regime 1 (Descendant of Native) at the most negative end of PC Axis 1. Regime 3 (Carryover) accounts for a majority of the variation on PC Axis two, extending in the positive direction.

PCA 3.1 (Figure 10) displays the first and second axes of Regime 1 (Descendant of Native; 13 species). There appears to be one very strong group and two more diffuse groups in the initial distribution. The most positive and negative loading coefficients for PC Axis one (46.9% variance) are Commissure Shape and Proximal Shape respectively. The most positive and negative loading coefficients for PC Axis two (28.6%) are Lateral Shape and

Middle Maximum Width respectively. The groups strongly correlate with genera. All *Strophomna* species in Regime 1 plot to the positive of PC Axis one and all of the *Vinlandostrophia* (*Platystrophia*) and the single *Hebertella* species plot to the negative of PC Axis one. Distribution along PC Axis two is a bit more diffuse and separates both *Strophomena* and *Platystrophia* into a total of four groups, each with their own quadrant. PCA 3.1 produced 12 PC Axes which account for the total variation in this dataset which leaves the remaining six characters invariant.

PCA 3.2 (Figure 10) displays the first and second PC Axes employing on species of Regime 2 (Maysvillian Restricted; 15 species). The initial spread appears to be well distributed with the exception on a single species, *Sowerbyella rugosa*, which is plotting away from the main cloud. The most positive and negative loading coefficients for PC Axis one (38.9% variance) are Proximal Shape & Folds and Median Sagittal Shape of the Dorsal Valve respectively. The most positive and negative loading coefficients for PC Axis two (18.4% respectively) are Commissure Shape and Surface Texture. All but one species is well distributed along PC axis one and do not vary much in the vertical direction along PC axis two. *Sowerbyella rugosa* plots at the most positive extent of PC Axis two, away from the main cloud. PCA 3.2 provided 14 PC axes that accounted for all variance in the dataset, as a result of four invariant characters.

PCA 3.3 (Figure 10) displays the first and second PC Axes employing only species of Regime 3 (Carryover; 8 species). The initial spread is scattered with no clear pattern. The species within Regime 3 (Carryover) appear to be well distributed with a few loose groupings of species with no greater than 3 species per group. The most positive and negative loading coefficients for PC Axis one (54.7 % variance) are Distal Shape and Shape of the Dorsal

Valve & Median Sagittal Shape of the Dorsal Valve & Median Sagittal Shape of the Ventral Valve respectively. The most positive and negative loading coefficients for PC Axis two (20.4% variance) are Proximal Shape & Distal Shape and Lateral Shape respectively.

Hebertella occidentalis and *Vinlandostrophia (Platystrophia) cypha* are the only two species in the third quadrant and this most distant separated from the rest of the species in this regime. There is a cluster of three species in the second quadrant, and the first and fourth quadrant contain a total of three fairly similarly plotted species. PCA 3.3 provided 7 PC Axes that expressed the variability within the dataset, the fewest of the four individual regimes. The remaining 11 axes are invariant.

PCA 3.4 (Figure 10) displays the first and second PC Axes for the species within Regime 4 (Extrabasinal Invaders; 11 species). There is a small group of tightly clustered species and a handful of more scattered species, but no clear definite grouping. The most positive and negative loading coefficients for PC Axis one (38.9% variance) are Commissure Shape and Folds respectively. The most positive and negative loading coefficients for PC Axis two (20.6% variance) are Shape of the Dorsal Valve and Surface Texture respectively. *Thaerodonta clarksvillensis*, *Leptaena richmondensis*, *Holtedahlinea sulcata*, and *Tetraphalerlla neglecta* are more spread out and plot to the positive direction of PC axis one. All species in Regime 4 (Extrabasinal Invaders) are well distributed along PC Axis two. PCA 3.4 provided 10 PC axes that accounted for all variance in the dataset, leaving eight invariant characters.

PCA 4.1 analyzes Specialist regimes (Regime 1 (Descendant of Native) and Regime 2 (Maysvillian Restricted); 28 species) (Figure 11a). The initial plot shows a relatively condensed Regime 2 (Maysvillian Restricted) and a diffusely plotted Regime 1 (Descendant

of Native). *Sowerbyella rugosa* plots outside of the 95% confidence interval of Regime 2 (Maysvillian Restricted) and falls within Regime 1 (Descendant of Native). The most positive and negative loading coefficients for PC Axis one (33.4% variance) are Distal Shape & Proximal Shape and Shape of the Dorsal Valve respectively. The most positive and negative loading coefficients for PC Axis two (18.7%) are Commissure Shape and Proximal Shape. Regime 2 (Maysvillian Restricted) plots diffusely along PC Axis one and does not vary much along PC Axis two, whereas Regime 1 (Descendant of Native) plots in all four quadrants rather diffusely. The two groups that fall into the negative of PC Axis two from PCA 3.1 have directly overlap with all but one, *Sowerbyella rugosa*, members of Regimes 2 (Maysvillian Restricted).

PCA 4.2 analyzes Generalist regimes (Regimes 3 (Carryover) and 4 (Extrabasinal Invader); 19 species) (Figure 11b). The initial distribution of species within Regimes 3 (Carryover) and 4 (Extrabasinal Invader) is fairly concentrated towards the center of the plot with a few stragglers including *Leptanea richmondensis*, *Holtedohlina sulcata*, and *Platystrophia cypha*. The most positive and negative loading coefficients for PC Axis one (33.4% variance) are Distal Shape & Proximal Shape and Shape of the Dorsal Valve respectively. The most positive and negative loading coefficients for PC Axis two (18.6% variance) are Commissure Shape and Proximal Shape. Regime 3 (Carryover) accounts for most of the variation along PC Axis one and Regime 4 accounts for most of the variation along PC Axis two with a large amount of overlap where the axes meet.

CVA All Regimes (Figure 12) includes all 47 species and analyzes their morphology within the a priori groups Regimes 1-4. The initial spread shows a reasonable grouping of each regime within itself and a fair amount of overlap of all four towards the intersection of

axes one and two. Regimes 1 (Descendant of Native) and 3 (Carryover) are more diffuse whereas Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) are more tightly associated. Regime 2 (Maysvillian Restricted) falls almost entirely within the 95% confidence interval ellipse of Regime 4 (Extrabasinal Invader) with the exception of two species and Regime 1 (Descendant of Native) is entirely encompassed within the largest 95% confidence interval ellipse belonging to Regime 3 (Carryover). The most positive and negative loading coefficients for axis one are Surface Texture and Lateral Shape respectively. The most positive and negative loading coefficients for axis two are Lateral Shape and Proximal Shape respectively. The reclassification and reorganization of species between regimes moved 11 species of which six species were directly exchanged between Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader). Of the remaining five species reclassified, one was moved from Regime 1 (Descendant of Native) to Regime 2 (Maysvillian Restricted), one was moved from Regime 1 (Descendant of Native) to Regime 4 (Extrabasinal Invader), one was moved from Regime 2 (Maysvillian Restricted) to Regime 3 (Carryover), one was moved one was moved from Regime 3 (Carryover) to Regime 1 (Descendant of Native), and one was moved from Regime 3 (Carryover) to Regime 4 (Extrabasinal Invader) (Table 6). The direct exchange of a sum of 6 species between Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) is further investigated in PCA 5.0.

PCA 5.0 analyzes Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) together (26 species) (Figure 13). The initial spread shows Regime 4 (Extrabasinal Invader) clustering to the left of the Regime 2 (Maysvillian Restricted) cloud with a large amount of overlap. All of the Regime 4 (Extrabasinal Invader) species plot within the 95% confidence

interval ellipse of Regime 2 (Maysvillian Restricted). The most positive and negative loading coefficients for PC Axis one (27.5% variance) are Folds and Median Sagittal Shape of the Dorsal Valve & Median Sagittal Shape of the Ventral Valve respectively. The most positive and negative loading coefficients for PC Axis two (17.7% variance) are Commissure Shape and Middle Maximum Width & Length : Width respectively. The two confidence ellipses are perpendicular to each other with Regime 2 scattered along PC Axis one and Regime 4 (Extrabasinal Invader) scattered along Regime Axis two.

Of the total 90 possible positions in morphospace and the 47 possible positions using this dataset, 46 out of 47 species occupied their own unique position. Example of a fully coded species of each regimes are:

Regime 1 - Descendant of Native *Strophomena planumbona* = Dorsal View, 1. Proximal : Distal (3 – Distal Narrow) 2. Length : Width (1 – Wide); 3. Mid Max Width : Maximum Width (1 – Short); 4. Lateral Shape (4 – Compound 2); 5. Ventral Valve Extension (0 – Very Narrow or Absent); 6. Proximal Shape (1 – Planar); 7. Distal Shape (2 – Convex). Sagittal View, 8. Asymmetric Dorsal Valve (2 – Proximal-Distal Equal); 9. Asymmetric Ventral Valve (2 – Proximal-Distal Equal); 10. Median Sagittal Section Dorsal Valve (2 – Same); 11. Median Sagittal Section Ventral Valve (2 – Same); 12. Shape of Dorsal Valve (3 - Concave); 13. Shape of Ventral Valve (1 – Convex); 14. Beak Size Dorsal Valve (0 – Very Narrow or Absent); 15. Beak Size Ventral Valve (0 – Very Narrow or Absent). Other, 16. Commissure Shape (4 – Nested); 17. Number of Folds (0 – None); 18. Shell Texture (1 – Costae).

Regime 2 - Maysvillian Restricted *Plectorthis neglecta* = Dorsal View, 1. Proximal : Distal (2 – Equal) 2. Length : Width (1 – Wide); 3. Mid Max Width : Maximum Width (2 -

Equal); 4. Lateral Shape (1 – Narrow); 5. Ventral Valve Extension (0 – Very Narrow or Absent); 6. Proximal Shape (2 – Convex); 7. Distal Shape (2 – Convex). Sagittal View, 8. Asymmetric Dorsal Valve (2 – Proximal-Distal Equal); 9. Asymmetric Ventral Valve (4 – Distal High); 10. Median Sagittal Section Dorsal Valve (2 – Same); 11. Median Sagittal Section Ventral Valve (2 – Same); 12. Shape of Dorsal Valve (1 – Convex); 13. Shape of Ventral Valve (1 – Convex); 14. Beak Size Dorsal Valve (2 - Average); 15. Beak Size Ventral Valve (1 – Narrow). Other, 16. Commissure Shape (0 – Planar); 17. Number of Folds (0 – None); 18. Shell Texture (2 – Plications or Ridges).

Regime 3 - Carryover *Vinlandostrophia (Platystrophia) cypha* = Dorsal View, 1. Proximal : Distal (3 – Distal Narrow) 2. Length : Width (1 – Wide); 3. Mid Max Width : Maximum Width (1 – Short); 4. Lateral Shape (4 – Compound 4 ; 5. Ventral Valve Extension (0 – Very Narrow or Absent); 6. Proximal Shape (2 – Convex); 7. Distal Shape (4 – Compound). Sagittal View, 8. Asymmetric Dorsal Valve (3 – Distal High); 9. Asymmetric Ventral Valve (1 – Proximal High); 10. Median Sagittal Section Dorsal Valve (0 – High Above); 11. Median Sagittal Section Ventral Valve (0 – High Above); 12. Shape of Dorsal Valve (0 – High Convex); 13. Shape of Ventral Valve (1 – Convex); 14. Beak Size Dorsal Valve (1 – Narrow); 15. Beak Size Ventral Valve (1 – Narrow). Other, 16. Commissure Shape (3 – Highly Asymmetrical); 17. Number of Folds (2 – One); 18. Shell Texture (2 – Plication or Ridges) (Figure 7).

Regime 4 - Extrabasinal Invader *Glypthorthis insculpta* = Dorsal View, 1. Proximal : Distal (2 – Equal) 2. Length : Width (2 – Equal); 3. Mid Max Width : Maximum Width (2 – Equal); 4. Lateral Shape (1 – Convex); 5. Ventral Valve Extension (1 - Narrow); 6. Proximal Shape (2 – Convex); 7. Distal Shape (1 - Planar). Sagittal View, 8. Asymmetric Dorsal Valve

(1 – Proximal High); 9. Asymmetric Ventral Valve (1 – Proximal High); 10. Median Sagittal Section Dorsal Valve (2 – Same); 11. Median Sagittal Section Ventral Valve (2 - Same); 12. Shape of Dorsal Valve (1 - Convex); 13. Shape of Ventral Valve (1 - Convex); 14. Beak Size Dorsal Valve (0 – Very Narrow or Absent); 15. Beak Size Ventral Valve (1 – Narrow). Other, 16. Commissure Shape (1 – Single Curve); 17. Number of Folds (0 - None); 18. Shell Texture (4 - Compound).

Discussion

The applicability and viability of the Multilevel Morphology Index

Taxonomic classification and phylogenetic relationships determined from the fossil record are largely based on morphological features preserved in the hard parts of the fossil (Carlson, 2016). Therefore, the use of taxonomic classification across all brachiopods is an organized and predefined way to test the validity of the Multilevel Morphology Index without the noise of additional parameters such as environmental or ecological niche. When family is overlain onto the total dataset of 47 species from Stigall (2010) on PCA 1.1 (Table 4; Figure 8a) families group together, separated into two larger groups among the 10 families along PC Axis one. The ability of the Multilevel Morphology Index to identify this higher level of taxonomic levels using only shell shape morphology supports the viability of this approach for analyzing morphological disparity among and within a family as well as highlight the most distinguishing characters of families the separate families from each other. Genera exhibit a similar pattern and plot inside their respective families in smaller groups

regardless of regime or ecological niche tolerance and are further explored in PCAs 3.1-3.4 (Table 4; Figure 10).

A set of PCAs were run on each regimes individually (PCA 3.1-3.4; Table 4; Figure 10) to observe the variation of morphology within each strato-biogeographic regime and to test the limit of the dataset using the Multilevel Morphology Index. Plotting the regimes individually allows for the detailed analysis of 1) the distribution of character states within each regime, 2) which characters define the morphospace, 3) the common morphology of the species within these regimes. In PCA 3.1, Regime 1 (Descendant of Native) reveals moderately strong groups of the 15 species by two genera, *Strophomena* and *Vinlandostrophia* (*Platystrophia*) with some variation in how the species within each genus. The third genus in Regime 1 (Descendant of Native), *Hebertella*, is represented by a single species and plotted with *Vinlandostrophia* (*Platystrophia*). This supports the methods as viable for accounting for some aspects of intrageneric variation. Genera, while not highlighted on PCA 1.1, are also exhibiting the same groups based on genus (see clusters of species labelled 9, 10, and 11) (Table 6; Figure 8a; Figure 13d).

It is important to note although 18 variables (characters) were used in each of the individual regime analyses, none generated 18 PCA axis due to invariance of some variables among species restricted to regimes (Table 4; Figure 10). For example, PCA 3.1 (Table 4; Figure 10d) only produced 12 PC axes concluding that the presence of six invariant characters within the species of Regime 4 (Extrabasinal Invader). The goal of this new approach was met and the present level of detail accounted for in the characters and character states is more useful for generic and higher morphological analyses than for inter and intraspecific variability. The presence of invariant characters is a byproduct of the Multilevel

Morphology Index which does not account for more minute and subtle differences in morphology that often distinguish species, meaning that fewer variables are account for the morphological variation of the species present within the regime. One example are species *Strophomena concordensis* and *Strophomena planumbona* of Regime 1 (Descendant of Native) have the exact same code (3-1-1-4-0-1-2-2-2-2-3-0-0-1-4-0-1) and are the only two species to fall into the same morphospace position of the 90 possible (Figure 8; Figure 10d; Figure 11a; Figure 12). Any variation in visual plotting of species *Strophomena concordensis* and *Strophomena planumbona* are not due to morphological differences, but manual differentiation to distinguish two different datapoints that share the same position in morphospace. If inter and intraspecific variability is to be further explored, ways to expand the Multilevel Morphology Index are outlined in the methods section of this paper. It is also useful to refer to the traditional morphological terms organized within each character state to further investigate the variation within the individual regimes beyond the coding system and PCA analyses such as different expressions of Surface Texture within the character state Costae (ribs, striae, multicostellate, parvicostellate, costellation) (Appendix 1).

Morphological analyses of all four regimes (47 species)

PC axis one of PCA 1.1 and 1.2 separates groups based on proximal and distal shape for positive values and dorsal and ventral median sagittal shape and the shape of the dorsal valve in the negative values (Table 4; .Figure 8a-b). These characters, alongside the characters that weigh heavily on PC axis two, commissure shape, lateral shape, and mid-max width, are important in defining the valve outline and the relative relationship of the dorsal and ventral valve. Fursich and Hurst (1974) explored how the ecological implications and

functions of these features and defined the order Strophomenida, which contains the family Strophomenidae, as preferring intermediate environmental conditions with quiet water and soft sediment, but can be found in turbulent environments and the order Orthida (Playtystrophidae and Plectorithidae) as preferring intermediate to turbulent conditions. The familial groups in PCA 1.1 (Table 4; Figure 8a) may indicate key morphological features, such as alae (lateral wing-like extensions of the proximal end of the dorsal and brachial valve), degree of fold/sulcus (depth and height of the deflection along the anterior portion of the valves), and nesting (one concave valve sits inside the opposite convex valve) which are important functional features in filter feeding efficiency and position relative to the substrate (Fursich and Hurst, 1974; Shiino and Kuwazuru, 2010; Tyler and Leighton, 2011) (Appendix 1). The loading coefficient value for surface texture for every species across all four regimes in PCA 1.1 is the closest of the characters to 0, making surface texture the least variable character of the first two components. Another look at the dataset reveals that all species in this study displayed some sort of surface texture ranging from costae to compound (combination of two or more surface textures) (Appendix 1-2). For PC Axes 3 and 4 of all four regimes and 47 species (Table 4; Figure 8c-d) PCA 1.3 and 1.4 do not display taxonomic or strato-biogeographic regime -based groups. Rather, the third and fourth axes represent characters that differentiate species within genera.

The presence of raised surface texture and/or plicated commissures in all species of Cincinnati-type fauna included in this study suggest a common morphological character that may be reflective of environment. Patzkowsky and Holland (2007) note that most of the brachiopod taxa that occur in C1-C6 horizons (Figures 1-2) occur in the C2-C5 shallow subtidal and deep subtidal zones. Radial variations in surface texture, coded as “Costae” or

“Plications or Ridges” in the Multilevel Morphology Index are found in modern brachiopods that have setae, a soft body feature sensitive to sediment and allow the organisms to snap shut to prevent the intake of sediment while filter feeding which is necessary in turbulent shallow subtidal zones of the continental shelf that fall in the fair weather wavebase as well as deep subtidal zones which are often subject to storm weather waves in order to prevent physical blockage of filter feeding mechanisms and desiccation (Fursich and Hurst, 1975; Rudwick, 1970).

Descendant of Native species niche differentiation

Regime 1 (Descendant of Native) species account for majority of the variation in the entire dataset (Table 4; Figure 8b) and is the most morphologically variable of the four regimes, establishing the morphological limits of three out of four axes on PCA 1.2 (Table 4; Figure 8b) and PCA 4.1 (Table 4; Figure 11a), while also being the least taxonomically diverse, composed of only three genera and two families. This high amount of morphological variability across three genera and within an ecological specialist regime is unusual. Species of Regime 1 (Descendant of Native) also plot far from the other members of the three regimes in PCA 2.0 (Table 4; Figure 9) which reflects the majority of Regime 1 (Descendant of Native) species as morphologically dissimilar from the remaining three regimes. The stress and pressure of significant changes in ecological, environmental, and geologic conditions during the Richmondian Invasion caused specialist native taxa to alter their niche parameters during invasions due to a decline in niche stability following the invasion (Malizia and Stigall, 2011). The variable morphology of brachiopod specialists that evolved from native taxa (Regime 1; Descendant of Native) across the Richmondian Invasion is

likely reflective of multiple morphotypes within a regime that fit into the newly altered niche parameters (e.g. strain of competition with new invaders and generalist carryover species). The vast difference in morphology of nearly half of all Regime 1 (Descendant of Native) species supports these taxa as inhabiting different environmental conditions or serving different ecological functions than the species of the remaining three regimes (Maysvillian Restricted, Carryover, and Extrabasinal Invaders). The half of species within Regime 1 (Descendant of Native) that overlap with Regimes 2-4 (Maysvillian Restricted, Carryover, Extrabasinal Invader) (Table 4; Figure 8b) are more morphologically similar and therefore occupy a more similar, but not identical, niche as do the majority of the total 34 species in the other three regimes.

Niche occupation of Maysvillian Restricted and Extrabasinal Invaders

Regime 2 (Maysvillian Restricted) is composed specialist endemic species, as defined by paleobiogeographic range in Stigall (2010), which did not persist across the Maysvillian – Richmondian boundary (Bauer and Stigall, 2014; Stigall, 2010). Regime 4 (Extrabasinal Invader) is composed of quite the opposite type of species: generalist, invasive migrating species from marginal and intracratonic basins including the peripheral basins, palaeoequator region north of the Transcontinental Arch, and from the midcontinent (Bauer and Stigall, 2014; Stigall, 2010).

The nested relationship of Regime 4 (Extrabasinal Invaders) within Regime 2 (Maysvillian Restricted) in PCA 1.2 (Table 4; Figure 8b) and the near identical positions of the modal values of Regimes 4 (Extrabasinal Invader) and 2 (Maysvillian Restricted) along

PC Axis one and two in PCA 2.0 (Table 4; Figure 9) independently display the highest level of similarity in morphology between Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) than of all the other possible combinations of regimes. A CVA was conducted to observe how all four regimes would interact in a space that organizes species to decrease the morphological disparity within the regime and increase the morphological disparity between regimes. The post-hoc groups showed the highest mutually reassignment took place between Regime 2 (Maysvillian Restricted) and Regime 4 (Extrabasinal Invader) out of all four regimes (CVA All Regimes; Tables 4, 6; Figure 12). This output is consistent with the building evidence of highly similar external morphology between the regimes.

An additional PCA was conducted on only Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) species (PCA 5.0; Table 4; Figure 13) to determine the specific morphological characters that were shared between the regimes. In PCA 5.0 (Table 4; Figure 13), PC Axis one displays the morphological variability of mostly Regime 2 (Maysvillian Restricted) species which is dominated by characters that are associated with fold and sulcus height. Along PC Axis two, the distribution of both Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) are nearly the same and since PC Axis one accounted for the main morphological differences within Regime 2 (Maysvillian Restricted) and not between Regimes 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader), it can be assumed Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) are well mixed along PC Axis two and therefore PC Axis two is a more representative sample of the actual variability between the Regime 2 (Maysvillian Restricted) and Regime 4 (Extrabasinal Invader). Along PC Axis two of PCA 5.0 (Table 4; Figure 13) plot characters Commissure Shape, Middle Maximum

Width, and Length: Width which are all indicators of shape outline and relationship to substrate.

The full 18 character codes of the modes of Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) in PCA 2.0 of modal regime values (Table 4; Figure 9) only differ on four characters (Ventral Valve Extension, Proximal Shape, Beak Size Ventral Valve, and Folds) by no more than a single character state categorical value, none of which are the variables with the highest loading coefficients in PCA 5.0 (Table 4; Figure 13) where both Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) are plotted together, meaning that these dissimilarities in the mode of each regime are not contributing meaningfully in terms of variability in the total dataset. Since the code of the modal values of the two regimes are only different on characters that do not contribute to variation in the dataset with all Regime 2 (Maysvillian Restricted) and Regime 4 (Extrabasinal Invader), it suggests that the majority of species within their respective regimes do not differ much from each other and the minority of species are contributing to the variation displayed on both of the PC Axes in PCA 5.0 (Table 4; Figure 13). In the individual analyses of each regime, PCA 3.4 (Regime 4 – Extrabasinal Invader) (Table 4; Figure 10a) and PCA 3.2 (Regime 2 – Maysvillian Restricted) (Table 4; Figure 10b) shares Commissure Shape as one of the four characters that account for the most variability in their respective datasets. A single feature that contributes to the variability in three separate analyses confirms that the morphological variability is similar within each PCA, further confirming that the majority of morphological character in the individual regimes are similar to each other.

Assuming external morphology serves a function that is related to the individual's ecological role and behavioral capacity, the similarity between Regimes 2 (Maysvillian

Restricted) and 4 (Extrabasinal Invader) species reflect a shared ecological functional relationship within the Cincinnati Arch prior to (C1-C3; Regime 2 – Maysvillian Restricted) and following (C4-C6; Regime 4 – Extrabasinal Invader) the Richmondian Invasion (Wainwright, 1994). Studies conducted on a portion the same native and invasive species from the Cincinnati Arch during the Richmondian Invasion determined that most native taxa, belonging to Regime 2 (Maysvillian Restricted), became locally extinct in C2 (Figure 2) and the invasive taxa, belonging to Regime 4 (Extrabasinal Invader), did not appear until C4 and did not persist with much success until C5, following a secondary invasive event (Patzkowsky and Holland, 2007).

The amount of similarity in the morphology of Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader) species is substantial, which suggests that the ecological function of Regime 2 (Maysvillian Restricted) taxa was likely fulfilled by Regime 4 (Extrabasinal Invader) species. The morphology is so similar between Regime 2 (Maysvillian Restricted) and Regime 4 (Extrabasinal Invader) that it is not likely that competitive exclusion of native Maysvillian taxa, but rather an open niche was fulfilled through the slow migration of invasive species into the Cincinnati Arch during the C4 and C5 sequences. This gap in time between native Regime 2 (Maysvillian Restricted) and invasive Regime 4 (Extrabasinal Invader) species coupled with the similarity in paleobiogeographic range between native and invader taxa further support invasive species as not directly competing with native taxa (Patzkowsky and Holland, 2007; Stigall, 2010).

Unusual morphology of Sowerbyella rugosa within Maysvillian Restricted

Sowerbyella rugosa, a Regime 2 (Maysvillian Restricted) species that appears for a brief period in during the Edenian C1 sequence, is the only species to plot outside of their respective 95% confidence interval ellipse of its regime. This occurs in PCA 1.2 (Table 4; Figure 8b) and PCA 4.1 (Table 4; Figure 11a), but not in PCA 5.0 (Table 4; Figure 13) or CVA All Regimes (Table 4; Figure 12) where *S. rugosa* plots within both the 95% confidence interval of both Regime 4 (Extrabasinal Invader) and 2 (Maysvillian Restricted). Additionally, *S. rugosa* was also reclassified from Regime 2 (Maysvillian Restricted) to Regime 4 (Extrabasinal Invader) as seen in Table 6. With the exception of uncoded species *Leptaena gibbosa*, *S. rugosa* is the only species in the entire dataset restricted to C1. One possible explanation for the similarity between this C1 Maysvillian restricted species and the invasive species from C3-C6 is the change in environment prior to the Maysvillian. Prior to C1 was the M6 sequence belonging to Mowhawkian (Figure 2) (Holland and Patzkowsky, 1996; Patzkowsky and Holland, 1996; Patzkowsky and Holland, 2007). The transition from M6 to C1 is marked by a shift from tropical to temperate lithology (Holland and Patzkowsky, 1996; Patzkowsky and Holland 1996). Patzkowsky and Holland (1996) noted that carbonate build-ups, known to occur more in more tropical settings, are uncommon above the M5 boundary but reappear in the late Cincinnati around C4; the same time as invasive species of a similar morphology to *S. rugosa* migrate into the Cincinnati Arch. It has been documented that many of the many of the M3-M6 extirpated species reappeared in the Cincinnati Arch following the Richmondian Invasion, including *Rhynchotrema* of Regime 4 (Extrabasinal Invader) which abundant in the region during the Richmondian and was also present prior to the Edenian (Patzkowsky and Holland, 1997). Additionally, the timing of the extirpation of endemic species occurred from the upper M4 to C1 (Patzkowsky and Holland,

1998). It is possible that *S. rugosa*, only present during C1 and sharing many of the same morphological features as Regime 4 (Extrabasinal Invader) invasive species, was one of the last of the endemic tropical species to go extinct and did not reappear in Regime 4 (Extrabasinal Invader) with the rest of the tropical-adapted species present in the Richmondian. More research on the occurrence and abundance data needs to be done to make any further conclusions.

Generalists Carryover and Extrabasinal Invaders

The two generalist regimes, native Regime 3 (Carryover) and invasive Regime 4 (Extrabasinal Invader) provide an opportunity to directly observe morphospace occupation of invasion and native taxa during the same time in the same space. Assuming Regime 3 (Carryover) species are morphologically identical in the Maysvillian and Richmondian (Stigall, 2010) and Regime 4 (Extrabasinal Invader) both has highly similar morphology and occupies the same ecological niche as Regime 2 (Maysvillian Restricted) did prior to the Richmondian Invasion, interpretations of the morphology of Regimes 3 (Carryover) and 4 (Extrabasinal Invader) can be directly compared to observe differentiation in morphology with niche partitioning. Confirmation that niche partitioning is exhibited between Regime 3 (Carryover) and Regime 4 (Extrabasinal Invader) species based on functional morphological characters through time are outlined in Tyler and Leighton (2011).

Members of Regime 3 (Carryover), like Regime 4 (Extrabasinal Invaders), are ecological generalist species, meaning that carryover species would have been more tolerant of the shift from temperate to tropical conditions and would have occupied a similar, but not

the same, ecological niche across the Maysvillian – Richmondian boundary. Studies of invasive and native generalists species have supported a pattern of niche stability of invasive taxa equal to native generalists before, during, and after the Richmondian Invasion (Malazia and Stigall, 2010). Regime 3 (Carryover) and Regime 4 (Extrabasinal Invaders) are plotted together in PCA 4.2 (Table 4; Figure 11b) and the general distribution of the members of the two regimes are perpendicular with a moderate amount of overlap around the center of the two axes (Table 4; Figure 11b). Continuing the thought that morphology reflects ecological occupation, the perpendicular relationship between Regime 4 (Extrabasinal Invader)), which now occupies a similar niche Regime 2 (Maysvillian Restricted) once did, and Regime 3 (Carryover) which has been present throughout, reflects morphological differences that are adapted to occupy a different niche than Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invader).

In PCA 2.0 (Table 4; Figure 9) the modal morphology of Regime 3 (Carryover) plots higher on PC Axis 2 than Regime 2 (Maysvillian Restricted) and 4 (Extrabasinal Invaders), differentiated mainly by lateral shape. Within PCA 3.3 on Regime 3 (Carryover) species only (Table 4; Figure 10c), lateral shape is included in the first four characters that contribute to variability within the regime. It is important that the morphological features, which are presumed to have functional characteristics that are variable in generalist regimes, because it reflects the taxa's ability to adjust to changing environment. Characters including Commissure Shape (PCA 4.2 and 3.4; Table 4; Figure 11), Median Sagittal Shape of the Dorsal Valve, Median Sagittal Shape of the Ventral Valve low on PC Axis one (PCA 3.3; Table 4; Figure 10c), and Folds (PCA 3.4; Table 4; Figure 11a) all have an influence on the

efficiency and competition for food particulates during filter feeding (Fursich and Hurst, 1975; Tyler and Leighton, 2011).

Conclusions

This study establishes a new approach for simplifying current brachiopod morphological terms for clearer and more accessible communication with quantitative applications that are comparable and prove useful in determining morphological patterns at generic and familial level. The application of this new approach onto Cincinnati-type brachiopods support the methods as applicable and useful for determining differences and similarities between and within different levels of niche tolerance as well as identifying variable functional morphological features alongside changing ecological and environmental parameters. The most significant result of this study is the notable morphological similarity between specialist locally extinct species and the invasive generalist species that later fill in the open niche. Studies of brachiopod niche differentiation on the same set of species is also further supported through the morphological disparities between the generalist carryover and invasive species which suggests niche differentiation of native and invasive generalist species. The morphological disparity exhibited in the species that descended from Maysvillian fauna exhibit the highest variability in morphological characters which is representative of specialist species attempting to fill in similar niches to those in Maysvillian during the Richmondian which increases the species habitat tracking and forces them to rapidly adapt to the changing ecological parameters. Additionally, the morphology of *Sowerbyella rugosa*, a Maysvillian Restricted species, placed *S. rugosa* consistently within

the invasive regime which has implications for delayed extirpation from earlier sequences during the Mohawkian where many of the invasive species from C3-C6 were once locally extant. Further studies using these methods are required to fully test the limits and ability of the methods as a comparable, concise, and simplified methodology for analyzing external brachiopod morphology in rhynchonelliform brachiopods. The potential applications for these methods are immense and include studying the morphological aspects of ontogeny, paleobiogeographic distribution, niche tolerance, intrageneric variation, phylogenetics, and functional morphology.

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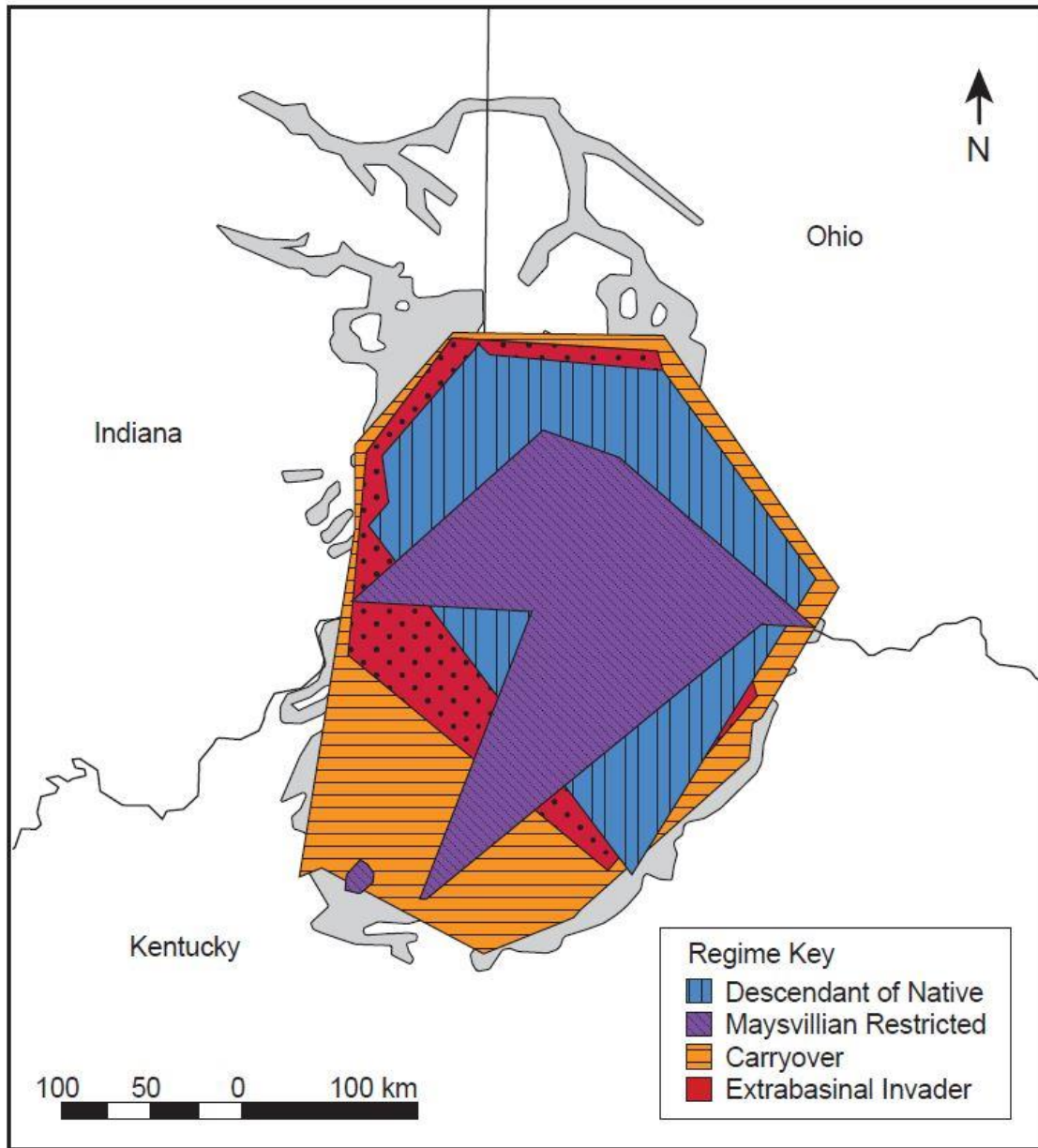


Figure 1. Generalized paleobiogeographic range reconstructions of representative brachiopod fauna in the Cincinnati region prior to and following the Richmondian Invasion. Modified from Stigall (2010).

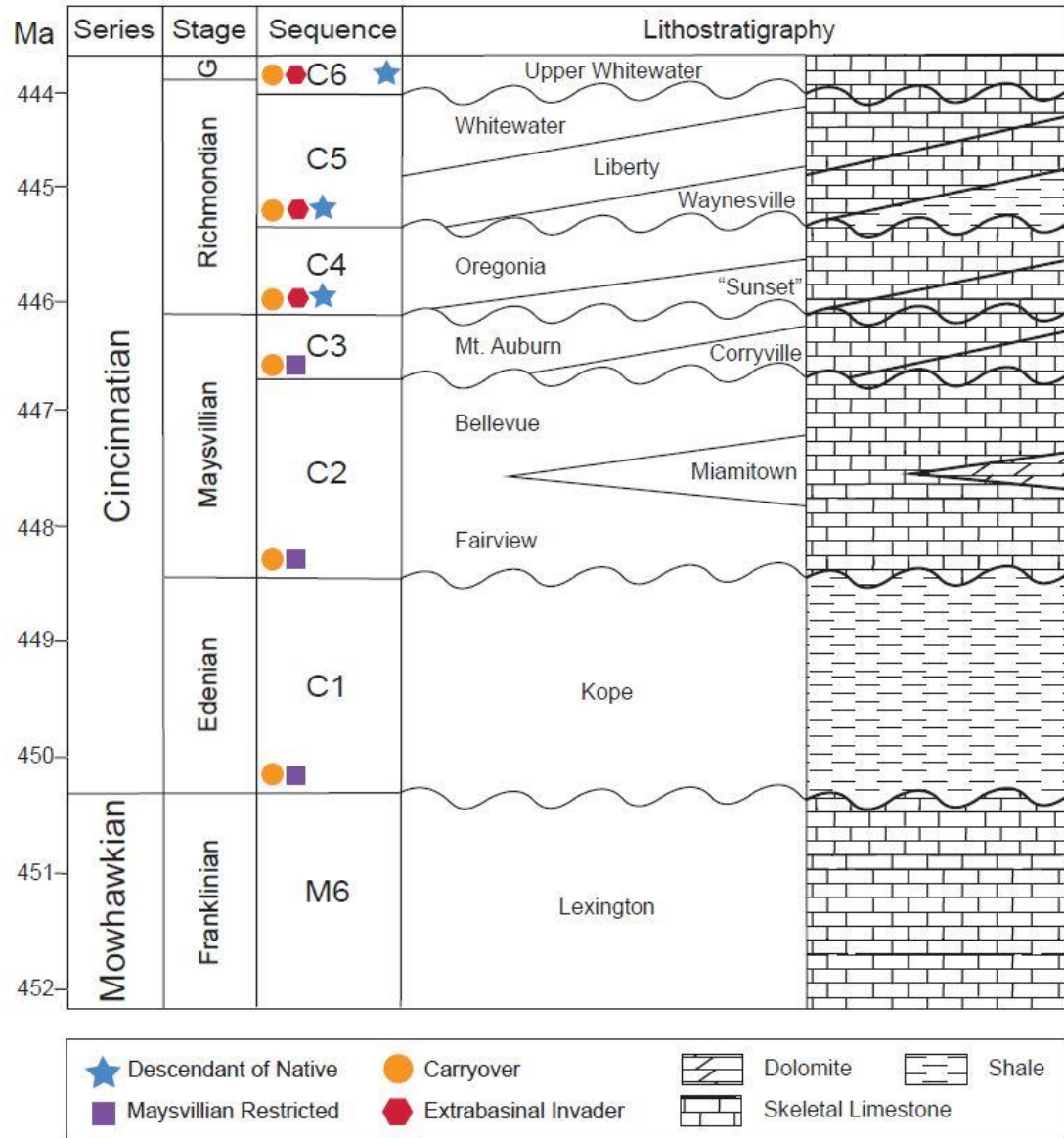


Figure 2. Stratigraphic column of Cincinnatian sequences C1-C6. Modified from Stigall (2010), Patzkowsky and Holland (1996) and Holland and Patzkowsky (1996).

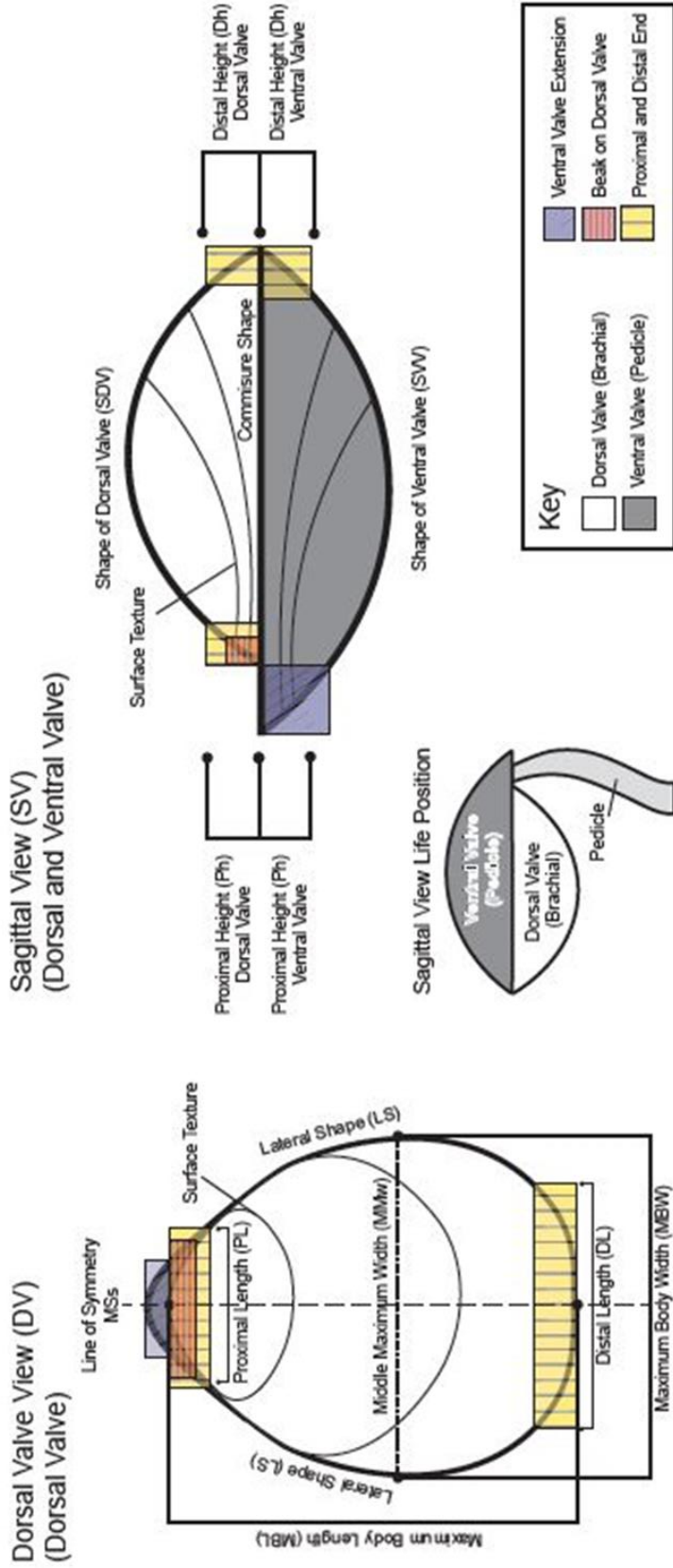
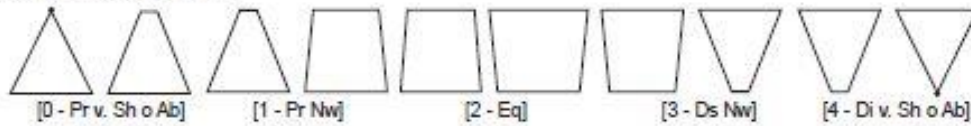


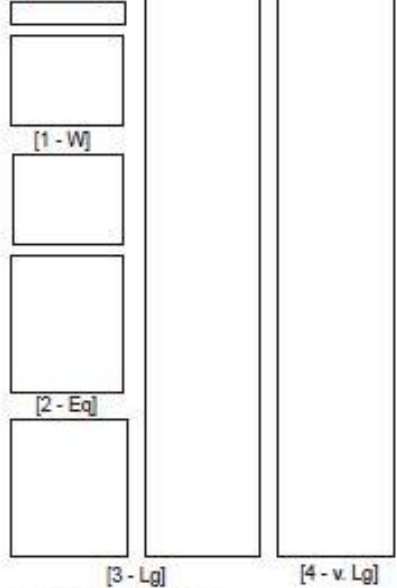
Figure 3. Brachiopod morphology with new features labels used in the new approach with correct orientation for photographs and analysis.

Dorsal View (DV)

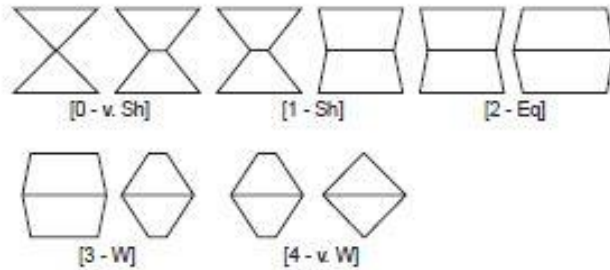
1. P : D, Proximal : Distal



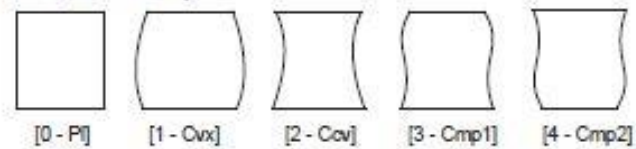
2. L : W, Length : Width



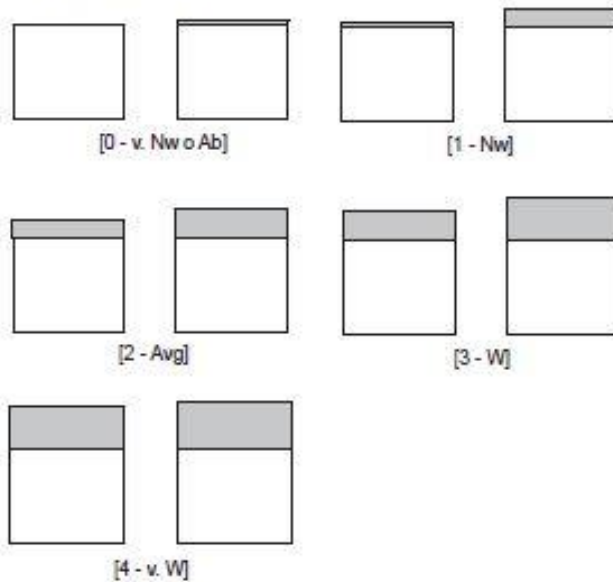
3. M : Mw, Mid Max Width



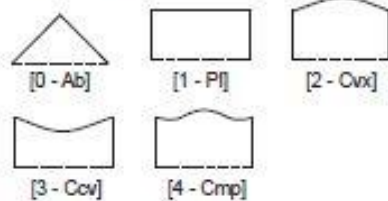
4. LS, Lateral Shape



5. VVe, Ventral Valve Extension



6. PS, Proximal Shape



7. DS, Distal Shape

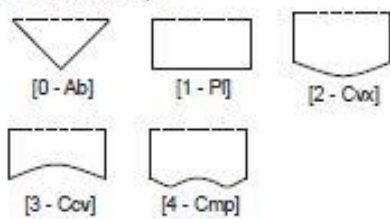
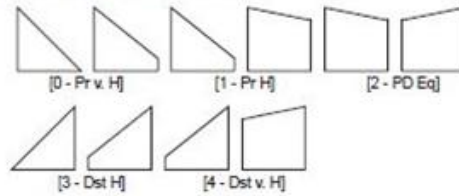


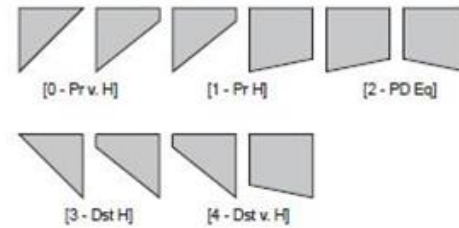
Figure 4. Visualization of characters each with all five character states bounded by end member character pairs. Dorsal View characters, 1-7. Dorsal valve: white. Ventral valve: gray. See Appendix 1 for full descriptions.

Sagittal View (SV)

8. AsDV, Asymmetric Dorsal Valve

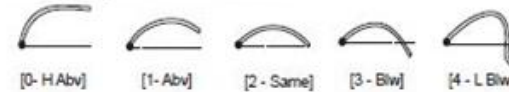


9. AsDV, Asymmetric Ventral Valve



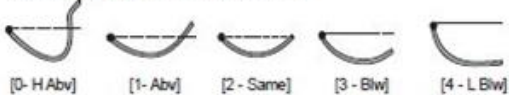
10. MSsDV

Median Sagittal Section Dorsal View

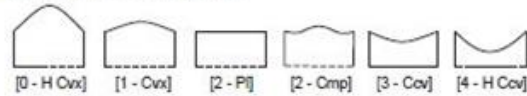


11. MSsVV

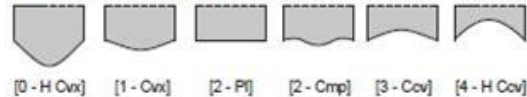
Median Sagittal Section Ventral View



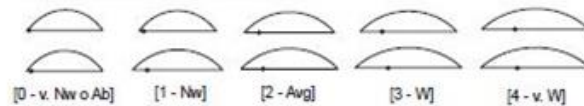
12. SDV, Shape of Dorsal Valve



13. SVV, Shape of Ventral Valve



14. BSDV, Beak Size Dorsal Valve



15. BSVV, Beak Size Ventral Valve

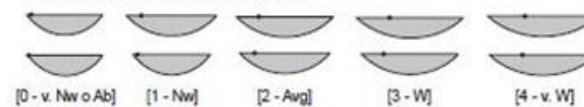


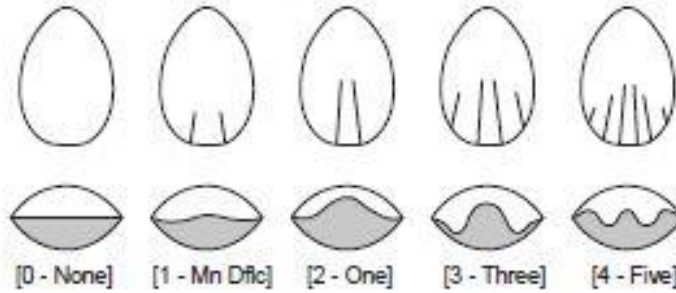
Figure 5. Visualization of characters each with all five character states bounded by end member character pairs. Sagittal View characters, 8-15. Dorsal valve: white. Ventral valve: gray. See Appendix 1 for full descriptions.

Other (0)

16. CommS, Commisure Shape



17. Folds, Number of Folds



18. STxt, Surface Texture

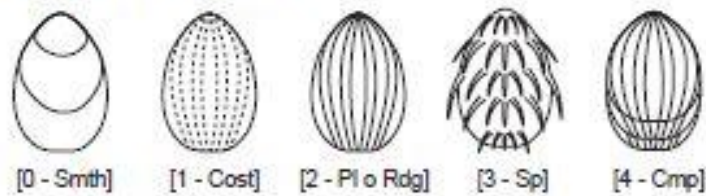


Figure 6. Visualization of characters each with all five character states bounded by end member character pairs. Other characters, 16-18. Dorsal valve: white. Ventral valve: gray. See Appendix 1 for full descriptions.

Vinlandostrophia (Platystrophia) cypha

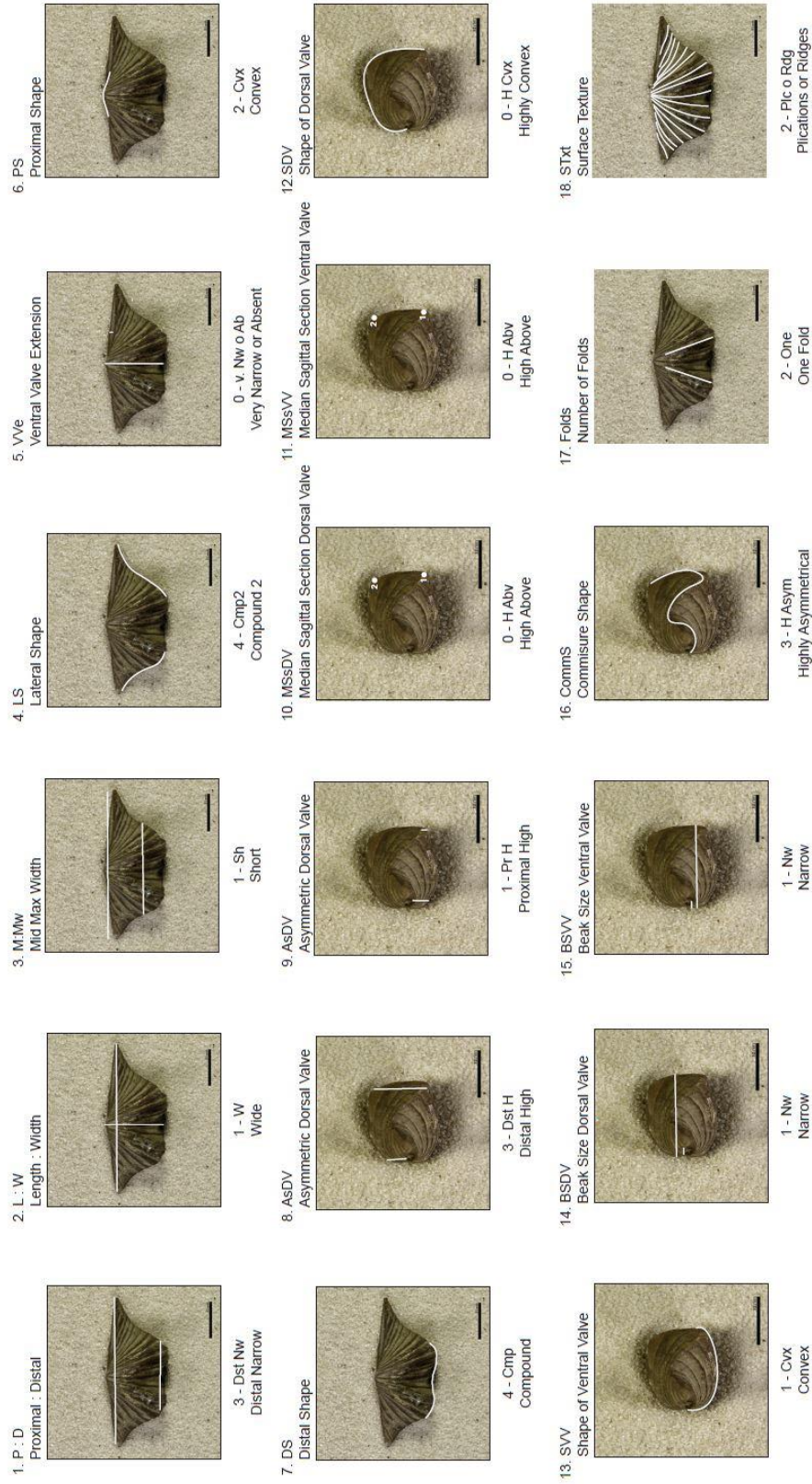


Figure 7. Visualization of Carryover species *Platystrophia cypha* with all 18 characters overlain with appropriate character states written below each image. Fully coded *V. cypha*: 3-1-1-4-0-2-4-3-1-0-0-1-1-1-3-2-2. Refer to Appendix 1 and 2 for elaboration on characters and character states.

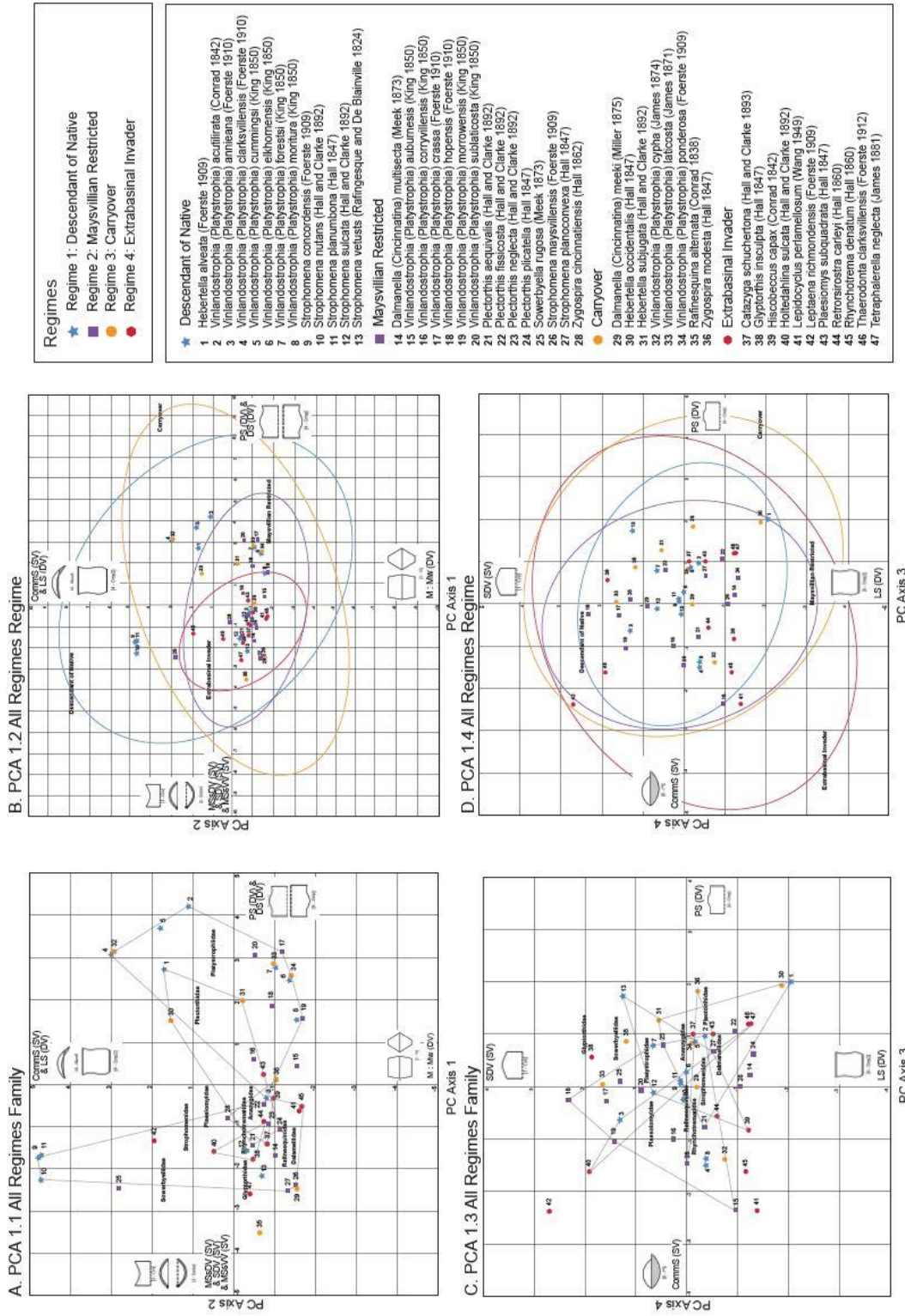


Figure 8. A. PCA 1.1, principal component analysis of component axes one and two of all four regimes. B. PCA 1.2, principal component analysis of component axes one and two of all four regimes with 95% confidence interval ellipses. 53.2% variance. C. PCA 1.3, principal component analysis of component axes three and four of all four regimes. D. PCA 1.4, component axes three and four of all four regimes with 95% confidence interval ellipses. 17.6% variance.

PCA 2.0 Modal Values of All Regimes

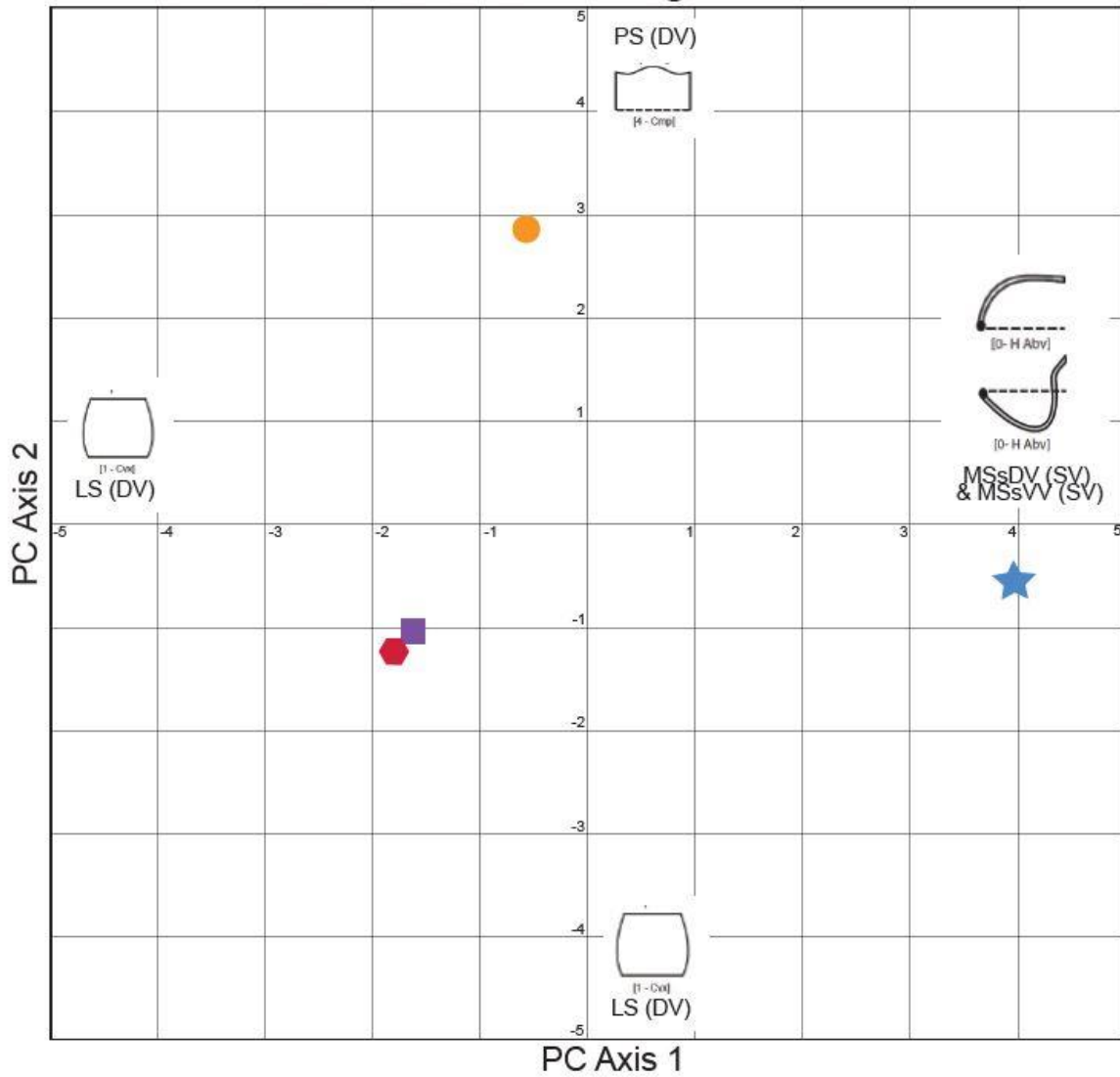


Figure 9. PCA 2.0, Principal component analysis of components one and two for the modal values of Descendant of Native, Maysvillian Restricted, Carryover and Extrabasinal Invader species.

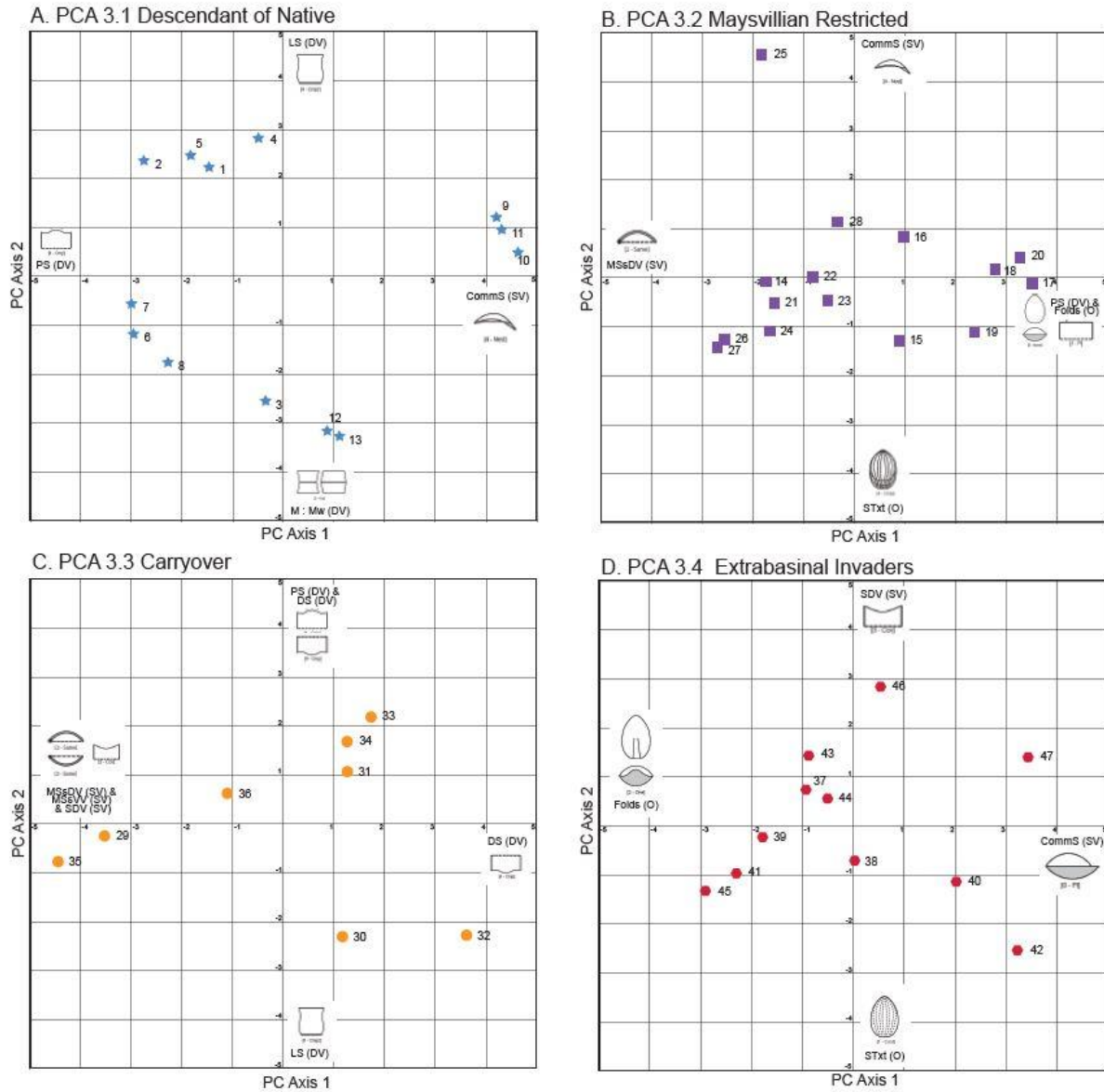


Figure 10. Four separate PCA analyses by regime. A. PCA 3.1, principal component analysis of components one and two of Descendant of Native fauna. 75.5% variance. B. PCA 3.2, principal component analysis of components one and two of Maysvillian Restricted fauna. 57.3% variance. C. PCA 3.3, principal component analysis of components one and two of Carryover fauna. 75.1% variance. D. PCA 3.4, principal component analysis of components one and two of Extrabasinal Invader fauna. 59.6% variance.

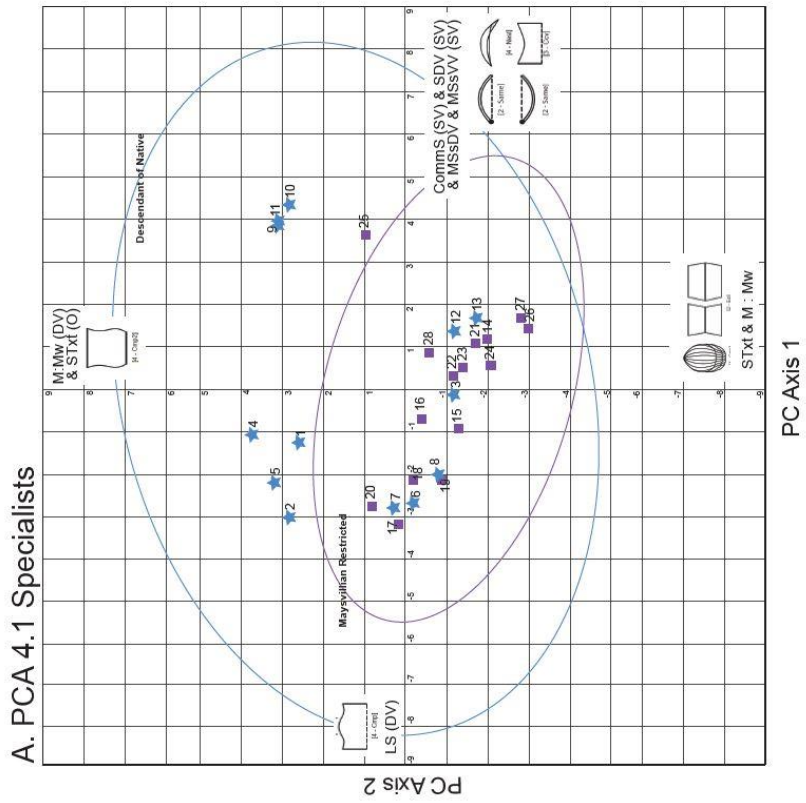
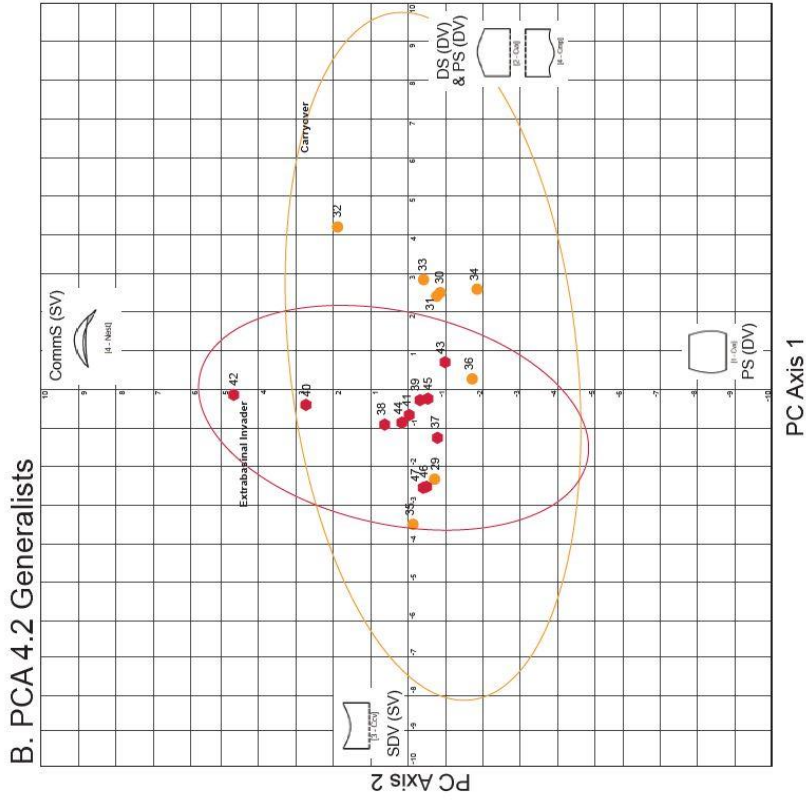


Figure 11. A. PCA 4.1, principal component analysis of components one and two of the two specialist regimes: Descendant of Native and Maysvillian Restricted. 60.1% variance. B. PCA 4.2, principal component analysis of components one and two of the two generalist regimes: Carryover and Extrabasal Invaders. 52.1% variance.

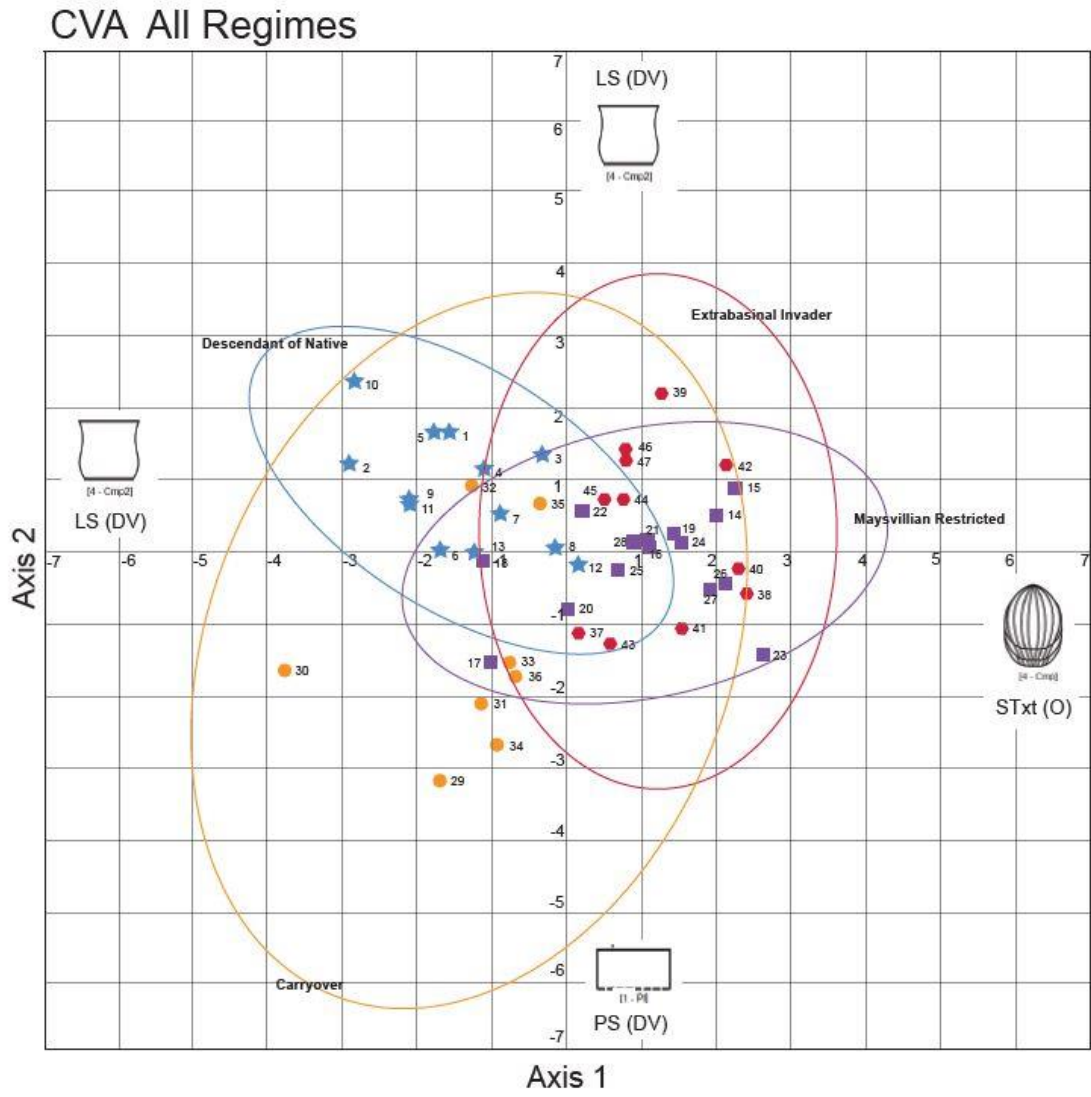


Figure 12. CVA All Regimes, canonical variance analysis of axes one and two of all four regimes.

PCA 5.0 Maysvillian Restricted and Extrabasinal Invaders

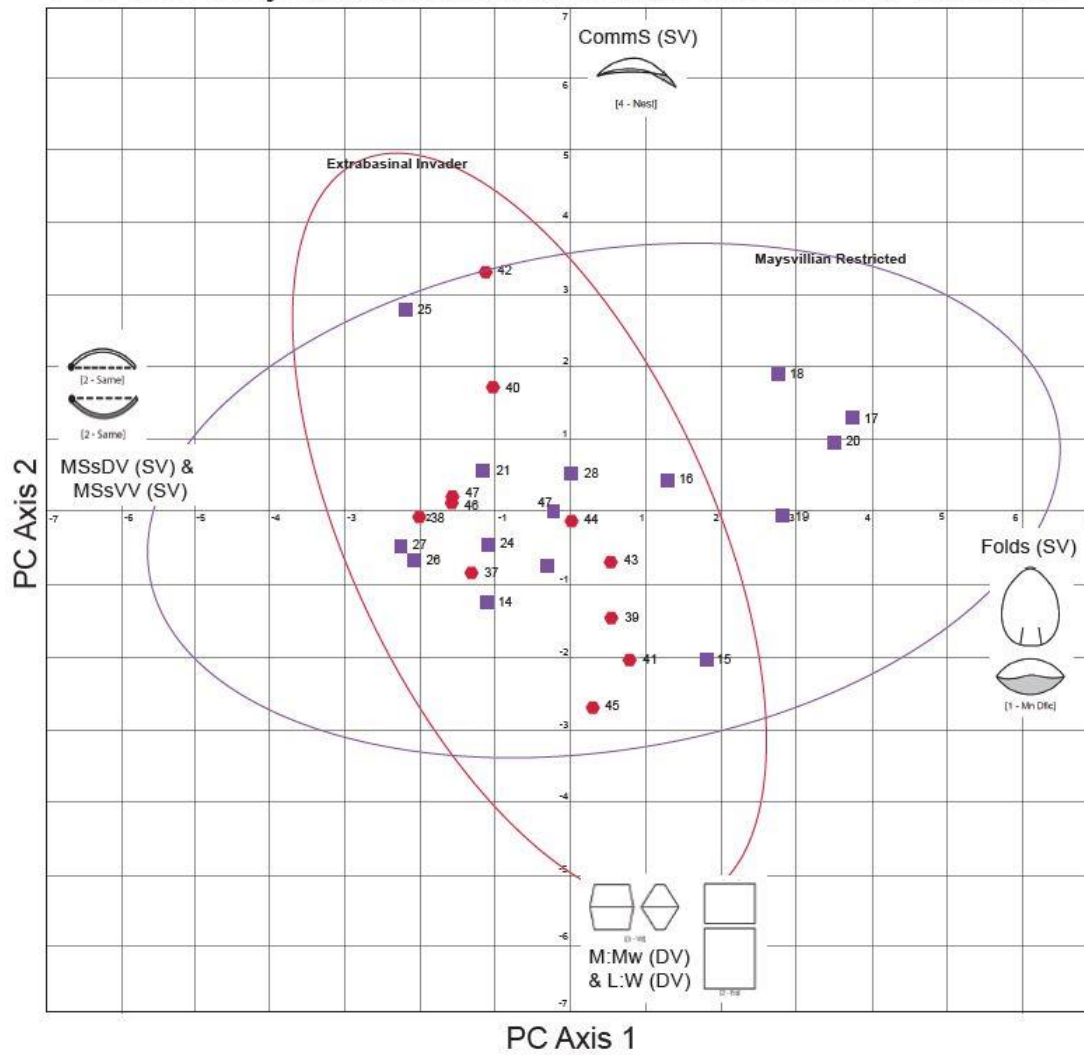


Figure 13. PCA 5.0, principal component analysis of components one and two of the Maysvillian Restricted and Extrabasinal Invader regimes. 45.2% variance.

Table 1. Presence - absence data of brachiopod taxa in the Cincinnati Region across depositional sequences C1-C6 (Stigall, 2010).

Species	C1	C2	C3	C4	C5	C6	Invasion Regime
<i>Hebertella alveata</i> (Foerste 1909)	0	0	0	0	1	1	Descendant of native
<i>Vinlandostrophia (Platystrophia) acutilirata</i> (Conrad 1842)	0	0	0	0	1	1	Descendant of native
<i>Vinlandostrophia (Platystrophia) annieana</i> (Foerste 1910)	0	0	0	0	1	0	Descendant of native
<i>Vinlandostrophia (Platystrophia) clarksvillensis</i> (Foerste 1910)	0	0	0	1	1	1	Descendant of native
<i>Vinlandostrophia (Platystrophia) cummingsi</i> (King 1850)	0	0	0	0	1	0	Descendant of native
<i>Vinlandostrophia (Platystrophia) elkhornensis</i> (King 1850)	0	0	0	0	1	1	Descendant of native
<i>Vinlandostrophia (Platystrophia) forestsii</i> (King 1850)	0	0	0	0	1	0	Descendant of native
<i>Vinlandostrophia (Platystrophia) moritura</i> (King 1850)	0	0	0	0	1	1	Descendant of native
<i>Strophomena concordensis</i> (Foerste 1909)	0	0	0	1	1	0	Descendant of native
<i>Strophomena nutans</i> (Hall and Clarke 1892)	0	0	0	0	1	0	Descendant of native
<i>Strophomena planumbona</i> (Hall 1847)	0	0	0	1	1	1	Descendant of native
<i>Strophomena sulcata</i> (Hall and Clarke 1892)	0	0	0	0	1	1	Descendant of native
<i>Strophomena vetustus</i> (Rafinesque and De Blainville 1824)	0	0	0	0	1	1	Descendant of native
<i>Dalmanella (Cincinnatiina) multisepta</i> (Meek 1873)	1	1	0	0	0	0	Maryvillian restricted
<i>Leptaena gibbosa</i> (James 1874)	1	0	0	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) auburnensis</i> (King 1850)	0	0	1	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) corryvillensis</i> (King 1850)	0	0	1	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) crassa</i> (Foerste 1910)	0	1	1	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) hopensis</i> (Foerste 1910)	1	1	1	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) morrowensis</i> (King 1850)	0	0	1	0	0	0	Maryvillian restricted
<i>Vinlandostrophia (Platystrophia) sublaticosta</i> (King 1850)	0	1	1	0	0	0	Maryvillian restricted
<i>Plectorthis aequivalis</i> (Hall and Clarke 1892)	0	1	1	0	0	0	Maryvillian restricted
<i>Plectorthis fissicosta</i> (Hall and Clarke 1892)	0	1	0	0	0	0	Maryvillian restricted
<i>Plectorthis neglecta</i> (Hall and Clarke 1892)	0	1	0	0	0	0	Maryvillian restricted
<i>Plectorthis plicatella</i> (Hall 1847)	0	1	0	0	0	0	Maryvillian restricted
<i>Sowerbyella rugosa</i> (Meek 1873)	1	0	0	0	0	0	Maryvillian restricted
<i>Strophomena maysvillensis</i> (Foerste 1909)	1	1	0	0	0	0	Maryvillian restricted
<i>Strophomena planoconvexa</i> (Hall 1847)	1	1	0	0	0	0	Maryvillian restricted
<i>Zygospira cincinnatiensis</i> (Hall 1862)	1	1	0	0	0	0	Maryvillian restricted
<i>Dalmanella (Cincinnatiina) meeki</i> (Miller 1875)	0	0	1	1	1	1	Carryover
<i>Hebertella occidentalis</i> (Hall 1847)	1	1	1	1	1	1	Carryover
<i>Hebertella subjugata</i> (Hall and Clarke 1892)	0	1	0	0	1	1	Carryover
<i>Vinlandostrophia (Platystrophia) cypha</i> (James 1874)	0	1	1	1	1	1	Carryover
<i>Vinlandostrophia (Platystrophia) laticosta</i> (James 1871)	0	1	1	1	1	0	Carryover
<i>Vinlandostrophia (Platystrophia) ponderosa</i> (Foerste 1909)	1	1	1	1	0	0	Carryover
<i>Rafinesquina alternata</i> (Conrad 1838)	1	1	1	1	1	1	Carryover
<i>Zygospira modesta</i> (Hall 1847)	1	1	1	1	1	1	Carryover
<i>Austinella scovellei</i> (Foerste 1909)	0	0	0	0	1	0	Invader
<i>Catazyga schuchertona</i> (Hall and Clarke 1893)	0	0	0	0	1	0	Invader
<i>Thaerodonta clarksvillensis</i> (Foerste 1912)	0	0	0	0	1	1	Invader
<i>Glyptorthis insculpta</i> (Hall 1847)	0	0	0	0	1	1	Invader
<i>Hiscobeccus capax</i> (Conrad 1842)	0	0	0	0	1	1	Invader
<i>Holtedahliina sulcata</i> (Hall and Clarke 1892)	0	0	0	0	1	1	Invader
<i>Lepidocyclus perlamellosum</i> (Wang 1949)	0	0	0	0	1	0	Invader
<i>Leptaena richmondensis</i> (Foerste 1909)	0	0	0	1	1	1	Invader
<i>Plaesiomys subquadrata</i> (Hall 1847)	0	0	0	0	1	1	Invader
<i>Retrorsirostra carleyi</i> (Hall 1860)	0	0	0	1	1	0	Invader
<i>Rhynchotrema denatum</i> (Hall 1860)	0	0	0	1	1	1	Invader
<i>Tetraphalerella neglecta</i> (James 1881)	0	0	0	0	1	0	Invader

Table 2. Full character and character state descriptions of all 18 characters alongside traditional morphological terms from the Treatise of Invertebrate Paleontology (Williams and Rowell, 1965).

N	Character Descriptors	Abbreviation	Orientation	Traditional Morphological Terms	Definitions of New Terms
1	Proximal : Distal	P:D	Dorsal (DV)	Size	Ratio of Proximal Length to Distal Length
2	Length : Width	L:W	Dorsal (DV)	Size	Ratio of Maximum Body Width to Maximum Body Length
3	Mid Max Width : Maximum Width	M:MW	Dorsal (DV)	Brachiopod Outline	Ratio of Maximum Width of the middle portion of the Dorsal Valve to Proximal or Distal Length (depending on which is wider)
4	Lateral Shape	LS	Dorsal (DV)	Lateral Margin - Brachiopod Outline	Shape of lateral edges of the dorsal valve parallel to the line of symmetry relative to a straight line
5	Ventral Valve Extension	Vve	Dorsal (DV)	Ventral Interearea or Ventral Palintrope seen above Dorsal Valve	Maximum Ventral Valve Extension as seen from dorsal view compared to the Maximum Body Length
6	Proximal Shape	PS	Dorsal (DV)	Posterior Margin - Brachiopod Outline	Description of the shape of the proximal portion of the dorsal valve perpendicular to line of symmetry
7	Dorsal Shape	DS	Dorsal (DV)	Anterior Margin - Brachiopod Outline	Description of the shape of the distal portion of the dorsal valve perpendicular to line of symmetry
8	Asymmetric Dorsal Valve	AsDV	Sagittal (SV)	Valve Thickness	Ratio of the Proximal Height to Distal Height of the Dorsal Valve in Sagittal view
9	Asymmetric Ventral Valve	AsVV	Sagittal (SV)	Valve Thickness	Ratio of the Proximal Height to Distal Height of the Ventral Valve in Sagittal view
10	Median Sagittal Section Dorsal Valve	MSSDV	Sagittal (SV)	Medial and Commissural Plane - Opposite Folding	Change in dorsal valve height along median line of symmetry relative to the distal position of external Comms to determine the relative relationship of valves and level of folding
11	Median Sagittal Section Ventral Valve	MSsW	Sagittal (SV)	Medial and Commissural Plane - Opposite Folding	Change in ventral valve height along median line of symmetry relative to the distal position of external Comms to determine the relative relationship of valves and level of folding
12	Shape of Dorsal Valve	SDV	Sagittal (SV)	Convexity or Concavity	Shape of the Dorsal Valve relative to the Ventral Valve
13	Shape of Ventral Valve	SVV	Sagittal (SV)	Convexity or Concavity	Shape of the Ventral Valve relative to the Dorsal Valve
14	Beak Size Dorsal Valve	BSDV	Sagittal (SV)	Dorsal Valve Posterior Extension past Hinge Line	Extension of the valve beyond hinge line on the posterior portion of the dorsal valve
15	Beak Size Ventral Valve	BSVV	Sagittal (SV)	Ventral Valve Posterior Extension past Hinge Line	Extension of the valve beyond hinge line on the posterior portion of the ventral valve
16	Commissure Shape	CommS	Sagittal (SV)	Commissure	Relationship between the Dorsal and Ventral Valve along the Commissure Line
17	Number of Folds	Folds	Other (O)	Folds and Sulci - Opposite Folding and Alternate Folding	The number of axes in a fold/sulcus pair divided by two along the distal-most portion of the commissure
18	Surface Texture	STxt	Other (O)	Ornamentation	Texture or variation on the surface of the brachiopod shell

Table 3. Description of features used to define character states and characters using traditional morphological terms from the Treatise of Invertebrate Paleontology (Williams and Rowell, 1965).

Measured Features	Abbreviation	Used in	Traditional Morphological Terms	Definitions
Proximal Length	PL	1. P:D (DV); 3. MiMw (DV)	All Lengths between either side of the line of symmetry of the Posterior Margin and Lateral Margin including the Hinge Line Length in the 10% most posterior portion of the dorsal valve	All lengths encompassed in the most proximal 10% the dorsal valve perpendicular to the line of symmetry excluding the beak
Distal Length	DL	1. P:D (DV); 3. MiMw (DV)	All Lengths between either side of the line of symmetry of the Anterior Margin and Lateral Margin in the 10% most anterior portion of the dorsal valve	All lengths encompassed in the most distal 10% of the dorsal valve perpendicular to the line of symmetry
Proximal or Distal Maximum Width	PDW	3. MiMw (DV)	Maximum Width of the Dorsal Valve at the Proximal 10% or Distal 10% perpendicular to the Line of Symmetry	Maximum width of the dorsal valve at the proximal or distal most 10%, use only distal 10% maximum width or proximal 10% maximum width depending on which is wider
Maximum Body Width	MBW	2. L:W (DV)	Maximum Width	Maximum width of the dorsal valve perpendicular to the line of symmetry
Maximum Body Length	MBL	2. L:W (DV); 5. VVe (DV); 14. BSDV (SV); 15. BSVV (SV)	Length of Dorsal Valve	Maximum length of the dorsal valve parallel to the line of symmetry
Middle Maximum Width	MiMw	3. MiMw (DV)	Maximum Width	Maximum body width in the middle 80% of the dorsal valve
Beak Length	BL	14. BSDV (SV); 15. BSVV (SV)	Extension of Dorsal and Ventral Valves past Hinge Line	Length of beak measured beyond Hinge Line for Dorsal and Ventral Valves
Ventral Valve Height	VvH	5. VVe (DV)	Ventral Interarea or Ventral Palintrope seen above Dorsal Valve	Maximum width where ventral valve (ventral interarea and delthyrium) can be seen extending past dorsal valve at proximal end of dorsal view
Proximal Height	Ph	8. AsDV (SV); 9. AsVV (SV)	Shell Thickness	Height of the proximal end of a valve in sagittal view
Distal Height	Dh	8. AsDV (SV); 9. AsVV (SV)	Shell Thickness	Height of the distal end of a valve in dorsal view
Lateral Shape	LS	4. LS (DV)	Lateral Margin - Brachiopod Outline	Shape of lateral edges of the dorsal valve parallel to the line of symmetry relative to a straight line
Beak Size	BS	14. BSDV (SV); 15. BSVV (SV)	Dorsal or Ventral Valve Posterior Extension above Hinge Line, Umbo	Extension of the valves beyond the hinge line
Proximal Shape	PS	6. PS (DV)	Posterior Margin - Brachiopod Outline	Description of the shape of the proximal portion of the dorsal valve perpendicular to line of symmetry
Dorsal Shape	DS	7. DS (DV)	Anterior Margin - Brachiopod Outline	Description of the shape of the distal portion of the dorsal valve perpendicular to line of symmetry
Shape of Dorsal Valve	SDV	12. SDV (DV)	Convexity or Concavity	Shape of the Dorsal Valve relative to the Ventral Valve
Median Sagittal Section	MMS	10. MSSDV (SV); 11. MSSW (SV)	Opposite Folding	The relative relationship of the distal portion of the commissure along the line of symmetry
Shape of Ventral Valve	SVV	13. SVV (DV)	Convexity or Concavity	Shape of the Ventral Valve relative to the Dorsal Valve
Commissure Shape	CommS	16. CommS (SV)	Commissure	Relationship between the Dorsal and Ventral Valve along the Commissure Line
Numbers of Folds	Folds	17. Folds (O)	Folds and Sulci - Opposite Folding and Alternate Folding	The number of axes in a fold/sulcus pair divided by two along the distal-most portion of the commissure
Surface Texture	STxt	18. STxt (O)	Ornamentation	Texture or variation on the surface of the brachiopod shell

Table 4. Guide to the principal component and canonical variance analyses included in this study. PCA 6.0 plots four modal values calculated from all the species within each regime.

Figure	Title	Regimes	N Species	N Invariant Characters	A Priori Groups	Genera	Families
Figure 8a	PCA 1.2	All Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	0	Family	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 8b	PCA 1.2	All Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	0	Regime	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 8c	PCA 1.3	All Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	0	Family	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 8d	PCA 1.4	All Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	0	Regime	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 9	PCA 2.0	All Regime Modes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	15	None	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 10a	PCA 3.4	R1 (Descendant of Native)	13	6	None	3: <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Strophomena</i>	3: Plectorthisidae, Platystrophiidae, Strophomenidae
Figure 10b	PCA 3.2	R2 (Maysvillian Restricted)	15	4	None	7: <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Rafinesquina</i> , <i>Zygospira</i>	7: Dalmanellidae, Rafinesquinidae, Platystrophiidae, Plectorthisidae, Soverbyellidae, Strophomenidae, Anazygidae
Figure 10c	PCA 3.3	R3 (Caryover)	8	11	None	5: <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Rafinesquina</i> , <i>Zygospira</i>	4: Dalmanellidae, Plectorthisidae, Platystrophiidae, Rafinesquinidae, Anazygidae
Figure 10d	PCA 3.4	R4 (Extrabassal Invaders)	11	8	None	11: <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i> , <i>Tetraphalerella</i>	8: Plaesiomyidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Strophomenidae, Rafinesquinidae, Strophomenidae, Soverbyellidae
Figure 11a	PCA 4.1	Specialist Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted)	28	0	Regime	8: <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Leptaena</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Plectorthis</i> , <i>Soverbyella</i> , <i>Strophomena</i> , <i>Zygospira</i> , <i>Hebertella</i>	6: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Rafinesquinidae, Soverbyellidae, Anazygidae
Figure 11b	PCA 4.2	Generalist Regimes: R2 (Maysvillian Restricted), R4 (Extrabassal Invaders)	19	0	Regime	16: <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Rafinesquina</i> , <i>Zygospira</i> , <i>Caazaga</i> , <i>Theaerodonta</i> , <i>Glyptorthis</i> , <i>Hiscobecus</i> , <i>Holteobolina</i> , <i>Leipodocyclus</i> , <i>Leptaena</i> , <i>Plaesiomya</i> , <i>Retrosirostra</i> , <i>Rhychnotrema</i> , <i>Tetraphalerella</i>	10: Dalmanellidae, Plectorthisidae, Platystrophiidae, Rafinesquinidae, Anazygidae, Plaesiomyidae, Glyptorthisidae, Glyptorthisidae, Rhychnotremitidae, Strophomenidae, Soverbyellidae
Figure 12	CVA All Regimes	All Regimes: R1 (Descendant of Native), R2 (Maysvillian Restricted), R3 (Caryover), R4 (Extrabassal Invader)	47	0	Regime	18: <i>Soverbyella</i> , <i>Leptaena</i> , <i>Strophomena</i> , <i>Holteobolina</i> , <i>Rafinesquina</i> , <i>Tetraphalerella</i> , <i>Theaerobonia</i> , <i>Glyptothyris</i> , <i>Caazaga</i> , <i>Retrosirostra</i> , <i>Zygospira</i> , <i>Plectorthis</i> , <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Hebertella</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Hiscobecus</i> , <i>Leipodocyclus</i> , <i>Rhychnotrema</i>	10: Plectorthisidae, Platystrophiidae, Strophomenidae, Dalmanellidae, Soverbyellidae, Anazygidae, Glyptorthisidae, Rhychnotremitidae, Plaesiomyidae, and Rafinesquinidae
Figure 13	PCA 5.0	R2 (Maysvillian Restricted), R4 (Extrabassal Invaders)	26	0	Regime	7: <i>Dalmanella</i> (<i>Cincinnatiina</i>), <i>Leptaena</i> , <i>Vinlandostrophia</i> (<i>Platystrophia</i>), <i>Plectorthis</i> , <i>Soverbyella</i> , <i>Strophomena</i> , <i>Zygospira</i>	11: Dalmanellidae, Plectorthisidae, Platystrophiidae, Rafinesquinidae, Anazygidae, Plaesiomyidae, Glyptorthisidae, Rhychnotremitidae, Strophomenidae, Strophomenidae, Soverbyellidae

A

Item	Proximal : Distal		P/D	Range
	Proximal Length	Distal Length		
0	0.00 0.20	1.00 1.00	0.00 0.20	20
1	0.20 0.80	1.00 1.00	0.20 0.80	60
2	0.80 1.20 1.00	1.00 1.00 0.83	0.80 1.20 1.20	40
	1.00	1.25	0.80	
3	1.00 1.00	0.83 0.20	1.20 5.00	60
4	1.00	0.20	5.00	20
	1.00	0.00	∞	200

C

Item	Mid Max Width			Range
	Prox or Dist Max	Mid Max Width	PDM/MMw	
0	1.00 1.00	0.00 0.20	0.00 5.00	20
1	1.00 1.00	0.20 0.80	5.00 1.25	60
2	1.00 0.83 1.25	0.80 1.20 1.00	1.25 0.83 0.83	40
3	0.83 0.20	1.00 1.00	0.83 0.20	60
4	0.20 0.00	1.00 1.00	0.20 ∞	20
				200

B

Item	Length : Width & Asymmetric Dorsal Valve & Asymmetric Ventral Valve			Range
	L & Ph	W & Dh	L/W & Ph/Dh	
0	1.00 1.00	0.20 0.00	5.00 ∞	20
1	1.00 1.00	0.83 0.20	1.20 5.00	60
2	1.00 0.80	0.83 1.00	1.20 0.80	40
	1.20	1.00	1.20	
3	0.20 0.80	1.00 1.00	0.20 0.80	60
4	0.00 0.20	1.00 1.00	0.00 0.20	20
				200

D

Item	Beak Size & Ventral Valve Extension			Range
	MbL or Vve	MBL	MbL/MBL or Vve/MBL	
0	0.00 0.05	1.00 1.00	0.00 0.05	5
1	0.05 0.20	1.00 1.00	0.05 0.20	15
2	0.20 0.30	1.00 1.00	0.20 0.30	10
3	0.30 0.45	1.00 1.00	0.30 0.45	15
4	0.45 0.50	1.00 1.00	0.45 ∞	5
				50

Table 5. Criteria for delimitating the five character states for the continuous and combination-type characters. Ratio calculations of character state percent weight of measurable and non-measurable features. A. For categories 1, B. For categories 2, 8-9. C. For category 3. D. For categories 5-6.

Table 6. Canonical variance analysis reclassification table. 74.47% of taxa were correctly classified. Rows highlight in gray are species that were assigned to a post-hoc group different from the a priori group.

Species	A Priori	Post-Hoc
1 <i>Hebertella alveata</i> (Foerste 1909)	Descendant of Native	Descendant of Native
2 <i>Vinlandostrophia (Platystrophia) acutilirata</i> (Conrad 1842)	Descendant of Native	Descendant of Native
3 <i>Vinlandostrophia (Platystrophia) annieana</i> (Foerste 1910)	Descendant of Native	Descendant of Native
4 <i>Vinlandostrophia (Platystrophia) clarksvillensis</i> (Foerste 1910)	Descendant of Native	Descendant of Native
5 <i>Vinlandostrophia (Platystrophia) cummingsi</i> (King 1850)	Descendant of Native	Descendant of Native
6 <i>Vinlandostrophia (Platystrophia) elkhornensis</i> (King 1850)	Descendant of Native	Descendant of Native
7 <i>Vinlandostrophia (Platystrophia) forestsi</i> (King 1850)	Descendant of Native	Descendant of Native
8 <i>Vinlandostrophia (Platystrophia) moritura</i> (King 1850)	Descendant of Native	Maysvillian Restricted
9 <i>Strophomena concordensis</i> (Foerste 1909)	Descendant of Native	Descendant of Native
10 <i>Strophomena nutans</i> (Hall and Clarke 1892)	Descendant of Native	Descendant of Native
11 <i>Strophomena planumbona</i> (Hall 1847)	Descendant of Native	Descendant of Native
12 <i>Strophomena sulcata</i> (Hall and Clarke 1892)	Descendant of Native	Invader
13 <i>Strophomena vetustis</i> (Rafinesque and De Blainville 1824)	Descendant of Native	Descendant of Native
14 <i>Dalmanella (Cincinnatina) multisepta</i> (Meek 1873)	Maysvillian Restricted	Maysvillian Restricted
15 <i>Vinlandostrophia (Platystrophia) auburnensis</i> (King 1850)	Maysvillian Restricted	Maysvillian Restricted
16 <i>Vinlandostrophia (Platystrophia) corryvillensis</i> (King 1850)	Maysvillian Restricted	Maysvillian Restricted
17 <i>Vinlandostrophia (Platystrophia) crassa</i> (Foerste 1910)	Maysvillian Restricted	Carryover
18 <i>Vinlandostrophia (Platystrophia) hopensis</i> (Foerste 1910)	Maysvillian Restricted	Descendant of Native
19 <i>Vinlandostrophia (Platystrophia) morrowensis</i> (King 1850)	Maysvillian Restricted	Maysvillian Restricted
20 <i>Vinlandostrophia (Platystrophia) sublaticosta</i> (King 1850)	Maysvillian Restricted	Maysvillian Restricted
21 <i>Plectorthis aequivalis</i> (Hall and Clarke 1892)	Maysvillian Restricted	Maysvillian Restricted
22 <i>Plectorthis fissicosta</i> (Hall and Clarke 1892)	Maysvillian Restricted	Maysvillian Restricted
23 <i>Plectorthis neglecta</i> (Hall and Clarke 1892)	Maysvillian Restricted	Maysvillian Restricted
24 <i>Plectorthis plicatella</i> (Hall 1847)	Maysvillian Restricted	Maysvillian Restricted
25 <i>Sowerbyella rugosa</i> (Meek 1873)	Maysvillian Restricted	Invader
26 <i>Strophomena maysvillensis</i> (Foerste 1909)	Maysvillian Restricted	Invader
27 <i>Strophomena planoconvexa</i> (Hall 1847)	Maysvillian Restricted	Invader
28 <i>Zygospira cincinnatiensis</i> (Hall 1862)	Maysvillian Restricted	Maysvillian Restricted
29 <i>Dalmanella (Cincinnatina) meeki</i> (Miller 1875)	Carryover	Carryover
30 <i>Hebertella occidentalis</i> (Hall 1847)	Carryover	Carryover
31 <i>Hebertella subjugata</i> (Hall and Clarke 1892)	Carryover	Carryover
32 <i>Vinlandostrophia (Platystrophia) cypha</i> (James 1874)	Carryover	Descendant of Native
33 <i>Vinlandostrophia (Platystrophia) laticosta</i> (James 1871)	Carryover	Carryover
34 <i>Vinlandostrophia (Platystrophia) ponderosa</i> (Foerste 1909)	Carryover	Carryover
35 <i>Rafinesquina alternata</i> (Conrad 1838)	Carryover	Invader
36 <i>Zygospira modesta</i> (Hall 1847)	Carryover	Carryover
37 <i>Catazyga schuchertona</i> (Hall and Clarke 1893)	Invader	Invader
38 <i>Thaerodonta clarksvillensis</i> (Foerste 1912)	Invader	Invader
39 <i>Glyptorthis insculpta</i> (Hall 1847)	Invader	Invader
40 <i>Hiscobeccus capax</i> (Conrad 1842)	Invader	Maysvillian Restricted
41 <i>Holtedahlina sulcata</i> (Hall and Clarke 1892)	Invader	Invader
42 <i>Lepidocyclus perlamellosum</i> (Wang 1949)	Invader	Invader
43 <i>Leptaena richmondensis</i> (Foerste 1909)	Invader	Maysvillian Restricted
44 <i>Plaesiomys subquadrata</i> (Hall 1847)	Invader	Maysvillian Restricted
45 <i>Retrorsirostra carleyi</i> (Hall 1860)	Invader	Invader
46 <i>Rhynchotrema denatum</i> (Hall 1860)	Invader	Invader
47 <i>Tetraphalerella neglecta</i> (James 1881)	Invader	Invader

Appendix 1. Coding scheme for characters with numerical constraints and brief definitions (Williams and Roswell, 1995). See Tables 1-2 for a definition of characters, character states, and features and Table 4 for an explanation of numerically constrained character states.

Number for Coding	Character Descriptions	Shorthand	Definition	Traditional Morphological Terms		Example Genera
				P.D.(D/V)	New Term	
1	Proximal...Distal (Dorsal Valve)		P/D			
	0 Proximal very Short or Absent	Pr v, Sh o Ab	$\infty - 0.2$	New Term	Tetracera (Weiler 1910)	
	1 Proximal Narrow	Pr Nw	0.2-0.8	New Term	Pseudoglossophrys (Buckman 1901)	
	2 Equal	Eq	0.8-1.2	New Term	Costistriclania (Amsden 1903)	
2	Distal very Short or Absent	Dj v, Sh o Ab	1.2-5.0	New Term	Artispriifer (Williams 1916)	
	0 Length - Width (Dorsal Valve)	LW (DV)	5.0 - ∞	New Term	Eurhectonema (Crickmay 1950)	
	1 Very Wide	vW	MH/MBW	Shell Length	Eurhectonema (Crickmay 1950)	
	2 Wide	W	5.0 - ∞	New Term	Dipaleasma (Ulrich and Cooper 1936)	
3	Equal	Eq	1.2-5.0	New Term	Grypus (Megerle con Muhlfeld 1811)	
	1 Long	Lq	0.8-1.2	New Term	Rouillieria (Makidin 1960)	
	2 Very Long	vLq	0.2-0.8	New Term		
	4 Mild Max Width - Maximum Width (Dorsal Valve)	M.Mw (DV)	$\infty - 0.2$	Valve Width		
4	Very Short	vSh	$\infty - 5.00$	New Term	Granulirhychia (Buckman 1918)	
	1 Short	Sh	5.00-1.25	New Term	Cyrtopelta (Schuchert and Cooper 1931)	
	2 Equal	Eq	1.25-0.83	New Term	Semipanus (Sarycheva 1952)	
	3 Wide	W	0.83-0.2	New Term		
5	Very Wide	vW	0.2 - ∞	Often exhibit alae		
	Lateral Shape (Dorsal Valve)	LS (DV)		Lateral Margin		
	0 Planar	Pl	Straight	New Term	Konnickia (Blitner 1893)	
	1 Convex	Cvx	Curved Outwards	New Term	Basiloda (Dall 1906)	
6	Concave	Cvc	Curved Inwards	New Term	Austrihychia (Ager 1959)	
	Compound 1	Cmp1	Distal Convex & Proximal Concave	New Term	Grathorhychia (Buckman 1918)	
	Compound 2	Cmp2	Distal Concave & Proximal Convex	New Term	Otusia (Walcott 1905)	
	Very Narrow or Absent	v, Nw o Ab	$\infty - 0.05$	Ventral Inclination of the Cardinal Areas Relative to the Commissural Plane.		
7	Narrow	Nw	0.05-0.2	0° - 15°, Straight	Ingria (Opik 1930)	
	Average	Avq	0.2-0.3	15° - 60° Straight, Nearly Straight, Suberect	Septarria (Muir-Wood and Cooper 1960)	
	Wide	W	0.3-0.45	60° - 105° Suberect, Erect, Incurved	Bouchardia (Davidson 1950)	
	Very Wide	v, W	0.45 - ∞	105° - 135° Incurved (>90°)	Inflata (Muir-Wood and Cooper 1960)	
8	Proximal Shape (Dorsal Valve)	PS (DV)		135° - 150° Incurved (>90°)	Orychodreta (Ulrich and Cooper 1926)	
	0 Absent	Ab	Point	Cardinal Margin Shape including Ears and Alae		
	1 Planar	Pl	Flat Line	New Term	Cyrtophrys (Middlemiss 1959)	
	2 Convex	Cvx	Curved Outwards	New Term	Ingria (Opik 1930)	
9	Concave	Cvc	Curved Inwards	New Term	Gibbithyris (Sahni 1925)	
	Compound	Cmp	Combination of Proximal Shapes (0-3)	New Term	Paraespirifer (Wedekind in Salomon 1926)	
	Distal Shape (Dorsal Valve)	DS (DV)		Anterolateral Commissure Shape		
	0 Absent	Ab	Point	New Term	Rugivetis (Muir-Wood and Cooper 1960)	
10	Planar	Pl	Flat Line	New Term	Basiloda (Dall 1906)	
	1 Convex	Cvx	Curved Outwards	New Term	Orthotoma (Quenstedt 1869)	
	2 Concave	Cvc	Curved Inwards	New Term	Paraespirifer (Wedekind in Salomon 1926)	
	Compound	Cmp	Combination of Distal Shapes (0-3)	New Term	Panvirhychia (Buckman 1918)	

8		Asymmetric Dorsal Valve (Sagittal View)		Ph/Dh		New Term	
		AsDV (SV)		Ph/Dh			
0	Proximal very High	Pr v. H	1,2-5,0	New Term			<i>Mimella</i> (Cooper 1930)
1	Proximal High	Pr H	5.0 - ∞	New Term			<i>Nisusia</i> (Walcott 1905)
2	Proximal - Distal Equal	PD Eq	0.8-1.2	New Term			<i>Psychopteurilla</i> (Schuchert and Cooper 1931)
3	Distal High	Dst H	0.2-0.8	New Term			<i>Haeticakia</i> (Boucot 1963)
4	Distal very High	Dst v. H	∞ - 0.2	New Term			
9	Asymmetric Ventral Valve (Sagittal View)	AsV (SV)	Ph/Dh	New Term			
0	Proximal very High	Pr v. H	1,2-5,0	New Term			<i>Teichertina</i> (Veivers, 1959)
1	Proximal High	Pr H	5.0 - ∞	New Term			<i>Psychopteurilla</i> (Schuchert and Cooper 1931)
2	Proximal - Distal Equal	PD Eq	0.8-1.2	New Term			<i>Cryptothyrus</i> (Bancroft 1945)
3	Distal High	Dst H	0.2-0.8	New Term			<i>Eremioechia</i> (Cooper 1966)
4	Distal very High	Dst v. H	∞ - 0.2	New Term			<i>Rhynchonella</i> (Muir-Wood 1966)
10	Median Sagittal Section Dorsal Valve (Sagittal View)	MSSDV (SV)	H/Abv	Medial and Commissural Plane-Opposite and Alternate Folding			<i>Eucheritina</i> (Schmidt, 1965)
0	High Above			Uniplicate, Sulciplicate, Parasulcate, Episulcate			
1	Above	Abv		Uniplicate, Sulciplicate, Parasulcate, Episulcate			<i>Herbertella</i> (Hall and Clarke, 1982)
2	Same	Same		Rectimarginate, Ornithellid, Melacarnate, Ligate, Strangulate, Bilobate, Asymmetrical			<i>Pentameroides</i> (Schuchert and Cooper, 1931)
3	Below	Blw		Sulcate, Intraplicate, Paraplicate, Antiplicate			<i>Imermia</i> (Opik, 1934)
4	Low Below	L Blw		Sulcate, Intraplicate, Paraplicate, Antiplicate			<i>Pisirhychia</i> (Buckman, 1918)
11	Median Sagittal Section Ventral Valve (Sagittal View)	MSSV (SV)	H/Abv	Medial and Commissural Plane-Opposite and Alternate Folding			
0	High Above			Uniplicate, Sulciplicate, Parasulcate, Episulcate			<i>Eucheritina</i> (Schmidt, 1965)
1	Above	Abv		Uniplicate, Sulciplicate, Parasulcate, Episulcate			<i>Herbertella</i> (Hall and Clarke, 1982)
2	Same	Same		Rectimarginate, Ornithellid, Melacarnate, Ligate, Strangulate, Bilobate, Asymmetrical			<i>Pentameroides</i> (Schuchert and Cooper, 1931)
3	Below	Blw		Sulcate, Intraplicate, Paraplicate, Antiplicate			<i>Imermia</i> (Opik, 1934)
4	Low Below	L Blw		Sulcate, Intraplicate, Paraplicate, Antiplicate			<i>Pisirhychia</i> (Buckman, 1918)

	SDV (SV)		SDV (SV)	
12		Shape of Dorsal Valve (Sagittal View)		
		Highly Convex	H Cox	Highly Curved Outwards relative to commissural line
0				Concave, Calina
1		Convex	Cvx	Convex, Sub-Carinale
2		Planar or Compound	Pl o Comp	Straight or Combination of Concavity and Convexity
3		Concave	Ccv	Concave
4		Highly Concave	H Ccv	Highly Curved Inwards
13		Shape of Ventral Valve (Sagittal View)	SV (SV)	
0		Highly Convex	H Cox	Highly Curved Outwards
1		Convex	Cvx	Curved Outwards
2		Planar or Compound	Pl o Comp	Flat or Compound of Dorsal Shapes
3		Concave	Ccv	Concave
4		Highly Concave	H Ccv	Highly Curved Inwards
14		Beak Size Dorsal Valve (Sagittal View)	BSDV (V.V)	
0		Very Narrow or Absent	v. Nw o Ab	∞, 0.05
1		Narrow	Nw	0.05-0.2
2		Average	Avd	0.2-0.3
3		Wide	W	0.3-0.45
4		Very Wide	v. W	0.45 - ∞
15		Beak Size Ventral Valve (Dorsal View)	BSDV (SV)	
0		Very Narrow or Absent	v. Nw o Ab	∞, 0.05
1		Narrow	Nw	0.05-0.2
2		Average	Avd	0.2-0.3
3		Wide	W	0.3-0.45
4		Very Wide	v. W	0.45 - ∞
16		Commissure Shape (Sagittal View)	ComMS (SV)	
0		Planar	Pl	Commissure is Flat
1		Sinile Curve	SaCrv	Single Curve in Commissure
2		Multiple Curves	MultiCrv	Multiple Curves in Commissure
3		Highly Asymmetrical	H Asym	Highly Asymmetrical Deflection(s)
4		Nested	Nest	Partially (resupinate) or Nested Valves
17		Number of Folds (Other)	Folds	Number of Fold Axes
0		No Folds	None	No Folds
1		Minor Deflection	Min Dfic	Minor Deflection(s) too minor to cause noticeable variation in Dorsal Valve view
2		One Fold	One	One Fold
3		Three Folds	Three	Three Folds
4		Five Folds	Five	Five Folds
18		Shell Texture (Other)	STM	
0		Smooth	Smth	Ornamentation
1		Costae	Cost	Minor Concentric Growths
2		Plications or Ridges	Plc o Ridg	Ribbing that does not cause plications along the Commissure
3		Spines	Sp	Ribbing that causes plications along the commissure
4		Compound	Comp	Protrusions from the surface of the Valve
				Includes all surface textures not described by 0-3

Appendix 2. Entire dataset of species listed in Stigall (2010) coded using new approach. All specimens in this study are from the Cincinnati Museum Center (CMC) Geier Collections and Research Center.

Category Name	Weight	1. P.D (DV)	2. L.W (DV)	3. M.Mw (DV)	4. LS (DV)	5. VVe (DV)	6. PS (DV)	7. DS (DV)		
Extreme	20	0 Pr v. Sh o Ab	0 v. W	0 v. Sh	0 Pl	0 v. Nw o Ab	0 Ab	0 Ab		
Moderate	60	1 Pr Nw	1 W	1 Sh	1 Cvx	1 Nw	1 Pl	1 Pl		
Center	40	2 Eq	2 Eq	2 Eq	2 Ccv	2 Avg	2 Cvx	2 Cvx		
Moderate	60	3 Pr v	3 Lg	3 W	3 Cmp1	3 W	3 Ccv	3 Ccv		
Extreme	20	4 Di v. Sh o Ab	4 v. Lg	4 v. W	4 Cmp2	4 v. W	4 Cmp	4 Cmp		
Location	Catalog Number	Family	Species	1. P.D (DV)	2. L.W (DV)	3. M.Mw (DV)	4. LS (DV)	5. VVe (DV)	6. PS (DV)	7. DS (DV)
CMC	68987	Plectrothidae	<i>Heberella alvata</i> (Foerste 1909)	3 Dst Nw	1 W	1 Sh	4 Cmp2	1 Nw	4 Cmp	4 Cmp
CMC	27702	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) acutilirata</i> (Conrad 1842)	4 Dst v. Sh o Ab	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	20710	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) amiana</i> (Foerste 1910)	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	2 Cvx	1 Pl
CMC	20584	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) clarkivillensis</i> (Foerste 1910)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	2 Cvx	4 Cmp
CMC	21306	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) cummingsi</i> (King 1850)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	66741	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) eckhornensis</i> (King 1850)	2 Eq	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	4 Cmp	2 Cvx
CMC	63669	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) foerstei</i> (King 1850)	3 Dst Nw	1 W	2 Eq	1 Pl	1 Nw	4 Cmp	4 Cmp
CMC	20769	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) foerstei</i> (King 1850)	2 Eq	1 W	3 W	1 Cvx	0 v. Nw o Ab	2 Cvx	2 Cvx
CMC	69015	Strophomenidae	<i>Strophomena concordensis</i> (Foerste 1909)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	1 Pl	2 Cvx
CMC	23634	Strophomenidae	<i>Strophomena nutans</i> (Hall and Clarke 1892)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	1 Pl	0 Ab
CMC	18596	Strophomenidae	<i>Strophomena planumbona</i> (Hall 1847)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	1 Pl	2 Cvx
CMC	64339	Strophomenidae	<i>Strophomena sulcata</i> (Hall and Clarke 1892)	3 Dst Nw	1 W	2 Eq	0 Pl	1 Nw	1 Pl	2 Cvx
CMC	2119	Strophomenidae	<i>Strophomena vetustus</i> (Rafinesque and De Blainville 1824)	3 Dst Nw	1 W	2 Eq	0 Pl	1 Nw	2 Cvx	2 Cvx
CMC			Mode of Descent of Native	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	4 Cmp	2 Cvx
CMC	28121	Dalmanellidae	<i>Dalmanella (Cincinnatiina) multisepta</i> (Meek 1873)	2 Eq	1 W	3 W	1 Cvx	1 Nw	1 Pl	2 Cvx
CMC	13894	Rafinesquinidae	<i>Lepaena gibbosa</i> (James 1874)	1 Pr Nw	1 W	3 W	1 Cvx	0 v. Nw o Ab	0 Ab	4 Cmp
CMC	20713	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) auburnensis</i> (King 1850)	3 Dst Nw	1 W	3 W	1 Cvx	1 Nw	2 Cvx	2 Cvx
CMC	1447	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) conyssa</i> (Foerste 1850)	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	20601	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) crassa</i> (Foerste 1910)	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	4 Cmp	2 Cvx
CMC	80452	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) hopensis</i> (Foerste 1910)	2 Eq	1 W	2 Eq	0 Pl	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	27842	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) morrowensis</i> (King 1850)	2 Eq	1 W	2 Eq	0 Pl	0 v. Nw o Ab	2 Cvx	4 Cmp
CMC	20782	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) sublaetosa</i> (King 1850)	2 Eq	1 W	2 Eq	1 Cvx	1 Nw	4 Cmp	4 Cmp
CMC	16656	Plectrothidae	<i>Plectrothis aequalis</i> (Hall and Clarke 1892)	3 Dst Nw	1 W	3 W	1 Cvx	1 Nw	1 Pl	2 Cvx
CMC	65980	Plectrothidae	<i>Plectrothis fissicosta</i> (Hall and Clarke 1892)	2 Eq	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	2 Cvx	2 Cvx
CMC	63574	Plectrothidae	<i>Plectrothis neglecta</i> (Hall and Clarke 1892)	2 Eq	1 W	2 Eq	1 Cvx	1 Nw	2 Cvx	2 Cvx
CMC	33406	Plectrothidae	<i>Plectrothis plicatella</i> (Hall 1847)	3 Dst Nw	1 W	3 W	1 Cvx	0 v. Nw o Ab	2 Cvx	2 Cvx
CMC	51269	Sowerbyellidae	<i>Sowerbyella rigosa</i> (Meek 1873)	3 Dst Nw	1 W	1 Sh	1 Pl	2 Avg	1 Pl	2 Cvx
CMC	69474	Strophomenidae	<i>Strophomena maysvillensis</i> (Foerste 1909)	2 Eq	2 Eq	2 Eq	0 Pl	0 v. Nw o Ab	1 Pl	1 Ab
CMC	23807	Strophomenidae	<i>Strophomena planconvexa</i> (Hall 1847)	3 Dst Nw	2 Eq	2 Eq	0 Pl	0 v. Nw o Ab	1 Pl	2 Cvx
CMC		Ananzylidae	<i>Zygospira cincinnatiensis</i> (Hall 1862)	2 Eq	1 W	3 W	1 Cvx	1 Nw	1 Pl	2 Cvx
CMC			Mode of Maysvillian Restricted	3 Dst Nw	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	1 Pl	2 Cvx
CMC	28344	Dalmanellidae	<i>Dalmanella (Cincinnatiina) meeki</i> (Miller 1875)	2 Eq	2 Eq	3 W	0 Pl	0 v. Nw o Ab	1 Pl	1 Pl
CMC	21580	Plectrothidae	<i>Heberella occidentalis</i> (Hall 1847)	3 Dst Nw	1 W	2 Eq	4 Cmp	0 v. Nw o Ab	4 Cmp	2 Cvx
CMC	20578	Plectrothidae	<i>Heberella subjugata</i> (Hall and Clarke 1892)	3 Dst Nw	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	66207	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) typha</i> (James 1874)	3 Dst Nw	1 W	1 Sh	4 Cmp2	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	80186	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) laticosta</i> (James 1871)	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	20655	Platystrophiidae	<i>Vinlandostrophia (Platystrophia) ponderosa</i> (Foerste 1909)	2 Eq	2 Eq	2 Eq	1 Cvx	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC		Rafinesquinidae	<i>Rafinesquina alternata</i> (Conrad 1838)	3 Dst Nw	1 W	2 Eq	0 Pl	1 Nw	1 Pl	0 Ab
CMC	79403	Ananzylidae	<i>Zygospira modesta</i> (Hall 1847)	2 Eq	2 Eq	2 Eq	0 Pl	1 Nw	1 Pl	2 Cvx
CMC			Mode of Conroyer	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	4 Cmp	4 Cmp
CMC	63684	Pleesiomyidae	<i>Austinea scovellii</i> (Foerste 1909)	2 Eq	2 Eq	2 Eq	1 Cvx	1 Nw	2 Cvx	1 Pl
CMC	21375	Ananzylidae	<i>Catezoga schuchertoni</i> (Hall and Clarke 1893)	2 Eq	2 Eq	2 Eq	1 Cvx	1 Nw	2 Cvx	1 Pl
CMC	50760	Glyptonthidae	<i>Glyptonthis insculpta</i> (Hall 1847)	2 Eq	2 Eq	1 Sh	1 Cvx	0 v. Nw o Ab	1 Ab	2 Cvx
CMC	77518	Rhynchotrematidae	<i>Hiscoecus capax</i> (Conrad 1842)	3 Dst Nw	1 W	2 Eq	0 Pl	0 v. Nw o Ab	2 Cvx	2 Cvx
CMC	28327	Strophomenidae	<i>Holledahlina sulcata</i> (Hall and Clarke 1892)	2 Eq	2 Eq	3 W	1 Cvx	1 Nw	0 Ab	2 Cvx
CMC	68585	Rhynchotrematidae	<i>Lepidocycclus perlanellosus</i> (Wang 1949)	3 Dst Nw	1 W	2 Eq	1 Pl	0 v. Nw o Ab	1 Pl	1 Pl
CMC	28341	Rafinesquinidae	<i>Lepaena richmondensis</i> (Foerste 1909)	3 Dst Nw	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	2 Cvx	4 Cmp
CMC	74001	Pleesiomyidae	<i>Pleesiomys subquadratus</i> (Hall 1847)	3 Dst Nw	1 W	2 Eq	1 Cvx	0 v. Nw o Ab	2 Cvx	4 Cmp
CMC	79605	Pleesiomyidae	<i>Retrosirostra carleyi</i> (Hall 1860)	3 Dst Nw	1 W	3 W	1 Cvx	1 Nw	1 Pl	2 Cvx
CMC	78494	Rhynchotrematidae	<i>Rhynchotrema denatum</i> (Hall 1860)	1 Pr Nw	2 Eq	3 W	1 Cvx	0 v. Nw o Ab	0 Ab	2 Cvx
CMC	80227	Strophomenidae	<i>Tetraphalerella neglecta</i> (James 1881)	3 Dst Nw	1 W	1 Sh	0 Pl	1 Nw	1 Pl	2 Cvx
CMC	78944	Sowerbyellidae	<i>Thaerofonta clarkivillensis</i> (Foerste 1912)	3 Dst Nw	1 W	1 Sh	0 Pl	1 Nw	1 Pl	2 Cvx
CMC			Mode of Extrabasinal Invader	3 Dst Nw	1 W	2 Eq	1 Cvx	1 Nw	1 Pl	2 Cvx

