USING MORPHOMETRIC ANALYSIS TO DETERMINE PATTERNS OF EVOLUTION IN THE UPPER ORDOVICIAN BRACHIOPOD *SOWERBYELLA RUGOSA* FROM THE KOPE FORMATION OF NORTHERN KENTUCKY

by

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(Under the Direction of Steven Holland)

ABSTRACT

This study examines patterns of evolution in the Upper Ordovician brachiopod *Sowerbyella rugosa* from the Kope Formation using morphometric analysis. Landmark analysis was used to determine centroid size and shape coordinates, which were then tested against stratigraphic position, environment and a random walk. Neither centroid size nor any of the shape coordinates show correlation with stratigraphic position or environment. Centroid size and one shape coordinate exhibit stasis, while the other shape coordinates follow a random walk. Centroid size and shape coordinates were also measured for *Eochonetes clarksvillensis*, another Upper Ordovician brachiopod from the Liberty Formation, a descendant of *S. rugosa*. *S. rugosa* has a smaller centroid size but has a longer hingeline than *E. clarksvillensis*. The change in morphologies between *S. rugosa* and *E. clarksvillensis* may have resulted from punctuated equilibrium or may be attributable to very gradual evolution that cannot be seen at the resolution of a million years.

INDEX WORDS: Morphometrics, evolution, random walk, stasis, punctuated equilibrium, landmark analysis, brachiopods, Kope Formation

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DEDICATION

I would like to dedicate this effort to all of my family and friends, who never tire of my incessant talk about science and nature, and for their patience with many career changes until I found science again. I would also like to thank my high school science and math teachers, without them I would have never pursued this path.

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CHAPTER 1

INTRODUCTION

This thesis was written as a manuscript that will be published separately in a peer-reviewed journal. Chapter 2 is the body of the manuscript and contains a more thorough introduction to the subject. This introduction will serve as a brief overview of the project.

The goal of this study was to look at *Sowerbyella rugosa*, an Upper Ordovician brachiopod, and determine how its morphology changed throughout the Kope Formation. Landmark analysis was used to determine shape and size variables that were then compared with stratigraphic position and environment. Each morphologic character was also subjected to Bookstein's random walk test to determine if it showed stasis, anagenesis or followed a random walk. Because denticulation is a diagnostic character of genus differentiation and many denticulated *S. rugosa* were found, an investigation of denticulated versus non-denticulated *S. rugosa* was also done.

In addition, landmark analysis was used on another Upper Ordovician brachiopod, *Eochonetes clarksvillensis*, a descendant of *S*. rugosa from the Liberty Formation. *E. clarksvillensis* is found in a shallower environment, further up in stratigraphic position and a comparison between the two brachiopods was done to determine morphologic difference and assess whether the two are separated by a punctuated mode of evolution.

CHAPTER 2

USING MORPHOMETRIC ANALYSIS TO DETERMINE PATTERNS OF EVOLUTION IN THE UPPER ORDOVICIAN BRACHIOPOD *SOWERBYELLA RUGOSA* FROM THE KOPE FORMATION OF NORTHERN KENTUCKY[1]

[1] Levy, G.M. and S.M. Holland. To be submitted to *PALAIOS*.

To test evolutionary trends, high sampling intensity and sufficient sequence stratigraphic control are required. This study uses these constraints and aims to determine patterns of evolution in the Upper Ordovician brachiopod Sowerbyella rugosa *from the Kope Formation of Northern Kentucky by using morphometric analysis. Landmark analysis was used to determine centroid size and shape coordinates, which were then tested against stratigraphic position, environment and a random walk. Neither centroid size nor any of the shape coordinates show correlation with stratigraphic position or environment. Centroid size and one of six shape coordinates exhibit stasis, while the rest of the shape coordinates follow a random walk.* Eochonetes clarksvillensis, *a direct descendant of* S. rugosa *was used to test the mode of evolution between the two. Similar landmark features were measured, and* E. clarksvillensis *had a shorter hingeline and longer submedial septa than* S. rugosa *suggesting that there is a definite change between the genera.*

The jump in morphology between S. rugosa and E. clarksvillensis *may have resulted from a punctuated equilibrium event or may be attributable to very gradual evolution that takes place over a 4 m.y. gap that occurs between the last occurrence of* S. rugosa *and the first appearance of* E. clarksvillensis. *Since this gap is present, it is impossible to determine with certainty that this is a case of punctuated equilibrium rather than long-term gradualism that is too gradual to be seen at the resolution of a few million years.*

INTRODUCTION

The theory of punctuated equilibrium has been controversial since its inception over 30 years ago. Given the nature of the fossil record it is difficult to prove or disprove instances of hypothetical punctuation. However, consensus among scientists exists in two areas: First, the necessity for sufficient sampling intensity (Raup and Crick, 1981; Levinton, 1983; Charlesworth, 1984; Gingerich, 1985; Bookstein, 1987; Stanley and Yang, 1987; Gingerich, 1993; Roopnarine et al., 1999; Haney et al., 2001; Roopnarine, 2001; Sheets and Mitchell, 2001), and second, good sequence stratigraphic control (MacLeod, 1991; Brett, 1995; Holland, 1995; Patzkowsky and Holland, 1997; Daley, 1999) before any study of evolution is undertaken. This study employs both of these constraints and aims to examine patterns of the evolution in two Upper Ordovician brachiopods.

Recently, the gradualism versus punctuated equilibrium debate has renewed, owing to new ideas and methods. Coordinated stasis, introduced by Brett and Baird (1995), suggests that speciation is not only punctuated but also occurs contemporaneously among unrelated species occupying the same or closely related environments. Innovation in statistical methods of stasis, anagenesis and random walk now provide more robust tests for stasis (Charlesworth, 1984; Bookstein, 1988b; Roopnarine, 1999, 2001; McCormick and Fortey, 2002). Additionally, papers debating evolutionary rates have rekindled the interest in the gradualism versus punctuated equilibrium debate (Raup and Crick, 1981; Kitchell et al., 1987; Stanley and Yang, 1987;

Gingerich, 1993; Roopnarine, 1999; Sheets and Mitchell, 2001) and the causes of stasis in the fossil record (Van Valen, 1982; Levinton, 1983; Gingerich, 1985; Stanley and Yang, 1987; Williamson, 1987; Lieberman et al., 1994; Lieberman and Dudgeon, 1996; Sheldon, 1996; Jackson and Cheetham, 1999; Seaborg, 1999; Burt, 2001; Merila, 2001) have further fueled the debate over gradualism versus punctuated equilibrium. Lastly, evolution along a cline (gradient of change in a measurable character) has been found in some cases and provides another hypothesis to test (Cisne et al., 1980, 1982; Daley, 1999; Haney et al., 2001).

All paleontological evolutionary studies must deal with the possibilities of ecophenotypes and ecomorphotypes (ecophenotypes share a common genotype yet display a different phenotype, whereas ecomorphotypes may or may not be genetically the same). Without knowing the underlying genetic component, it is difficult to distinguish whether morphotypes are from the same species. With the advent of morphometric analysis, a quantitative approach can now be taken to determine species based on a suite of morphological characteristics (Tabachnick and Bookstein, 1990; Holtzmann and Pawlowski, 1997; Roopnarine and Vermeij, 2000; Kim et al., 2002; McGhee and McKinney, 2002). Therefore this analysis incorporates size and shape metrics as well as an investigation of hingeline denticulation, a character of genus differentiation to determine how the two genera in question differ.

Haney et al. (2001) tested the question of size and shape change over time and with environment to determine differences in five species of the Ordovician plectambonitacean brachiopod *Sowerbyella* from northern and central Kentucky with each species occurring in a separate formation. They found that size and shape changed over time among the five species and that a clinal variation in shape was related to onshore – offshore position. Haney et al. (2001) cited a need for more detailed temporal and spatial sampling to determine the existence of a contemporaneous cline for each of these five species of *Sowerbyella*. The present study looks at one of these five species, *Sowerbyella rugosa*, within the Upper Ordovician Kope Formation of northern Kentucky to test if a cline could be detected at a higher sampling resolution. Holland et al. (2001) showed that there were subtle biofacies changes within the Kope (a single lithofacies) by using gradient analysis to find a quantitative proxy for water depth. By using the methods presented in Holland et al. (2001), this study is able to test the conclusions of Haney et al. (2001) and use a higher resolution approach for testing ecomorphologic variation. By doing so, an assessment of the mode of evolution can be done between *S. rugosa* and a descendant species, *Eochonetes clarksvillensis*.

In addition, landmark analysis was used on another Upper Ordovician brachiopod, *Eochonetes clarksvillensis* from the Liberty Formation of southeastern Indiana. *Eochonetes clarksvillensis* is found in a shallower environment, occurs stratigraphically higher and is a descendant of *S. rugosa* (Howe, 1972). A comparison between the two brachiopods was done to determine morphologic difference and to assess whether the two species had a punctuated mode of evolution.

This study addresses two main questions: 1) Does the morphology of *S. rugosa* change within the Kope Formation either with environment or stratigraphic position as predicted by Haney et al. (2001)? 2) How similar is the morphology of *S. rugosa* compared with *Eochonetes clarksvillensis* and could this be a case for a punctuated mode of evolution?

BACKGROUND

Geologic Setting

Kope Formation

The established sequence stratigraphy of the Kope Formation (Holland et al., 1993) is used as the framework for this study. The Kope Formation is part of a broad band of Ordovician shallow-water carbonates and siliciclastic mudstones that extend from the Great Lakes to central Tennessee (Jennette and Pryor, 1993). The Kope Formation spans about 2 m.y., from roughly 451 to 449.5 Ma (Holland et al., 2001).

Part of the Cincinnatian Series, the Kope Formation is mostly composed of mudstone (80%) and bioclastic limestones and calcisiltites (20%) (Jennette and Pryor, 1993; Holland et al., 2000). The facies interpretation of the Kope is that of a distal offshore environment near normal storm wave base (Hay et al., 1981; Tobin and Pryor, 1981; Jennette and Pryor, 1993; Holland, 1997) as indicated by the dominance of mudstone, the presence of storm beds, small-scale hummocky and trough cross-lamination, and mega-ripples (Holland, 1993; Jennette and Pryor, 1993). The Kope spans most of the C1 depositional sequence (Holland and Patzkowsky, 1996), however *S. rugosa* are only found in the lower half of the Kope (Holland et al., 2000). The Kope Formation exhibits meter-scale cycles that consist of shale-rich intervals alternating with thin to medium beds of packstone and grainstones (Holland et al., 2000). The meter-scale cycles stack to form larger cycles up to 20-meters thick that are defined by changes in the thickness of meter-scale cycles. Although the Kope is largely a single lithofacies, it contains environmentally controlled faunal changes (Holland et al., 2001).

The environmental control needed to evaluate patterns of morphological evolution can be supplied through ecological ordination techniques. Detrended correspondence analysis (DCA) is one such multivariate statistical technique for ordinating samples based on changes in their taxonomic composition (Cisne and Rabe 1978, Cisne et al., 1980; Holland et al. 2001). Holland et al. (2001) used DCA to ordinate taxa from the Kope Formation. By comparing the ordination results to sequence-stratigraphic architecture, they found that DCA Axis 1 corresponded with water depth, giving them a quantitative proxy for environment (Fig. 1). These Axis 1 DCA scores are used in this study to compare brachiopod morphology to environment. The sampling intensity of this study is very high (a total of 274 specimens from 35 beds) and any trend in morphologic change ought to be detectable (Gingerich, 1985).

Liberty Formation

The Liberty Formation, like the Kope, is also part of the Ordovician-age shallow-water carbonates and siliciclastic mudstones that extend from the Great Lakes to central Tennessee (Jennette and Pryor, 1993). The Liberty Formation spans the period of time from roughly 445 to 444.5 Ma (Holland, 1997).

The Liberty is also part of the Cincinnatian Series but lies within the C5 depositional sequence (Holland and Patzkowsky, 1996). The Liberty was deposited in a shallower environment than the Kope below normal wave base and above storm wave base within a transition-zone environment (Hay et al., 1981; Tobin and Pryor, 1981;

Jennette and Pryor, 1993; Holland, 1997). The Liberty is characterized by mixed packstones and mudstones, contains storm beds, planar lamination, wave-ripple lamination, and small-scale hummocky cross-lamination (Holland, 1997). The lithologic components are fossiliferous packstones (45%), mudstones (45%) and wackestones, grainstones and calcisiltites (10%) (Holland, 1997).

The Species Studied

Sowerbyella rugosa is a model organism for evolutionary study for several reasons. First, it is found abundantly throughout the lower Kope Formation and is the only species of *Sowerbyella* found in the Kope (Caster et al., 1955). Second, it is found in a narrow range of environments within the offshore facies (Patzkowsky, 1995; Holland, 1997). Finally, the brachial valve is well preserved in most cases and the features of the brachial interior are easily seen on the abundant disarticulated valves so that morphometric analysis can be done. *Eochonetes clarksvillensis* was chosen for this study because it is a descendent of *S. rugosa* (Howe, 1972) and it also has good preservation, enabling morphometric analysis.

S. rugosa and *E. clarksvillensis* are closely related (Howe, 1972) and their history is complicated and intertwined. Both Meek (1873) and Foerste (1912) labeled *Sowerbyella rugosa* as *Plectambonites rugosa* and Foerste (1912) described *Eochonetes clarksvillensis* as a subspecies of *Sowerbyella rugosa* by naming it *Plectambonites rugosa clarksvillensis*. Cooper (1944) revised this designation by changing *Plectambonites rugosa* to *Sowerbyella rugosa*. Wang (1949) changed the *Sowerbyella* designation to *Thaerodonta* and compared *Thaerodonta rugosa* to *Thaerodonta clarksvillensis* (the previous designation of *Eochonetes clarksvillensis*). Caster et al. (1955) reaffirmed the *Sowerbyella* designation. Ross (1957) found *Sowerbyella* with denticulated hingelines, which he believed were intermediate forms of *Sowerbyella* and *Thaerodonta*. Howe (1972, 1979) also used the *Sowerbyella* designation. Cox and Rong (1989) returned to the original *Plectambonites* designation and listed *Thaerodonta* as a subgenus of *Sowerbyella*, with *Eochonetes* as a separate genus into which they wanted to move *Sowerbyella rugosa*. However, Cox and Rong (1989) found no differences between *Thaerodonta* and *Eochonetes* and therefore established them as synonyms. The most recent *Treatise on Invertebrate Paleontology* (Moore and Kaesler, eds., 1997) agrees with Cox and Rong's (1989) designation and changed *Thaerodonta* to *Eochonetes*, keeping the designation of *Sowerbyella*.

The currently recognized differences between *Sowerbyella* and *Eochonetes* are that members of *Eochonetes* have accessory teeth, hingeline denticulations and dorsal lateral septa, whereas members of *Sowerbyella* do not have these features (Howe, 1972). Both forms are closely related and *E. clarksvillensis* is thought to have descended from *S. rugosa* (Howe, 1972).

METHODS

Sample Methods

The *S. rugosa* samples for this study were collected from the K445 outcrop, which is located in northern Kentucky near Cincinnati, Ohio (Fig. 2). This study spans the entire interval in the Kope Formation over which *S. rugosa* occurs. Specimens were collected from bioclastic limestones, calcisiltites and mudstones. To describe the evolutionary pattern of *S. rugosa*, samples were collected from 35 beds in a 26-meter section of the Kope Formation, yielding 274 individuals that had at least half of the shell preserved, including the points defining the mirror plane. The *E. clarksvillensis* samples were collected from float in the Liberty Formation exposed at South Gate Hill in southeastern Indiana (Fig. 2), yielding over 100 total, but only 33 usable individuals for morphometric analysis.

Rock samples were collected in bulk and washed, and every *S. rugosa* and *E. clarksvillensis* was numbered. Each brachial interior was photographed with a Nikon digital camera, and a centimeter-scale was included in each photograph for later specimen calibration. Care was taken to ensure that the focal plane of the camera was exactly parallel to the individual to minimize distortion, which might lead to false conclusions about shape or size change (Hughes, 1999).

Morphometric Landmarks

Landmarks were chosen because they were some of the same ones that Haney et al. (2001) used and were picked because they, in combination with living tissue helped with valve movement and feeding, in addition to having good preservation (Fig. 3A). In almost every complete brachial interior, the points chosen as landmarks are well preserved. The endpoints of the shell (Fig. 3A: a, b) and the mirror plane endpoints (Fig 3A: c, d) reflect overall size and the combination of exterior and interior landmarks are an indication of shape. On each brachiopod, eight landmarks were identified and x-y pixel coordinates measured using Adobe Photoshop. Landmarks a and b are the tips of the hingelines, c is the tip of the cardinal process, d is at the anterior intersection of the commissure and the symmetry plane, e and f are the antero-lateral tips of the brachiophore processes, and g and h are the anterior tips of the submedial septa. Landmarks c and d are Type 1 landmarks, meaning that they are at discrete juxtapositions of tissues, or a triple-point intersection (Bookstein, 1991). All other landmarks are Type 2, that is, points representing the maxima of curvature or other local morphogenetic processes (Bookstein, 1991).

Not all brachiopods were preserved whole; therefore, landmarks were reflected across the mirror plane. If both landmarks of a pair were present (e.g., a and b, or g and h) they were averaged by reflecting the right point across the mirror plane and then averaging the positions of right and left landmarks (Fig. 3B). Reflection of landmarks allows for the maximum amount of data to be used and is a technique that has been used by others where specimens are incomplete (Haney 2001; McCormick and Fortey 2002).

Allometry

To ensure that size has no effect on shape, a null hypothesis of no allometry must be demonstrated. Without this proof, it is impossible to separate true evolutionary change from allometric growth. Tort and Laurin (2001) found that large morphologic variation might occur through ontogeny. Likewise Jaecks and Carlson (2001) have found that juvenile thecideide brachiopods have different internal features than adults because of ontogenetic change. Because different parts of an organism may grow at different rates, allometric differences can cause juvenile forms and adult forms of a single species to be interpreted as a different species. In this study, allometry was tested for by correlating each shape coordinate versus centroid size and finding the p-value for the correlation to determine significance. All size classes were included in this study and no differentiation was made between juveniles and adults.

Centroid Size and Shape Coordinates

Centroid size and shape coordinate data were calculated for the reflected landmarks. Centroid size is a size measure that is independent of shape and is calculated by summing the squared distances from each landmark to the centroid (Bookstein, 1991). In the absence of allometry, centroid size should be uncorrelated with shape (Bookstein, 1991). Centroid size (CS) is calculated by:

$$CS = \sqrt{\sum_{i=1}^{j} \left(M - Z_i\right)^2}$$

where M is the centroid, Z_i is the landmark and j is the number of landmarks.

Shape coordinates are Cartesian coordinates that are fixed to a constant baseline (see Bookstein, 1991). In this study, the baseline is defined as the mirror plane given by landmark points c and d. The shape coordinates of landmarks ab, ef, and gh are relative to the baseline c-d. Shape coordinates are symbolized by □, with each labeled by its composite landmark, with a subscript of 1 for the direction parallel to the baseline (symmetry-plane) and a subscript of 2 for the direction perpendicular to the baseline (direction of hingeline) throughout. Shape coordinates ($\square_1$ and $\square_2$) are calculated as:

$$\square_1 = \frac{(x_b - x_a)(x_c - x_a) + (y_b - y_a)(y_c - y_a)}{(x_b - x_a)^2 + (y_b - y_a)^2}$$

$$\square_2 = \frac{(x_b - x_a)(y_c - y_a) - (y_b - y_a)(x_c - x_a)}{(x_b - x_a)^2 + (y_b - y_a)^2}$$

where *a* and *b* are the baseline points, *c* is the landmark to be measured, and *x* and *y* are the Cartesian coordinates for the landmark.

Testing for stasis and anagenesis

One method of assessing anagenesis (directed evolution) and stasis (morphologic consistency) is by testing against a random walk model. Random walk models have long been used in a variety of scientific fields. In genetics, an unbiased random walk would occur when the probability of an allele becoming fixed or extinct in a population is equal (Futuyma, 1998). In paleontology, a random walk is used to describe evolution where change in a character occurs, but it is not directed and a net shift in morphology may not occur (Gingerich, 1993). Bookstein (1988b) developed a method for testing character change to determine if the character was showing stasis, anagenesis or a random walk. Recently, this method has been used to speculate about modes of evolution (Roopnarine et al., 1999; Roopnarine and Vermeij, 2000; Roopnarine, 2001; McCormick and Fortey, 2002).

The limits for stasis and anagenesis are easily calculated, and then can be compared to the maximum excursion of the character in question. Bookstein's (1988b) method is calculated by finding the standard deviation of the final step of the random walk ($\sigma\sqrt{n}$) so that

$$\sigma\sqrt{n} = \sqrt{\sum_i \left(Sn_i - Sn_{i-1}\right)^2}$$

where Sn is the corrected mean measurement per interval and i is the interval (in this case the interval is a bed containing *Sowerbyella*). Once $\sigma\sqrt{n}$ is calculated, it is then multiplied by the maximum and minimum cutoffs. For 95% confidence levels, the critical value for anagenesis would be $2.25\left(\sigma\sqrt{n}\right)$ meaning, any maximum excursion of a character (size or shape) equal to or greater than 2.25 times $\sigma\sqrt{n}$ would be regarded as indicating anagenesis (Bookstein, 1991). The critical value for stasis is $0.62\left(\sigma\sqrt{n}\right)$ and any maximum excursion equal to or less than that value would indicate stasis (Bookstein, 1991). Any value between those cut-offs would be regarded as following a random walk. Centroid size and shape coordinates were compared against a random walk to test for stratophenotypic patterns.

Denticulation

In addition to testing for shape and size differences in *S. rugosa* and *E. clarksvillensis*, differences in degree of hingeline denticulation were also examined. Denticulation is a diagnostic feature for distinguishing between the two genera (Howe, 1972). Thirty-five randomly chosen brachiopods from each genus were examined for denticulation. Denticulation was measured on a five-part scale: 1) Hingeline obscured, 2) No denticulation, 3) Possible denticulation, 4) Denticulation along part of hingeline, and 5) Denticulation along entire hingeline (Fig. 4). To determine if denticulated *S. rugosa* differed from non-denticulated *S. rugosa*, *t*-tests were performed on each morphologic character to compare between the groups. Since denticulation is a diagnostic feature of genus differentiation, these latter tests were run in order to ensure that all Kope *S. rugosa* truly belonged to the same genus.

RESULTS

Measurement Error

Measurement error was determined by replicating each of the eight landmark measurements on five randomly chosen brachial valves on five non-consecutive days. The centroid size error calculations based on those replicates resulted in a maximum variance per valve of 0.001 mm. Centroid size measurement error accounts for an average of 1.6% of the total observed variation in size. Shape variable error calculations on the replicates resulted in a maximum variance of 0.0013 mm. Measurement error of shape coordinates accounts for an average of 6.6% of the total observed variation. Error resulting from the reflection of the landmarks across the mirror plane is also small and constituted an average of 5.6% of the total observed variation in landmark positions.

Allometry

Three of the six shape coordinates show a statistically significant correlation with centroid size, indicating the possible presence of allometry (Fig. 5, Table 1). However, if the slope of the data is small, allometric changes in shape with size can be considered minimal because the correlation is small. Furthermore, the r^2 values for the correlation of shape coordinates with centroid size range from 0.004 to 0.099 meaning that only 0.4% to 9.9% of the variance in any shape coordinate is explained by size, suggesting that allometry contributes little to differences in shape among specimens. The presence of statistically significant allometry is likely the result of relatively large sample size (n=274).

Centroid Size

To test if mean size of *S. rugosa* changed over time, mean centroid size per bed was plotted against stratigraphic position (Fig. 6). The correlation between the centroid size and stratigraphic position is not significant (r=0.111, n=35, p=0.524), and little net change in size occurs over this roughly one million-year time interval. Centroid size does oscillate by a few millimeters throughout the section, but there is no overall trend.

To give an indication of changes in water depth, DCA Axis 1 scores (Holland et al., 2001) are shown next to centroid size for the stratigraphic section. Although size superficially appears to shift concurrently with water depth based on the DCA Axis 1 portion of the figure, no significant correlation is seen with DCA Axis 1 scores (see below for significance measures).

Centroid size was tested against a random walk to determine if it shows stasis, anagenesis or follows a random walk. In this test, at 95% confidence limits, the upper limit of stasis was 0.467 and the lower limit for anagenesis was 1.693; maximum excursion for centroid size is 0.276, therefore, centroid size falls within the range of stasis (Table 2).

To test for size change with environment, DCA Axis 1 scores were plotted against mean centroid size per bed (Fig. 7). The correlation of DCA Axis 1 scores and centroid size is not significant ($r=0.057$, $n=35$, $p=0.744$), indicating a lack of size change with environment. The overall pattern of centroid size oscillates slightly, but there is no consistent relationship of size change with environment.

Shape Coordinates

When all landmarks are aligned to the same shape space, the scatter of each landmark can be plotted against a consistent baseline (Fig. 8). The scatter is greatest for landmark gh, partly because gh has the greatest measurement error (~10%) but mostly because it has the greatest inherent variance.

Changes in shape coordinates were tested in the same manner as size. Each mean shape coordinate per bed was plotted against stratigraphic position (Fig. 9, Table 1), DCA scores (Fig. 10, Table 1), and tested for random walk (Table 2). When compared to stratigraphic position, □gh_1 is the only shape coordinate to show a significant correlation ($r^2=0.447$, $n=35$, $p=0.00001$) (Table 1), indicating that roughly 45% of the variation in shape is due to stratigraphic position.

Bookstein's (1988b) random walk test was also applied to each shape coordinate (Table 2). Of the shape coordinates, only □ab_1 falls within the limits of stasis. All other shape coordinates follow a random walk. Some of the shape coordinates show two apparent trends with respect to stratigraphic position, particularly in the intervals from 0 to 9 meters and from 22 to 24 meters. The □ef_2 shape coordinate is a good example of these trends for 0-9 m and 22-24 m (Fig. 9). Shape coordinates in both of these stratigraphic intervals were tested against an unbiased random walk (Tables 3 and 4). Shape coordinate □ef_1 falls on the cutoff between random walk and anagenesis for meters 22-24, and for meters 0-9 falls within the range of anagenesis. Shape coordinate □ef_2 falls within the range of anagenesis for the meters 22-24 but follows a random walk for meters 0-9. All other shape coordinates (□ab_2, □gh_1 and □gh_2) follow a random walk in both the upper and lower sections of the range of *S. rugosa*.

When compared to DCA Axis 1 scores, □ab_2 and □ef_1 show statistically significant correlations (Figure 10, Table 1). However, both of the corresponding r^2s are small (r^2=0.027 for □ab_2 and r^2=0.023 for □ef_1), suggesting that the vast majority (~97%) of the shape variation is not related to environment.

The morphological distinctiveness of *S. rugosa* and *E. clarksvillensis*

Because *S. rugosa* and *E. clarksvillensis* have had a long and tangled taxonomic history (Wang, 1949; Ross, 1957; Howe, 1972) the two genera were compared to test for their morphological distinctiveness. The defining traits of *E. clarksvillensis* such as denticulated hingeline, dorsal lateral septa and accessory teeth were sometimes absent in *E. clarksvillensis* and sometimes present in *S. rugosa* (Howe, 1972). In this study, denticulation was measured on 35 randomly selected individuals of each genus (Fig. 11). Typically, *E. clarksvillensis* had denticulation (87%), but not throughout the entire hingeline, and *S. rugosa* generally lacked denticulation (60%). In some cases, specimens of *E. clarksvillensis* lacked denticulation and specimens of *S. rugosa* had denticulated hingelines.

Mean centroid size was measured for each genus and then a *t*-test was employed to test for any significant difference in centroid size (Table 5). Mean centroid size of *S. rugosa* was 7.1 mm and is significantly smaller than mean centroid size for *E. clarksvillensis* which had a centroid size of 7.8 mm (t=2.62, n=33, p=0.009) although the actual size difference is not great.

Mean shape coordinates were also compared between *S. rugosa* and *E. clarksvillensis* (Fig. 12, Table 5). Of the shape coordinates, three ($\square ab_1$, $\square ab_2$ and $\square gh_1$) were significantly different. From this figure the position of the ef landmark (tip of the brachiophore process) is similar in both *S. rugosa* and *E. clarksvillensis*. Overall, *S. rugosa* has a wider hingeline, and shorter submedial septa than *E. clarksvillensis*.

Since denticulation is a primary characteristic that can distinguish between genera, denticulated versus non-denticulated *S. rugosa* were also tested for centroid size and shape coordinate differences (Table 6). No significant difference in any morphometric characters was seen. Therefore, denticulated and non-denticulated *S. rugosa* do not differ morphologically in size or shape.

DISCUSSION

Does the morphology of *S. rugosa* change throughout the Kope Formation?

Although some morphological characters follow a random walk, no net change in morphology is seen in *S. rugosa* through the Kope Formation. Centroid size of *S. rugosa* does not vary with stratigraphic position (Fig. 6), nor does it vary with environment (Fig. 7), and it displays stasis (Table 2). Shape coordinates also show no net change with stratigraphic position or environment throughout the Kope Formation, and only □ab_1 (endpoints of the hingeline) displays stasis with the rest following a random walk (Table 2). Despite two significant correlations with environment, the r^2 for each of those comparisons is so small (2.7% and 2.3%) that the result is not biologically meaningful when only a small percent of the observed variation comes from environmental change. However, shape coordinate □gh_1 (tips of the submedial septa) has an r^2 of 0.447 when compared to stratigraphic position. Though this relationship is statistically significant, the biological significance is not clear, as this difference is less than 1 mm and is close to the measurement error in replicates. Shape coordinates □ab_2, □ef_1, and □ef_2 each show a trend in both the upper and lower sections (meters 22-24 and 0-9) of the Kope study interval. These trends offset each other and the shape coordinate shows little net change. In the case of □gh_1, the submedial septa get shorter for the lowest 5 meters and then the septa increase in size to be larger than when they first appeared at meter 0. The trend in the lower study interval of the Kope is so strong that the reverse trend in the upper study interval in the Kope does not offset it and a statistically significant relationship is seen (Table 1).

Several shape coordinates do show persistent trends in the stratigraphic intervals of 0-9 m and 22-24 m. In each case the trend seen from 0-9 m is reversed in the interval from 22-24 m (Fig. 10). For shape coordinates that describe the tips of the brachiophore processes (□ef_1 and □ef_2) noteworthy trends were seen in both intervals. Shape coordinate □ef_1 shows anagenesis from 0-9 m and falls on the cut-off for anagenesis in 22-24 m.

Shape coordinate □ef$_2$ also shows anagenesis from 22-24 m but follows a random walk in 0-9 m. The tips of the brachiophore processes show evolutionary changes in portions of the Kope, but when looking at the scale of the entire study interval these same morphologic characteristics follow a random walk. Patterns of morphologic change are thus scale-dependant.

Because of the unsystematic nature of a random walk (Roopnarine et al., 2001), there is an increased chance of a Type II error (failure to reject a false null hypothesis), owing to the large variances of the predictions of the random walk model, which may cause non-random patterns to appear random (Roopnarine et al., 1999; Sheets and Mitchell, 2001; McCormick and Fortey, 2002). Also, the possibility of the pattern seen being produced by some other dynamic process such as genetic drift (Sheets and Mitchell, 2001) should be considered. Roopnarine et al. (1999) argued that the risk of committing a Type II error increases as stratigraphic completeness decreases because the resemblance of stratophenic series to random walks will increase. McCormick and Fortey (2002) state that the resolution of a Paleozoic stratophenic series may never be sufficient to test against a random walk model. However, this study is an example of what can be done with Paleozoic fossils. The sampling resolution in the Kope is good and conforms closely to McCormick and Fortey's (2002) "ideal field section", which includes: thick rock sequence that is continually fossiliferous with no stratigraphic condensation, confacial rock sequence, high sampling density, and good stratigraphic correlation.

Haney et al.'s (2001) study of *Sowerbyella* cited a need for more detailed temporal and spatial sampling to determine the existence of a contemporaneous cline within each of the five species of *Sowerbyella*. This study provides this detail for one of his five species, *S. rugosa*, by greatly increasing the sample size and specifically testing size and shape against stratigraphic position and environment. Haney et al. (2001) found that centroid size in *Sowerbyella* was not related to energy of environment, substrate condition or relative onshore-offshore position. However, Haney et al. (2001) did find that centroid size changed with stratigraphic position. In this study, centroid size was shown to be static and that it did not change with environment or stratigraphic position. The discrepancy between their findings and the ones of this study could be due to the longer stratigraphic interval (M5, C1 and C3 sequences) that Haney examined. Also, their study encompassed five species of *Sowerbyella*, whereas this study focuses on only one species of *Sowerbyella* in the Kope Formation. However, if there were a contemporaneous cline like they suspect, it ought to be reflected in this data, but is not. A more likely reason for the differences, especially the stepwise decrease in centroid size that Haney et al. (2001) found, is that there may be punctuated changes in size occurring between each of the species of *Sowerbyella*.

With regard to shape change, Haney et al. (2001) report a gradient in shape change between the five species of *Sowerbyella*, but not within each species. One gradient corresponds to onshore-offshore position and the other, stratigraphic position. They attribute the shape change between species to sequence stratigraphic position and note a marked change between species across the maximum flooding surface in the M5 sequence. This study, however, examined only one sequence and there are no condensed sections or major flooding surfaces within the section investigated. Haney et al. (2001) probably observe a cline because the five species of *Sowerbyella* are stratigraphically disjunct. However, each of Haney's species was not investigated independently to look for a continuous cline. When the morphology of *S. rugosa* was tested against environment, no gradient in shape was found.

Ecomorphologic variation between *Sowerbyella rugosa* and *Eochonetes clarksvillensis*

The comparison of *S. rugosa* and *E. clarksvillensis* can be made in this study much the same way that Haney et al. (2001) interpreted the differences between the species of *Sowerbyella*. In the deeper-water Kope Formation, *S. rugosa* have a statistically significant smaller mean centroid size than the shallower water *E. clarksvillensis* from the Liberty Formation. This is the same pattern that Haney et al. (2001) found: a stepwise decrease in centroid size as facies get deeper. Only half of the shape coordinates show any significant difference between *S. rugosa* and *E. clarksvillensis*. However, the ones that show significant differences are the hingeline shape coordinates ($\square ab_1$ and $\square ab_2$) and the submedial septa shape coordinate ($\square gh_1$). The direction in which these shape coordinates change is also reported by Haney et al. (2001) in their onshore-offshore gradient. In both studies, the nearshore brachiopods were narrower in the hingeline and longer in the submedial septa, where the offshore brachiopods had longer hingelines and shorter submedial septa. Haney et al. (2001) found a significant difference in brachial-valve shape with environment and attributed this mainly to lithofacies differences. The reasons are similar in this study in that shape differences between *S. rugosa* and *E. clarksvillensis* can be attributed to facies change.

Another aspect of the difference between *S. rugosa* and *E. clarksvillensis* is the pattern of denticulation on the hingeline, with *E. clarksvillensis* possessing a denticulated hingeline, and *S. rugosa* lacking denticulation (Howe, 1972). In the course of this study, it became clear that this was not always the case. It was found that 87% of *E. clarksvillensis* brachiopods were denticulated, whereas only 60% of *S. rugosa* were not denticulated (Figs. 4 and 11), indicating that not all specimens show this characteristic and that caution must be used in species identification using isolated specimens. Partial denticulation on *S. rugosa* was also found by Ross (1957) and Cox and Rong (1989).

The possibility of *S. rugosa* and *E. clarksvillensis* being ecomorphs of each other is not likely. *S. rugosa* occurs in the C1 depositional sequence where there are only offshore *S. rugosa* found. No sowerbyellid species occur in the transition zone of the C1 sequence. *E. clarksvillensis* occur in the C5 depositional sequence in the transition zone and there are no sowerbyellids present in other facies of the C5 sequence. Therefore, these species cannot be ecomorphs of each other because they do not co-occur. In addition, *S. rugosa* was tested against a cline and no clinal variation was found.

Punctuated Equilibrium versus Gradualism

One of the outcomes of this study was to comment on the mode of evolution in *S. rugosa* and *E. clarksvillensis*. The morphologic character overlap of denticulation in these two closely related brachiopods, stasis in centroid size (and one shape coordinate) of *S. rugosa* and the lack of morphologic change along a cline of *S. rugosa* all suggest punctuated equilibrium as the mode of evolution in these brachiopods. However, not all morphologic characteristics in *S. rugosa* show stasis; in fact, most of the shape coordinates follow a random walk. Cheetham (1987) found that despite morphologic change in single characters in the bryozoan *Metrarabdotos* there was an overall pattern of morphologic stasis, which is the implicit pattern in this study as well. McCormick and Fortey (2002) argue that punctuated and gradual change cannot be meaningfully separated unless there is consideration of stratigraphic resolution because an event that appears punctuated at a coarser resolution may appear gradual at a finer resolution. As a solution to this dilemma, McCormick and Fortey (2002) suggest statistically testing for sustained unidirectional change. As previously mentioned, this study tested for anagenesis over the entire Kope Formation and found none.

Despite the change between *S. rugosa* and *E. clarksvillensis* appearing to be punctuated, long-term gradualism cannot be ruled out as a cause of morphologic change because there is a time gap of roughly four million years between the last occurrence of *S. rugosa* and first appearance of *E. clarksvillensis* (Fig 13). While there is no net change in morphology of *S. rugosa* throughout the Kope, it could have undergone a gradual change that is too gradual to be detected at the resolution of this study.

The difficulty in determining the mode of evolution in fossil species is largely due to problems with the fossil record. Holland (2000) modeled the effects of sequence architecture on observed patterns of morphologic change and found that abrupt changes in morphology tend to occur near a transgressive surface, maximum flooding surface or at a sequence boundary.

Other problems interpreting such data arise from the four different biases of the fossil record (Holland, 2000) that consist of sampling bias, unconformity bias, facies bias, and condensation bias. In this study, these biases were avoided by consistency of sampling effort, sampling within one sequence so there were no unconformities, testing changes in morphology against changes in environment, and by the lack of strong variation in depositional rates (Holland et al., 1997). Sequence stratigraphy plays an important role in determining patterns of preservation of fossils and also how patterns of evolution appear (Bayer and McGhee,1985; Brett, 1995b; Holland, 1995, 2000; McCormick and Fortey, 2002). For non-sequence-stratigraphic example, Cheetham (1986: Fig. 5) shows the morphological evolution of the bryozoan *Metrarabdotos*, which has several punctuations in its lineage. However some of the punctuation events lie near sequence boundaries at the base of NN11 nannofossil biochrono- stratigraphic zone, the middle of NN11 and the base of NN15 (Haq et al.,1987). The record throughout this section is incomplete and though these speciation events appear punctuated, there is no way to be certain that gradual evolutionary change did not occur during these gaps.

Other problems such as time averaging and preservation can also obscure the patterns of evolution. Although time averaging may have a substantial effect on shell beds, Bush et al. (2002) recently found that if a morphologic character displays stasis, time averaging will have little affect on net preservation of that character. Although the most common durations of time averaging are on the order of thousands to tens of thousands of years (Kidwell and Flessa, 1996), time averaging should not have a notable affect on the outcome of this study because the Kope consists of numerous storm beds with an average recurrence time of hundreds of years (Kowalewski and Bambach, 2002). Furthermore, any pattern of stasis is unlikely to be falsely generated or removed by time averaging (Jablonski, 2000; Kidwell and Holland, 2002).

Given that the stratigraphic resolution of this study is high, *S. rugosa* are abundant, and that the Kope Formation lacks significant internal sequence boundaries or facies change, this section is nearly ideal for studying patterns of evolution (Gingerich, 1985; Jackson and Cheetham, 1999; McCormick and Fortey, 2002). More studies need to be done on morphologic change in which there is good sequence stratigraphic control and high sampling resolution. These "ideal" sections are difficult to find, but are necessary to assess evolutionary trends.

CONCLUSIONS

1. Morphology of *S. rugosa* displays no net change with stratigraphic position or depositional environment. Neither centroid size nor shape coordinates showed any significant correlation with time or with environment. Therefore no cline was present during the timespan of *S. rugosa*.
2. All morphologic characters of *S. rugosa* follow a random walk with the exception of centroid size and one of the six shape coordinates, which both display stasis. Although some shape coordinates show anagenesis over part of the stratigraphic section, no anagenesis is seen over the entire stratigraphic interval. In contrast, characters that show stasis do so consistently throughout the entire stratigraphic interval.
3. *S. rugosa* and *E. clarksvillensis* differ significantly in centroid size and half of the shape coordinates. *S. rugosa* is smaller in size and has a longer hingeline but shorter submedial septa than *E. clarksvillensis*. *S. rugosa* is found in a deeper water facies than *E. clarksvillensis*, and the same trend of mean size decrease in deeper water and increase in hingeline but decrease in septa length

in deeper water was reported by Haney et al. (2001) among five different species of *Sowerbyella*.

4. The change in morphologies between *S. rugosa* and *E. clarksvillensis* may have resulted from a punctuational event or may be attributable to slow gradual evolution that takes place over a 4 m.y. gap that occurs between the last occurrence of *S. rugosa* and the first appearance of *E. clarksvillensis*. Because this gap is present, it is impossible to determine with certainty that this is a case of punctuated equilibrium rather than long-term gradualism that is too gradual to be seen at the resolution of a few million years.

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CHAPTER 3

CONCLUSIONS

In order to investigate patterns of evolution, morphometric analysis was performed on the Upper Ordovician brachiopod *Sowerbyella rugosa* from the Kope Formation. Centroid size and shape coordinates were compared to both stratigraphic position and a quantitative proxy of environment. Neither shape nor size showed any significant correlation with either stratigraphic position or environment. Each of the morphologic characters (centroid size and all of the shape coordinates) was tested against Bookstein's (1988b) random walk to determine what evolutionary mode the character exhibited. Centroid size and one of six shape coordinate showed stasis throughout the Kope Formation, with the rest of the shape coordinates following a random walk through the Kope Formation. However, several shape coordinates displayed anagenesis in the 0-9 m and 22-24m stratigraphic ranges.

In addition, *Sowerbyella rugosa* was compared to *Eochonetes clarksvillensis* from the Liberty Formation to determine if their morphologies can be distinguished quantitatively. They were found to differ in mean centroid size, and in three of six shape coordinates. *S. rugosa* is smaller in size and has a wider but narrower shell than *E. clarksvillensis*. In addition, most *E. clarksvillensis* was found to have denticulation, whereas most *S. rugosa* did not. However, some *S. rugosa* were denticulated and some *E. clarksvillensis* were not.

The jump in morphologies between *S. rugosa* and *E. clarksvillensis* may have resulted from a punctuated equilibrium event or may be attributable to very gradual evolution that takes place over a 4 m.y. gap that occurs between the last occurrence of *S. rugosa* and the first appearance of *E. clarksvillensis*. Since this gap is present it is impossible to determine with certainty that this is a case of punctuated equilibrium rather than long-term gradualism that is too gradual to be seen at the resolution of a few million years.

TABLE 1 – r^2 values of shape coordinates versus centroid size, stratigraphic position and DCA Axis 1

	□ab_1	**□ab_2**	**□ef_1**	**□ef_2**	**□gh_1**	**□gh_2**
Centroid Size	0.008	0.024*	0.011	0.040*	0.004	0.099*
Stratigraphic Position	0.016	0.009	0.000	0.060	0.447*	0.033
DCA Axis 1	0.011	0.027*	0.023*	0.000	0.006	0.000

* significant at □=0.05

TABLE 2 – Bookstein's (1988b) test for anagenesis and stasis applied to centroid size and shape coordinates over the Kope Formation

Variable	Maximum excursion	Anagenesis limit	Stasis limit	Conclusion
Centroid Size	0.276	1.693	0.467	stasis
□ab_1	0.048	0.323	0.089	stasis
□ab_2	0.110	0.186	0.051	random walk
□ef_1	0.031	0.038	0.010	random walk
□ef_2	0.030	0.047	0.013	random walk
□gh_1	0.061	0.093	0.026	random walk
□gh_2	0.020	0.053	0.015	random walk

TABLE 3 – Bookstein's (1988b) test for anagenesis and stasis applied to centroid size and shape coordinates for meters 0-9 of the Kope

Variable	**Maximum excursion**	**Anagenesis limit**	**Stasis limit**	**Conclusion**
Centroid Size	0.210	1.209	0.333	stasis
□ab_1	0.048	0.187	0.051	stasis
□ab_2	0.110	0.122	0.034	random walk
□ef_1	0.031	0.028	0.008	anagenesis
□ef_2	0.030	0.038	0.011	random walk
□gh_1	0.061	0.071	0.019	random walk
□gh_2	0.016	0.040	0.011	random walk

TABLE 4 – Bookstein's (1988b) test for anagenesis and stasis applied to centroid size and shape coordinates for meters 22-24 of the Kope

Variable	Maximum excursion	Anagenesis limit	Stasis limit	Conclusion
Centroid Size	0.276	1.056	0.291	stasis
□ab_1	0.035	0.164	0.045	stasis
□ab_2	0.096	0.135	0.037	random walk
□ef_1	0.022	0.022	0.006	anagenesis
□ef_2	0.026	0.024	0.007	anagenesis
□gh_1	0.030	0.058	0.016	random walk
□gh_2	0.020	0.034	0.015	random walk

TABLE 5 – t-test comparison of centroid size and shape coordinates in *Sowerbyella and Eochonetes* (n=33, □=0.05)

Variable	**t**	**p**
Centroid Size	2.62	0.009
$□ab_1$	3.04	0.004
$□ab_2$	-11.39	<0.001
$□ef_1$	-0.94	0.352
$□ef_2$	-1.68	0.092
$□gh_1$	5.85	<0.001
$□gh_2$	1.18	0.247

TABLE 6 – t-test comparison of centroid size and shape coordinates in denticulated versus non-denticulated *Sowerbyella* (n=274, α=0.05)

Variable	**t**	**p**
Centroid Size	0.062	0.950
□ab_1	0.450	0.653
□ab_2	0.004	0.997
□ef_1	1.190	0.235
□ef_2	1.419	0.157
□gh_1	1.531	0.127
□gh_2	0.299	0.764

FIGURE 1 – DCA Axis 1 scores for representative samples from the Kope Formation. Small axis 1 values are interpreted to reflect deeper-water settings, with large axis 1 values as indicative of shallower-water environments. Reprinted with permission from Holland et al., 2001.

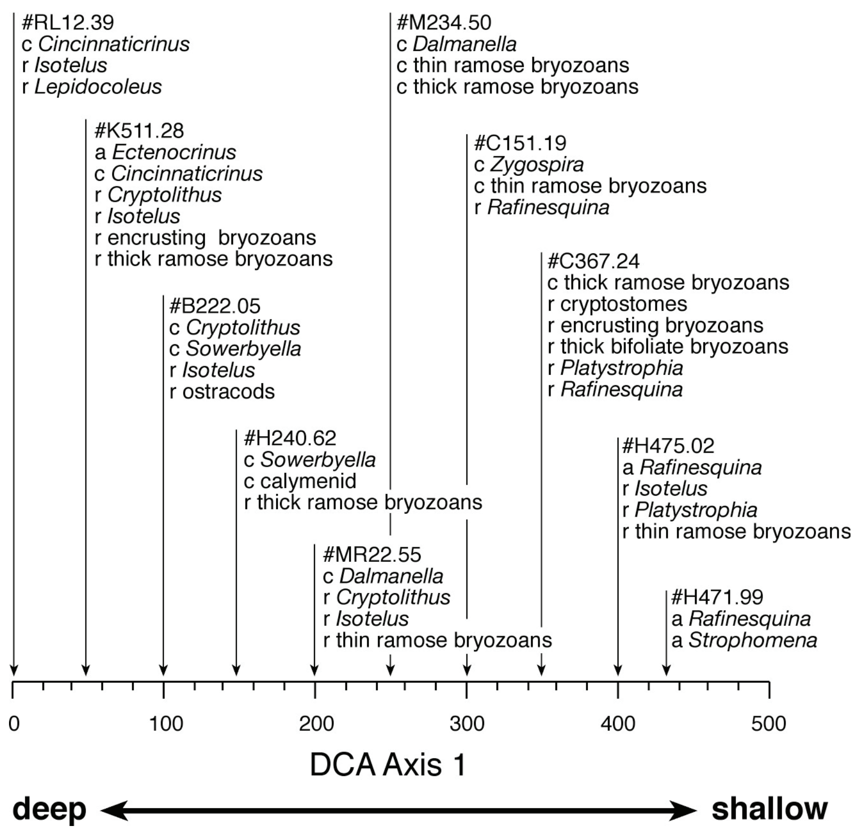

#RL12.39
c *Cincinnaticrinus*
r *Isotelus*
r *Lepidocoleus*
#K511.28
a *Ectenocrinus*
c *Cincinnaticrinus*
r *Cryptolithus*
r *Isotelus*
r encrusting bryozoans
r thick ramose bryozoans
#B222.05
c *Cryptolithus*
c *Sowerbyella*
r *Isotelus*
r ostracods
#H240.62
c *Sowerbyella*
c calymenid
r thick ramose bryozoans
#MR22.55
c *Dalmanella*
r *Cryptolithus*
r *Isotelus*
r thin ramose bryozoans
#M234.50
c *Dalmanella*
c thin ramose bryozoans
c thick ramose bryozoans
#C151.19
c *Zygospira*
c thin ramose bryozoans
r *Rafinesquina*
#C367.24
c thick ramose bryozoans
r cryptostomes
r encrusting bryozoans
r thick bifoliate bryozoans
r *Platystrophia*
r *Rafinesquina*
#H475.02
a *Rafinesquina*
r *Isotelus*
r *Platystrophia*
r thin ramose bryozoans
#H471.99
a *Rafinesquina*
a *Strophomena*
0
100
200
300
400
500
DCA Axis 1
deep
shallow

FIGURE 2 – Map showing locations of K445 where *S. rugosa* was collected from the Kope Formation and South Gate Hill, where *E. clarksvillensis* was collected from the Liberty Formation.

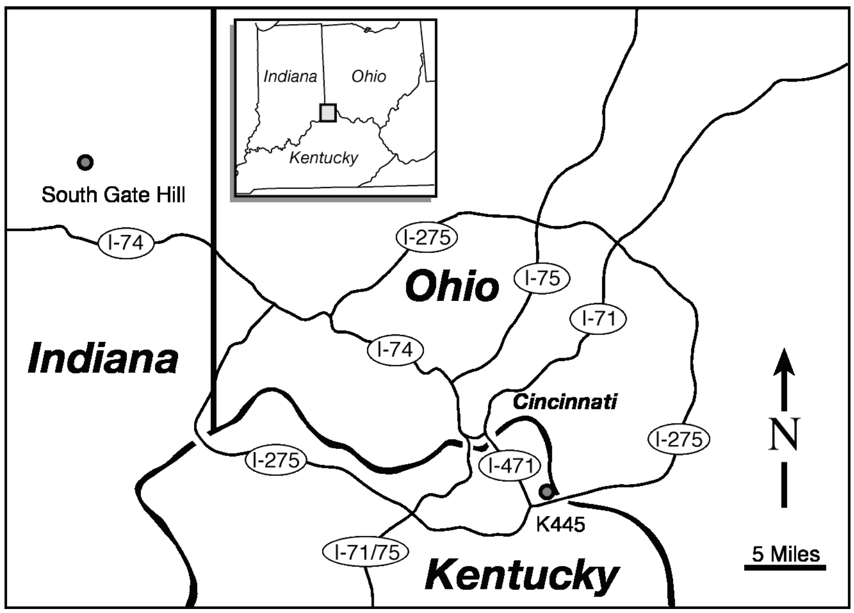
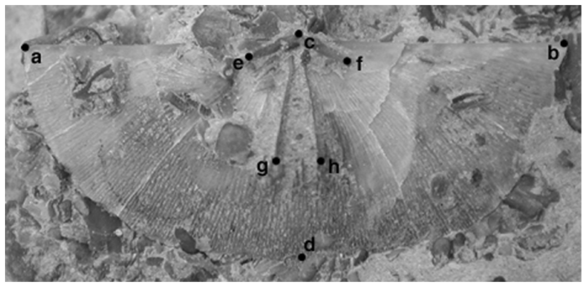

Indiana
Ohio
Kentucky
South Gate Hill
I-74
I-275
Ohio
I-75
I-71
Indiana
I-74
Cincinnati
I-275
I-275
I-471
K445
I-71/75
Kentucky
N
5 Miles

FIGURE 3 – A) Representative *S. rugosa* with landmarks. a and b are the tips of the hingeline, c is the beak, d is at the anterior intersection on the commissure and the symmetry plane, e and f are the anterior-lateral tips of the brachiophore processes, and g and h are the anterior tips of the submedial septa. B) Landmarks as reflected across the c-d baseline (the symmetry plane).

A Landmarks



B Reflected landmarks

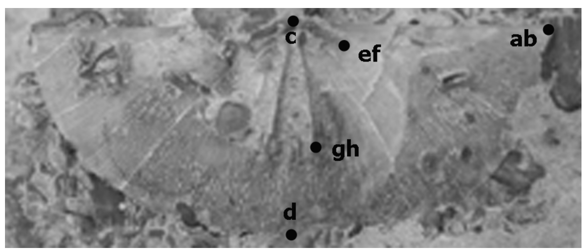


FIGURE 4 – Scale of hingeline denticulation, as illustrated by representative valves of *S. rugosa*.

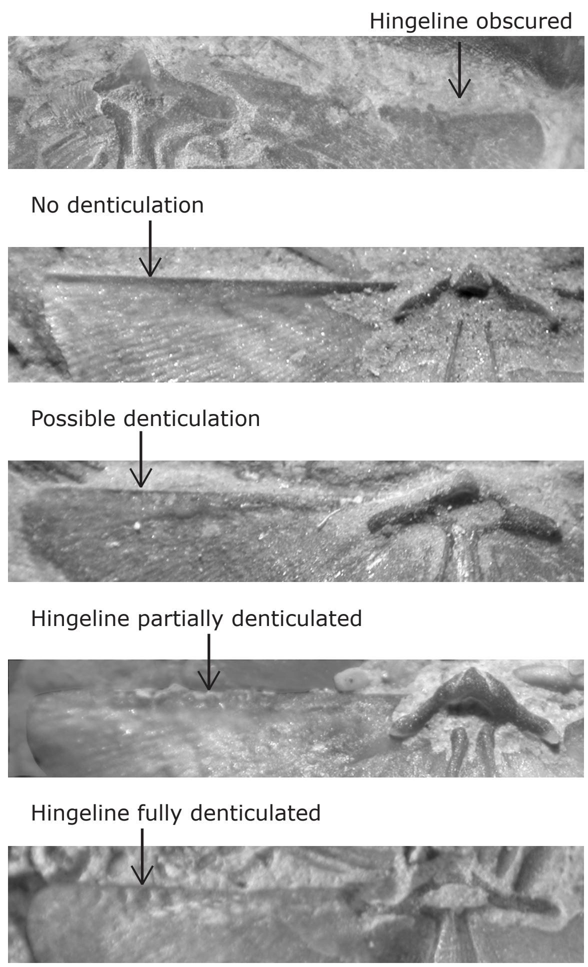
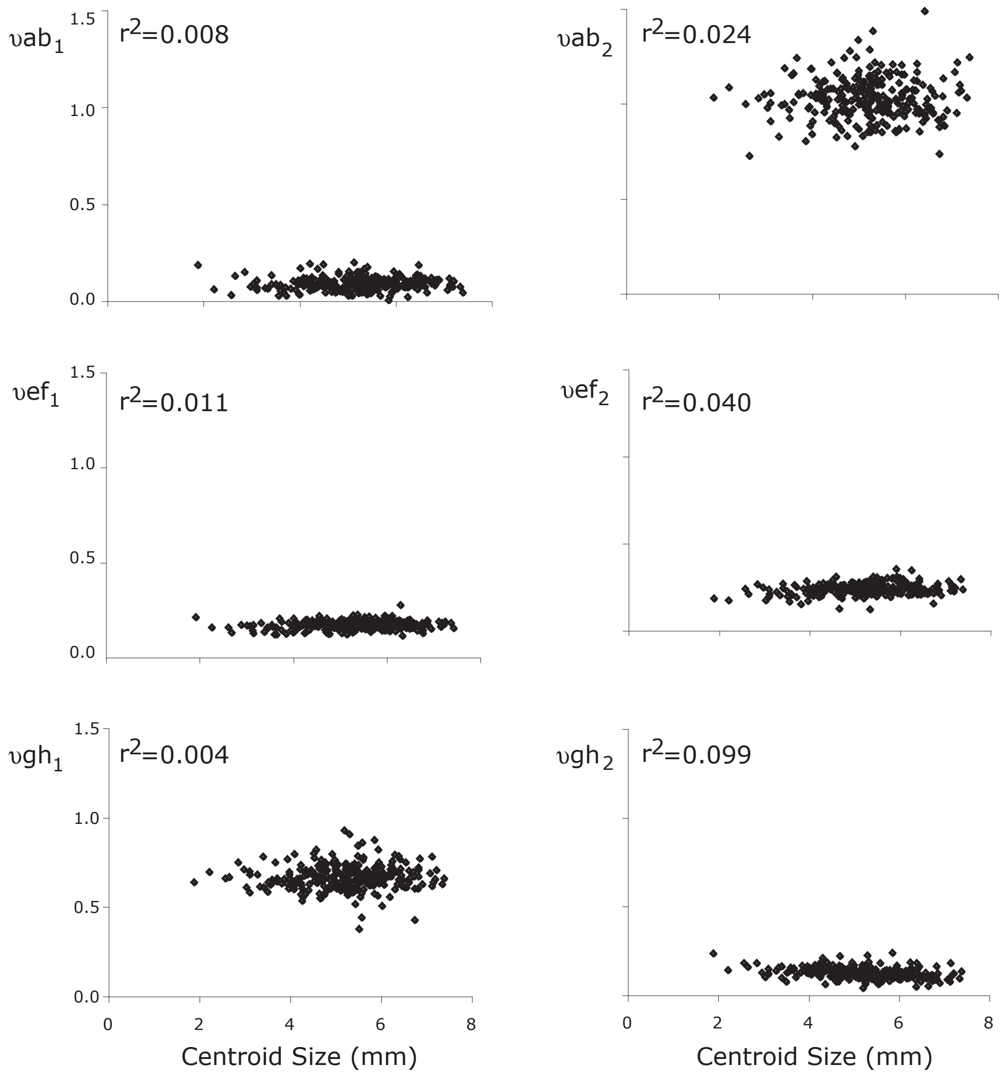
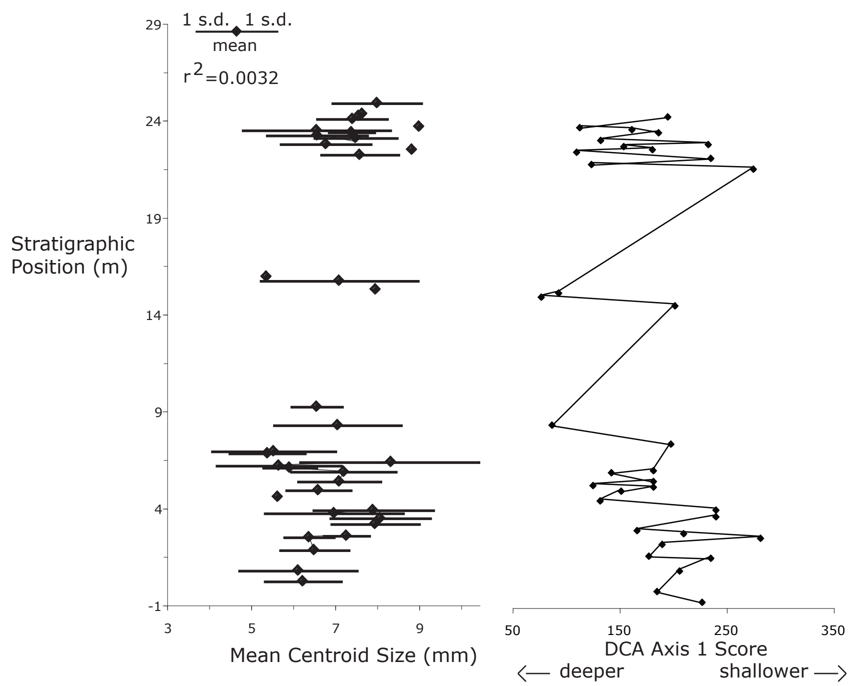

Hingeline obscured
No denticulation
Possible denticulation
Hingeline partially denticulated
Hingeline fully denticulated

FIGURE 5 – Plots of shape coordinates versus centroid size.



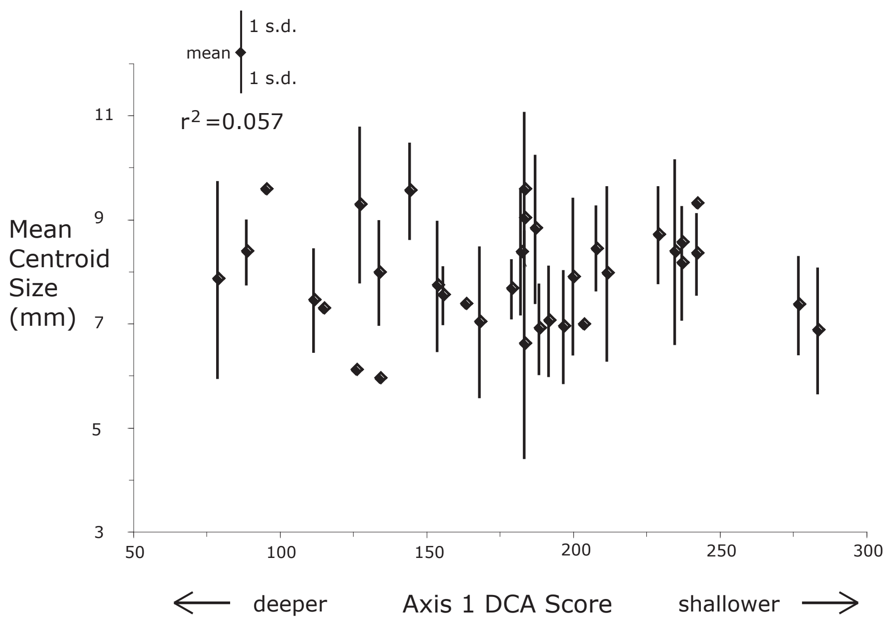
υab1
r2=0.008
υab2
r2=0.024
υef1
r2=0.011
υef2
r2=0.040
υgh1
r2=0.004
υgh2
r2=0.099
1.5
1.0
0.5
0.0
0
2
4
6
8
Centroid Size (mm)
Centroid Size (mm)

FIGURE 6 – Mean centroid size (diamond) of each *Sowerbyella*-bearing bed plotted against stratigraphic position. The DCA Axis 1 trend of Holland et al. (2001) is shown for comparison. The low r^2 indicates that minimal variation in centroid size is related to stratigraphic position.



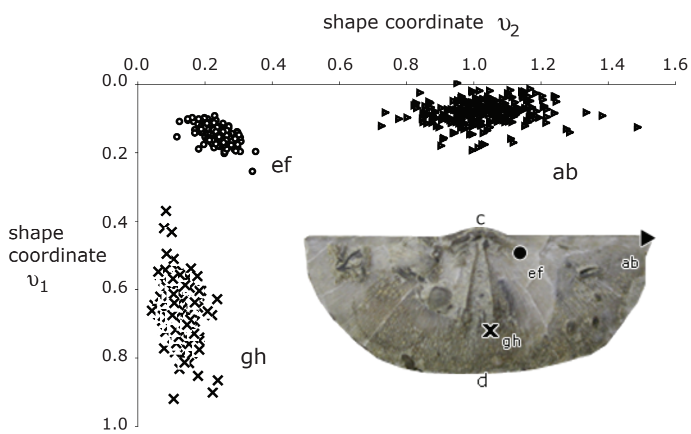
1 s.d. 1 s.d.
mean
r2=0.0032
Stratigraphic Position (m)
29
24
19
14
9
4
-1
3
5
7
9
Mean Centroid Size (mm)
50
150
250
350
DCA Axis 1 Score
deeper
shallower

FIGURE 7 – Mean centroid size plotted against DCA Axis 1 scores of Holland et al. (2001). As shown by the very small r^2, variation in centroid size is not related to environment.



1 s.d.
mean
1 s.d.
$r^2 = 0.057$
Mean Centroid Size (mm)
11
9
7
5
3
50
100
150
200
250
300
deeper
Axis 1 DCA Score
shallower

FIGURE 8 – Scatter plot of the shape coordinates with a representative *Sowerbyella rugosa* for reference. Composite landmark ab is shown by triangles, ef is shown by circles, and gh is shown by x's.



shape coordinate υ_2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
shape coordinate υ_1
ef
ab
gh
c
d

FIGURE 9 – Shape coordinates plotted against stratigraphic position for *S. rugosa*. Although many of the shape coordinates show trends over portions of the study interval, there are no significant correlations of shape with stratigraphic position as a whole.

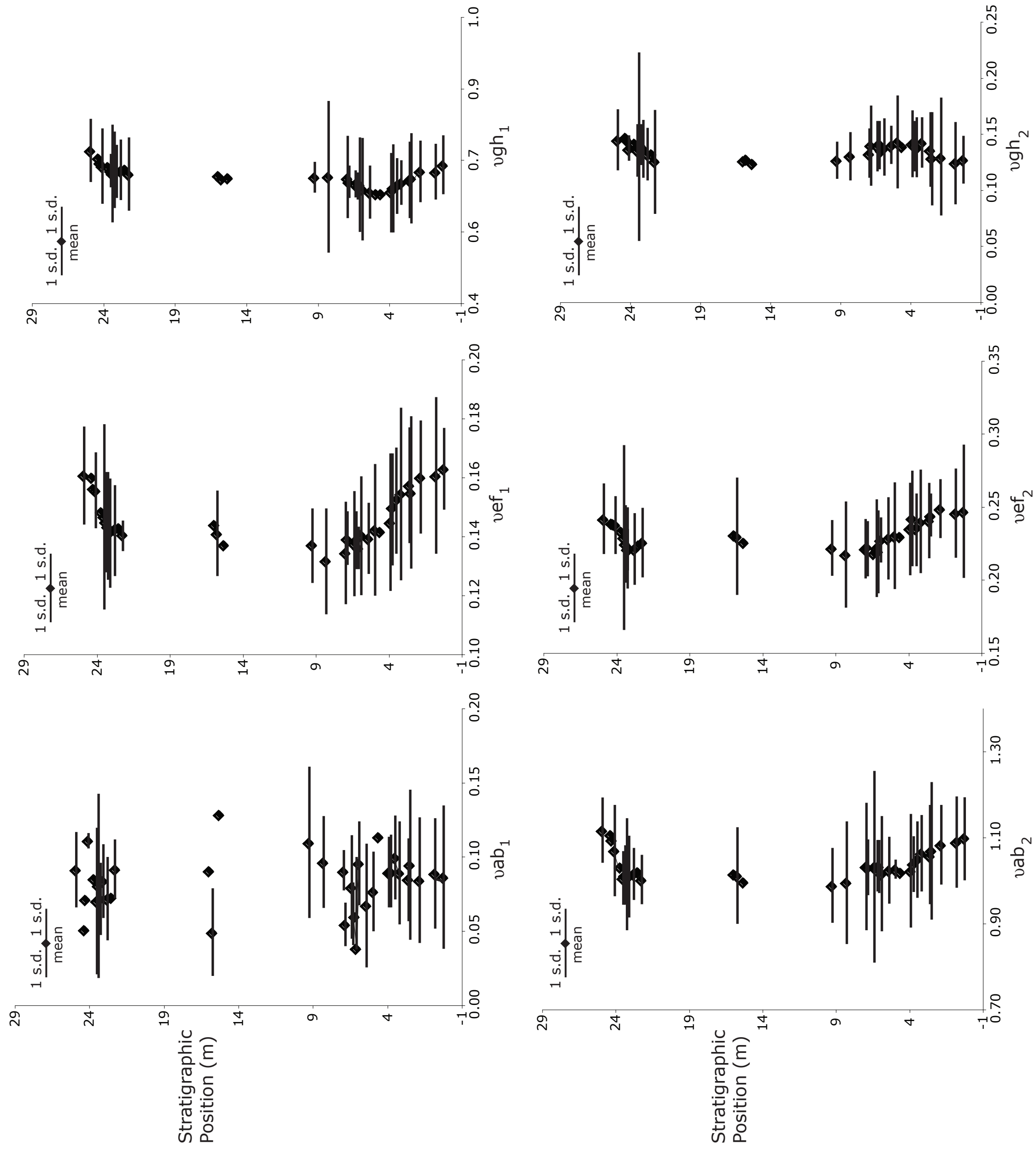
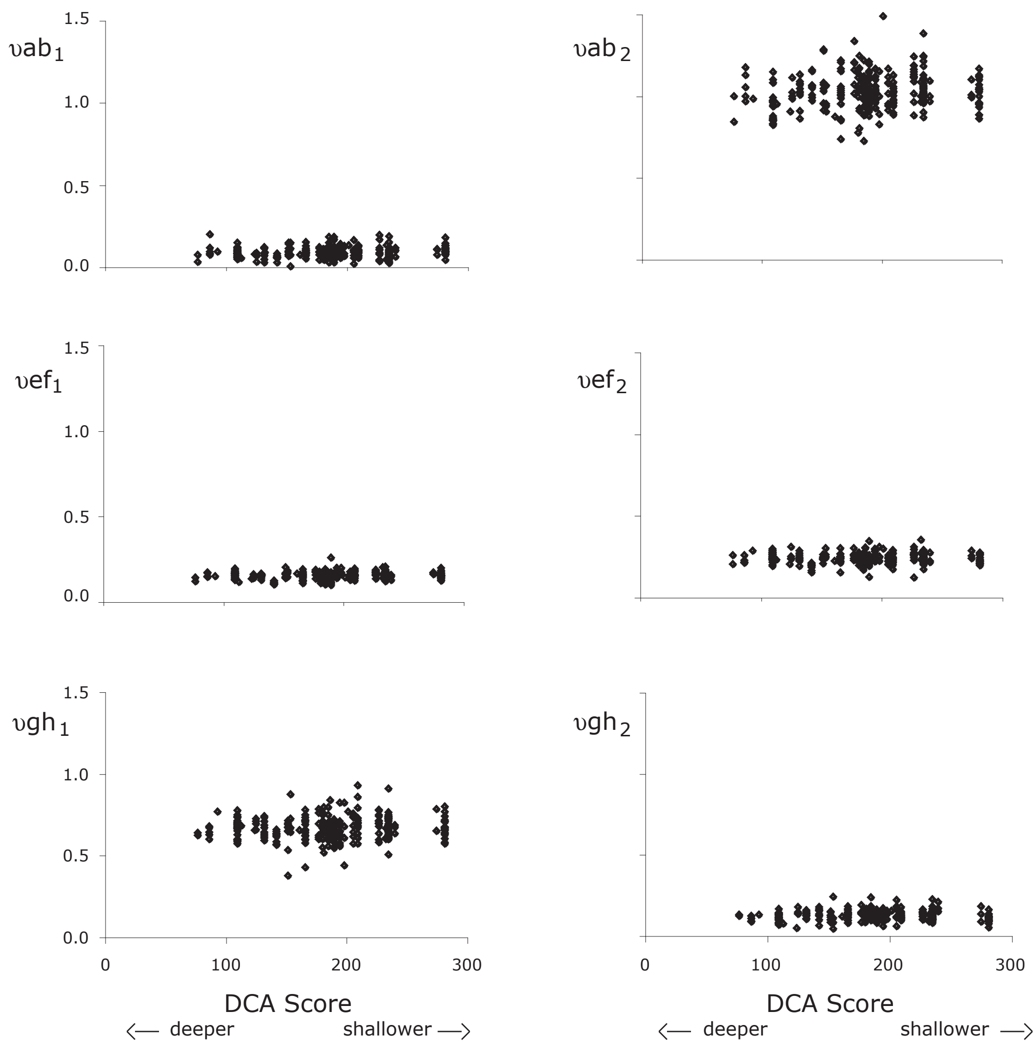

Stratigraphic Position (m)
Stratigraphic Position (m)
1 s.d. 1 s.d.
mean
υab1
υef1
υgh1
υab2
υef2
υgh2

FIGURE 10 – Shape coordinates plotted against DCA Axis 1 scores (Holland et al., 2001) for *S. rugosa*.



υab1
υab2
υef1
υef2
υgh1
υgh2
1.5
1.0
0.5
0.0
0
100
200
300
DCA Score
deeper
shallower

FIGURE 11 – Frequency distributions of denticulation for thirty-five randomly chosen specimens of *S. rugosa* and *E. clarksvillensis*. Although there is some overlap in this distinguishing characteristic, the majority for each genus falls where expected, with *Sowerbyella* displaying no overall denticulation and *Eochonetes* bearing hingeline denticulation.

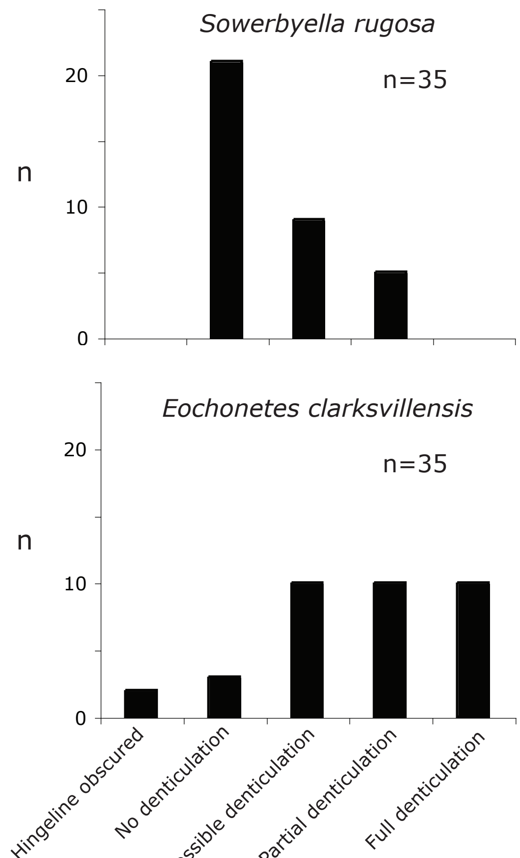
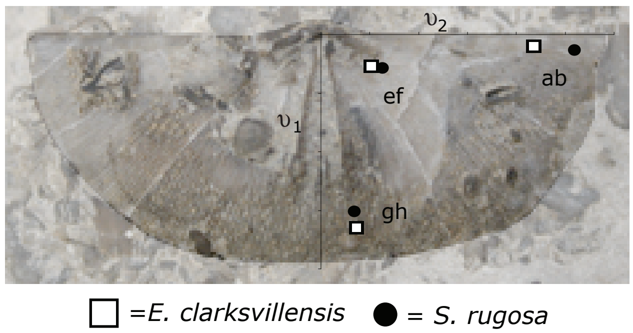
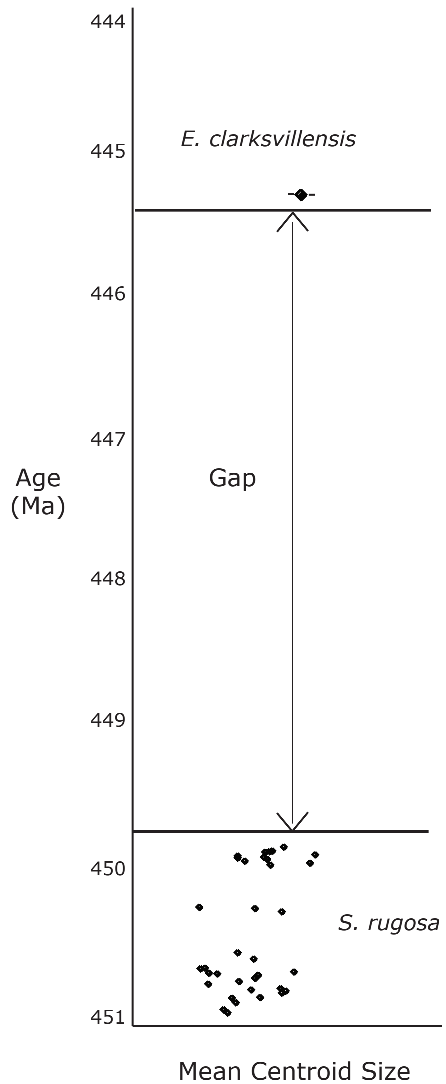

Sowerbyella rugosa
n=35
n
20
10
0
Eochonetes clarksvillensis
n=35
n
20
10
0
Hingeline obscured
No denticulation
Possible denticulation
Partial denticulation
Full denticulation

FIGURE 12 – Relative mean positions of landmarks on *S. rugosa* and *E. clarksvillensis*, displayed on a representative specimen of *S. rugosa*.



υ_2
ab
ef
υ_1
gh
□ =*E. clarksvillensis* ● = *S. rugosa*

FIGURE 13 – Illustration of the 4 m.y. time gap between the last appearance of *S. rugosa* and the first appearance of *E. clarksvillensis*. Each diamond represents the average centroid size per bed. One standard deviation is indicated for the *E. clarksvillensis* sample.


444
445
446
447
448
449
450
451
E. clarksvillensis
Gap
S. rugosa
Age (Ma)
Mean Centroid Size

APPENDIX A

Landmark Coordinates for *Sowerbyella rugosa* (in cm)

	a		b		c		d		e		f		g		h	
	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y
0a.5	0.23	0.12			0.65	0.10	0.65	0.45	0.56	0.17			0.60	0.36	0.70	0.36
0a.6	0.10	0.12			0.67	0.08	0.67	0.59	0.54	0.16	0.77	0.16	0.60	0.47	0.72	0.45
0a.11	0.10	0.24	1.11	0.25	0.59	0.23	0.59	0.66	0.47	0.31	0.70	0.29	0.53	0.56	0.63	0.57
0a.16	0.18	0.11			0.64	0.09	0.64	0.48	0.55	0.16			0.59	0.36	0.70	0.36
0a.21	0.06	0.40	1.25	0.45	0.65	0.41	0.65	0.93	0.51	0.50	0.79	0.50	0.59	0.77	0.69	0.78
0a.25	0.06	0.09	0.84	0.08	0.47	0.06	0.47	0.39	0.40	0.10	0.56	0.10	0.41	0.31	0.52	0.31
0a.27	0.07	0.17			0.68	0.08	0.68	0.64	0.54	0.18	0.67	0.16	0.62	0.48	0.76	0.45
0a.40	0.08	0.31	1.24	0.34	0.67	0.27	0.67	0.81	0.53	0.37	0.81	0.36	0.62	0.64		
0a.46	0.07	0.33	1.35	0.32	0.71	0.26	0.71	0.84			0.88	0.36			0.80	0.66
0a.47			1.01	0.50	0.52	0.41	0.52	0.89	0.38	0.49	0.63	0.49	0.44	0.74	0.55	0.75
0a.52	0.19	0.58	1.32	0.57	0.76	0.53	0.76	1.12	0.60	0.63	0.90	0.63	0.67	0.87	0.84	0.87
0a.53	0.07	0.52	1.33	0.55	0.72	0.50	0.72	1.06	0.57	0.58	0.87	0.58	0.63	0.82	0.78	0.84
0a.54			0.95	0.25	0.42	0.19	0.42	0.79	0.24	0.29	0.60	0.29	0.34	0.58	0.48	0.56
0b.1	0.77	0.81	1.79	0.83	1.28	0.80	1.28	1.25	1.17	0.86	1.39	0.87	1.24	1.05	1.34	1.05
0b.20			1.93	0.82	1.60	0.78	1.60	1.10	1.51	0.82	1.68	0.83	1.53	1.01	1.65	1.02
0b.23	1.11	0.98			1.70	0.93	1.70	1.52	1.59	0.99	1.82	0.99	1.65	1.28	1.78	1.28
0b.27	1.42	0.76	1.88	0.73	1.65	0.70	1.65	0.93	1.62	0.75	1.70	0.74			1.71	0.85
0b.28	1.27	0.96			1.81	0.92	1.81	1.36	1.69	0.97	1.92	0.99	1.72	1.18	1.88	1.21
0b.29			2.17	0.88	1.63	0.87	1.63	1.41			1.73	0.93			1.69	1.25
0b.30	1.04	1.11	1.93	1.10	1.50	1.08	1.50	1.53	1.41	1.13	1.60	1.13	1.44	1.36		
0b.31			2.05	1.15	1.61	1.11	1.61	1.61			1.69	1.16	1.56	1.41	1.68	1.41

0b.33	0.78	0.98	2.18	0.94	1.46	0.91	1.46	1.56	1.31	1.00	1.60	0.99	1.37	1.32	1.54	1.33
0b.34	1.21	1.06			1.80	1.01	1.80	1.54	1.66	1.10	1.94	1.10	1.71	1.38		
0b.37	1.20	0.72	2.37	0.72	1.77	0.67	1.77	1.30	1.63	0.75	1.91	0.74	1.73	1.06	1.85	1.06
0b.40	0.98	1.06	2.28	1.07	1.66	0.99	1.66	1.63	1.49	1.10	1.81	1.08	1.56	1.42	1.71	1.42
0b.41	1.12	0.98			1.66	0.95	1.66	1.44	1.55	1.02			1.58	1.29		
0b.45	1.29	0.79	2.49	0.82	1.89	0.76	1.89	1.31	1.74	0.84	2.02	0.85	1.82	1.13	1.92	1.14
0b.48	1.37	0.91	2.54	0.92	1.95	0.88	1.95	1.44	1.83	0.94	2.08	0.95	1.87	1.26	2.00	1.26
0b.49	0.74	0.80			1.34	0.76	1.34	1.37	1.23	0.83			1.24	1.13		
0b.52	1.11	1.13	2.01	1.13	1.55	1.09	1.55	1.52	1.46	1.15	1.66	1.15	1.50	1.43	1.62	1.42
0b.61			1.79	1.17	1.51	1.12	1.51	1.51	1.43	1.16	1.59	1.17	1.43	1.38	1.55	1.38
1a.9	1.00	0.60			1.49	0.51	1.49	1.05	1.36	0.60			1.46	0.87		
1a.10	0.95	0.51	2.14	0.46	1.54	0.43	1.54	0.98	1.40	0.51	1.68	0.49	1.50	0.78	1.62	0.76
1a.15	1.16	0.22			1.69	0.17	1.69	0.66	1.59	0.26	1.80	0.23			1.78	0.45
1a.17			1.63	0.45	1.15	0.41	1.15	0.84	1.05	0.48	1.25	0.48	1.11	0.73	1.20	0.72
1a.19	1.21	0.66			1.77	0.63	1.77	1.23	1.65	0.71			1.67	1.08	1.86	1.07
1a.23	1.71	1.34			2.41	1.33	2.41	1.93			2.53	1.42	2.30	1.78		
1a.26	0.69	0.33	1.62	0.36	1.16	0.30	1.16	0.79	1.06	0.38	1.27	0.38	1.11	0.62	1.22	0.61
1a.28			2.19	1.22	1.65	1.19	1.65	1.72			1.78	1.26	1.53	1.55		
2a.1	1.66	1.18	2.59	1.19	2.16	1.14	2.16	1.54	2.05	1.22	2.24	1.21	2.12	1.43	2.22	1.41
2a.3	1.91	1.72			2.50	1.71	2.50	2.29	2.34	1.78			2.39	2.05	2.54	2.06
2a.10			2.16	1.31	1.65	1.21	1.65	1.77	1.51	1.28	1.78	1.29	1.58	1.58	1.70	1.60
2a.24	0.99	1.24			1.60	1.20	1.60	1.64	1.48	1.27			1.51	1.60		
2a.28	1.34	0.95			1.97	0.89	1.97	1.41	1.84	0.99			1.92	1.24		
2a.31	1.47	0.85	2.57	0.87	2.03	0.82	2.03	1.27	1.92	0.90	2.14	0.90	1.95	1.16	2.09	1.15
2a.34	1.76	1.47			2.34	1.45	2.34	1.91	2.22	1.53	2.46	1.53	2.28	1.79	2.40	1.79
2b.5	0.08	0.43			0.70	0.41	0.70	0.92	0.56	0.49	0.83	0.49	0.61	0.80	0.76	0.82
2b.13	0.14	0.60	1.31	0.62	0.72	0.57	0.72	1.01			0.83	0.65			0.78	0.90

2b.17	0.32	0.36	1.69	0.31	1.01	0.28	1.01	0.92	0.81	0.41	1.19	0.38	0.94	0.68	1.10	0.67
2b.18	0.36	0.41	1.67	0.45	0.99	0.36	0.99	0.93			1.12	0.46	0.88	0.71		
2b.20			1.66	0.34	1.01	0.26	1.01	0.90			1.16	0.34			1.07	0.64
2b.24	0.12	0.30	1.47	0.30	0.79	0.26	0.79	0.82			0.93	0.35	0.72	0.65	0.87	0.64
3a.7	0.70	0.80			1.45	0.74	1.45	1.41	1.30	0.85	1.61	0.86	1.35	1.11	1.52	1.12
3a.8	0.19	0.93			0.80	0.88	0.80	1.39	0.67	0.97	0.93	0.96	0.75	1.25	0.86	1.24
3a.9	0.47	1.16	2.00	1.16	1.26	1.09	1.26	1.81	1.09	1.21	1.41	1.19	1.15	1.55	1.32	1.56
3a.10	0.53	0.91	1.83	0.90	1.15	0.83	1.15	1.50	1.02	0.93	1.32	0.91	1.07	1.19	1.20	1.23
3a.11			1.86	0.97	1.11	0.84	1.11	1.57			1.26	0.95	1.05	1.31	1.16	1.32
3a.14	0.87	1.14	2.27	1.11	1.53	1.08	1.53	1.76	1.35	1.16	1.70	1.15	1.41	1.54	1.59	1.53
3a.16	0.66	0.77	2.02	0.72	1.34	0.70	1.34	1.29	1.20	0.79	1.48	0.78	1.29	1.12	1.39	1.12
3a.17			1.36	1.31	0.76	1.24	0.76	1.86	0.63	1.32	0.88	1.32	0.67	1.64	0.83	1.65
3a.18	1.30	0.85	2.34	0.87	1.82	0.83	1.82	1.38	1.69	0.91	1.95	0.91	1.75	1.22	1.90	1.21
3a.20	0.74	0.74			1.28	0.72	1.28	1.21	1.18	0.77			1.22	1.02	1.34	1.02
3a.21			1.96	0.44	1.33	0.41	1.33	1.01	1.21	0.51	1.46	0.50	1.28	0.78	1.39	0.79
3a.22			1.11	1.19	0.51	1.13	0.51	1.69	0.37	1.22	0.62	1.21			0.56	1.49
3a.23	0.23	0.81	1.71	0.79	0.99	0.76	0.99	1.37	0.78	0.91			0.93	1.21	1.06	1.18
3a.25			1.95	1.02	1.34	0.98	1.34	1.60	1.22	1.06	1.45	1.07	1.25	1.38	1.38	1.37
3a.26	0.68	1.45			1.31	1.38	1.31	2.00	1.17	1.47	1.44	1.46	1.23	1.78	1.40	1.78
3a.27			2.45	1.20	1.69	1.10	1.69	1.97	1.50	1.20	1.87	1.21	1.58	1.62	1.76	1.62
3a.28			2.30	1.04	1.61	0.98	1.61	1.70	1.46	1.08	1.77	1.07	1.54	1.49	1.72	1.47
3a.35	1.21	0.92	2.51	0.92	1.85	0.86	1.85	1.52	1.71	0.96	2.02	0.96	1.78	1.29	1.94	1.28
3a.36	0.61	0.69	1.81	0.69	1.21	0.63	1.21	1.24	1.09	0.71	1.33	0.70	1.17	0.98	1.29	1.00
3a.37	1.42	0.57			2.06	0.56	2.06	1.12	1.93	0.64	2.19	0.63	2.01	0.94		
3a.38	0.84	0.86	2.13	0.82	1.47	0.78	1.47	1.42	1.35	0.87	1.61	0.87	1.43	1.19	1.56	1.19
3a.39	0.73	1.33	2.20	1.37	1.49	1.27	1.49	2.07	1.28	1.39	1.68	1.41	1.38	1.81	1.63	1.80
3a.40	0.47	0.98	1.54	0.94	1.01	0.93	1.01	1.49	0.94	0.99			0.93	1.22	1.10	1.25

3a.42			2.63	1.16	1.89	1.09	1.89	1.90	1.69	1.19	2.08	1.21	1.86	1.65	2.01	1.61
3a.44	0.59	0.91	2.03	0.90	1.32	0.84	1.32	1.61	1.14	0.92	1.49	0.91	1.18	1.29	1.40	1.31
3a.46	1.39	0.81			1.87	0.73	1.87	1.25	1.76	0.80			1.80	1.05	1.96	1.05
3a.50	0.48	0.80	2.10	0.84	1.31	0.72	1.31	1.58	1.13	0.84	1.51	0.84	1.23	1.24	1.38	1.27
3b.3			2.32	0.76	1.49	0.70	1.49	1.46	1.33	0.82	1.66	0.81	1.41	1.19	1.58	1.20
3b.4	1.19	1.16	2.50	1.14	1.84	1.10	1.84	1.66	1.73	1.16	1.98	1.18	1.76	1.50	1.91	1.49
3b.5	1.02	0.63	2.06	0.67	1.52	0.60	1.52	1.21	1.40	0.67	1.64	0.68	1.43	0.95	1.55	0.94
3b.6	1.05	0.98	2.47	0.98	1.76	0.89	1.76	1.59	1.59	1.03	1.93	1.01	1.70	1.36	1.85	1.35
3b.7	0.71	0.66			1.24	0.61	1.24	1.09	1.15	0.68			1.21	0.92		
3b.12			2.21	0.69	1.42	0.63	1.42	1.40			1.59	0.75			1.49	1.09
3b.13	0.94	0.61	2.38	0.60	1.64	0.52	1.64	1.34	1.45	0.63	1.82	0.64	1.52	1.14	1.72	1.15
3b.14	0.10	0.34	1.48	0.37	0.84	0.29	0.84	0.99			0.97	0.39	0.77	0.76		
3b.18	0.60	0.85	1.76	0.84	1.22	0.79	1.22	1.39	1.09	0.87	1.34	0.87	1.14	1.21	1.29	1.22
3b.24	0.54	0.65			1.13	0.58	1.13	1.15	1.02	0.66	1.27	0.66	1.09	0.97	1.22	0.95
3b.29			2.15	0.40	1.42	0.37	1.42	1.07	1.26	0.47			1.38	0.83		
3b.31	0.89	0.74	2.43	0.72	1.63	0.64	1.63	1.47	1.42	0.81	1.84	0.76	1.50	1.22	1.77	1.24
3b.32			1.91	0.82	1.19	0.75	1.19	1.42			1.37	0.85			1.26	1.19
3b.35			2.12	0.61	1.37	0.52	1.37	1.32			1.54	0.64			1.45	1.03
3b.36			2.41	1.18	1.82	1.13	1.82	1.67	1.71	1.21	1.94	1.22	1.77	1.47	1.87	1.48
3b.39	1.11	0.88	2.59	0.96	1.83	0.84	1.83	1.68	1.61	0.97	2.05	1.00	1.72	1.41	1.87	1.46
3b.40			2.54	1.04	1.92	0.94	1.92	1.50	1.78	1.03	2.05	1.02			1.98	1.35
3b.44	1.48	0.58			1.97	0.53	1.97	1.04	1.84	0.63	2.10	0.63	1.92	0.95	2.05	0.93
3b.47			3.40	0.80	2.76	0.72	2.76	1.33			2.89	0.81			2.83	1.07
3b.48	1.66	0.63	3.11	0.61	2.36	0.54	2.36	1.31			2.57	0.65	2.28	1.03	2.41	1.01
3c.1			1.79	0.43	1.27	0.40	1.27	0.92			1.41	0.50	1.19	0.88	1.29	0.87
3c.2	0.83	0.63	1.78	0.67	1.33	0.61	1.33	1.08	1.25	0.67	1.43	0.68	1.27	0.89	1.39	0.89
3c.3	0.82	0.54	2.16	0.58	1.52	0.49	1.52	1.19	1.37	0.59	1.69	0.60	1.42	1.03	1.57	1.05

3c.4	0.91	0.61	1.91	0.57	1.42	0.52	1.42	1.07	1.28	0.62	1.55	0.61	1.38	0.92	1.50	0.89
3c.5			1.75	1.01	1.40	0.99	1.40	1.32	1.32	1.04	1.46	1.04	1.36	1.21	1.44	1.23
3c.8	0.83	0.95			1.47	0.87	1.47	1.50			1.61	0.95	1.38	1.23		
3c.10	0.57	1.15	2.08	1.09	1.32	1.05	1.32	1.83	1.16	1.17			1.24	1.52	1.39	1.52
3c.13			1.80	0.80	1.14	0.74	1.14	1.40			1.28	0.84	1.05	1.18		
3c.15	1.03	0.72	2.19	0.74	1.62	0.66	1.62	1.32			1.77	0.76			1.68	1.14
3c.16			2.04	1.12	1.43	1.06	1.43	1.70	1.28	1.15			1.37	1.49		
3c.20			1.55	0.66	1.06	0.62	1.06	1.09	0.96	0.70	1.16	0.70	1.00	0.93	1.10	0.91
3c.22			1.68	0.86	1.43	0.84	1.43	1.07			1.47	0.87	1.39	1.01	1.46	1.00
3c.28	0.62	0.86	1.97	0.85	1.21	0.78	1.21	1.48	1.02	0.91			1.10	1.29	1.27	1.29
3c.30	0.62	0.71	2.04	0.72	1.32	0.66	1.32	1.41	1.11	0.79	1.54	0.78	1.26	1.20	1.43	1.18
3c.39	0.45	0.39	1.67	0.38	1.07	0.31	1.07	0.92	0.90	0.42	1.25	0.43	0.97	0.83		
3c.40	0.40	0.26	1.68	0.30	1.04	0.23	1.04	0.80	0.89	0.31	1.20	0.32	0.97	0.62		
3d.1			1.74	0.64	1.06	0.61	1.06	1.18			1.19	0.68	0.98	1.00	1.14	1.00
3d.2	0.59	1.00	1.91	1.00	1.25	0.93	1.25	1.59	1.09	1.04	1.41	1.03	1.15	1.41	1.30	1.39
3d.3	0.55	0.79	1.87	0.89	1.21	0.76	1.21	1.54	1.04	0.85	1.37	0.86	1.13	1.20	1.27	1.21
3d.4	0.78	0.67			1.55	0.58	1.55	1.62	1.40	0.68	1.71	0.70	1.47	1.03	1.63	1.01
3d.5	1.08	1.05	2.33	1.06	1.71	1.02	1.71	1.62	1.56	1.09	1.84	1.11	1.62	1.37	1.77	1.37
3d.13	1.20	0.67	2.16	0.69	1.68	0.64	1.68	1.11	1.56	0.71	1.79	0.71	1.61	0.93	1.74	0.96
3d.14	0.49	0.62	2.19	0.58	1.32	0.53	1.32	1.34	1.13	0.66	1.53	0.67	1.18	1.04		
3d.15	0.84	0.52	2.01	0.54	1.43	0.47	1.43	1.16	1.27	0.54	1.60	0.57	1.35	0.88	1.50	0.88
3d.17	0.83	0.70	2.22	0.71	1.51	0.65	1.51	1.24	1.39	0.73	1.65	0.74	1.43	1.01		
3d.18	0.74	0.86			1.34	0.79	1.34	1.31	1.21	0.86			1.27	1.11		
3d.19			2.21	0.81	1.63	0.76	1.63	1.32	1.49	0.86	1.79	0.85	1.55	1.16	1.73	1.16
3d.20			2.24	0.55	1.82	0.52	1.82	0.93	1.74	0.58	1.91	0.57	1.76	0.79	1.87	0.78
3d.23	0.67	1.01	2.04	0.99	1.32	0.90	1.32	1.60			1.52	1.03			1.43	1.42
3d.24			2.05	1.00	1.25	0.95	1.25	1.61			1.42	1.04			1.30	1.46

3d.26	0.76	0.52	2.14	0.49	1.46	0.44	1.46	1.16	1.28	0.56			1.37	0.97		
3d.28	0.79	0.45			1.50	0.40	1.50	1.15	1.34	0.49			1.43	0.92		
4b.2			1.06	0.17	0.56	0.12	0.56	0.57	0.47	0.19					0.64	0.41
4d.6			1.88	0.58	1.38	0.55	1.38	1.05	1.24	0.61	1.51	0.61			1.49	0.89
4d.16			2.19	0.89	1.60	0.84	1.60	1.44	1.47	0.93			1.51	1.25		
5a.2	1.37	0.87			1.79	0.86	1.79	1.27	1.71	0.92	1.86	0.91	1.74	1.12	1.84	1.12
5a.3	1.10	1.03			1.60	1.03	1.60	1.59	1.46	1.11	1.74	1.13	1.49	1.44	1.65	1.44
5a.5	0.82	0.81			1.44	0.75	1.44	1.31	1.31	0.84	1.56	0.83	1.35	1.11	1.51	1.09
5a.6	0.86	0.69			1.49	0.67	1.49	1.29	1.33	0.76	1.62	0.74	1.40	1.03	1.55	1.04
5a.7	0.82	0.64	2.02	0.62	1.43	0.58	1.43	1.14	1.30	0.67	1.55	0.66	1.36	0.98	1.49	0.95
5a.10	0.82	0.73			1.44	0.64	1.44	1.36			1.64	0.75	1.37	1.07	1.52	1.08
5a.11	0.56	0.51	1.77	0.49	1.27	0.47	1.27	1.06	1.11	0.55			1.21	0.90	1.37	0.89
5a.14	1.31	0.80	2.31	0.78	1.82	0.74	1.82	1.23	1.71	0.81	1.93	0.81	1.74	1.04	1.90	1.04
5a.17	0.65	0.98	2.06	0.96	1.36	0.92	1.36	1.58	1.20	1.03	1.52	1.02	1.30	1.40	1.47	1.38
5b.18	0.90	0.76	2.31	0.77	1.61	0.71	1.61	1.37	1.46	0.80	1.76	0.79	1.56	1.15	1.69	1.14
5b.24	1.03	1.19			1.56	1.16	1.56	1.67	1.46	1.23			1.50	1.49		
5b.29			2.52	1.10	1.90	1.03	1.90	1.52			2.03	1.13			1.94	1.38
5b.31	0.99	1.19	2.47	1.21	1.74	1.12	1.74	1.94			1.94	1.25	1.63	1.68	1.81	1.69
5b.32			2.16	1.14	1.51	1.06	1.51	1.75	1.35	1.14	1.66	1.17	1.38	1.51	1.55	1.50
5b.33	1.00	1.12	2.02	1.11	1.52	1.08	1.52	1.55	1.41	1.14	1.63	1.14			1.59	1.40
5b.36	1.74	0.78	2.90	0.86	2.28	0.76	2.28	1.21	2.16	0.83	2.38	0.84	2.20	1.06	2.33	1.07
5b.37	0.92	1.02			1.60	0.95	1.60	1.67	1.43	1.07	1.77	1.06	1.55	1.17	1.66	1.27
5b.38	0.91	1.59	1.93	1.58	1.42	1.55	1.42	2.04	1.31	1.62	1.54	1.63			1.47	1.81
6a.4	0.74	0.60	1.99	0.56	1.43	0.53	1.43	1.10	1.25	0.62			1.37	0.94	1.52	0.94
6a.5			1.26	0.86	0.97	0.85	0.97	1.15	0.90	0.89			0.93	1.05	1.03	1.05
6a.7	0.73	1.11			1.21	1.08	1.21	1.57	1.10	1.15	1.34	1.15	1.12	1.42	1.26	1.42
6a.8	0.96	0.94			1.45	0.91	1.45	1.39	1.34	0.98	1.56	0.97	1.39	1.24	1.51	1.25

6b.7	1.06	0.66			1.47	0.65	1.47	1.00	1.41	0.68	1.52	0.68	1.41	0.87	1.50	0.87
6b.9	0.97	0.53	2.18	0.52	1.57	0.48	1.57	1.05	1.46	0.55			1.54	0.80		
6b.11	1.22	0.87	2.23	0.86	1.74	0.83	1.74	1.31	1.64	0.89			1.66	1.10		
6b.13	1.48	0.88	2.32	0.89	1.91	0.87	1.91	1.23	1.84	0.90			1.85	1.10		
6b.14	1.39	0.67			1.78	0.65	1.78	1.04	1.70	0.69	1.85	0.69	1.71	0.89	1.83	0.89
6b.15			1.91	0.71	1.43	0.69	1.43	1.14	1.34	0.74			1.35	0.99		
6b.19			2.01	0.89	1.58	0.86	1.58	1.27	1.52	0.90			1.53	1.12		
6b.23			2.18	0.90	1.67	0.87	1.67	1.41	1.57	0.93	1.76	0.92	1.62	1.21		
6b.28	1.44	0.94	2.16	1.01	1.80	0.96	1.80	1.32	1.73	1.00	1.86	1.01	1.74	1.17	1.83	1.17
6c.6			2.70	1.10	2.16	1.10	2.16	1.58			2.29	1.16	2.10	1.47	2.25	1.48
6c.15			1.68	0.94	1.22	0.90	1.22	1.34			1.32	0.96	1.15	1.19		
6d.1			2.98	0.96	2.11	0.93	2.11	1.63	1.95	1.03	2.28	1.02			2.20	1.39
6d.3	0.50	0.78	1.36	0.80	0.93	0.74	0.93	1.28			1.06	0.82	0.85	1.09		
6d.4	1.06	0.97			1.89	0.89	1.89	1.67	1.70	1.02	2.08	1.02	1.80	1.44	1.99	1.43
6e.1	0.55	0.60	1.34	0.59	0.96	0.56	0.96	0.99	0.88	0.63	1.04	0.62	0.92	0.83	1.02	0.84
6e.3	0.63	0.49			0.98	0.45	0.98	0.83	0.88	0.49	1.06	0.48	0.94	0.70	1.05	0.71
6e.5			1.49	0.73	0.84	0.68	0.84	1.24	0.71	0.76	0.95	0.75	0.77	0.96	0.88	0.98
8b.3			1.40	0.45	0.71	0.36	0.71	1.06			0.88	0.48	0.62	0.67	0.76	0.67
8b.6			2.54	1.30	1.93	1.22	1.93	1.91			2.10	1.33			2.02	1.64
8b.7	0.78	0.42			1.45	0.37	1.45	0.95	1.27	0.48			1.36	0.85		
8b.10			1.18	0.33	0.82	0.30	0.82	0.73	0.73	0.37					0.88	0.59
9a.7			1.81	0.69	1.21	0.57	1.21	1.18	1.05	0.66	1.36	0.69	1.13	0.96	1.25	1.00
9a.31	1.06	1.16			1.54	1.11	1.54	1.57	1.44	1.17	1.63	1.17	1.48	1.38	1.59	1.39
9a.33	0.79	0.61			1.31	0.56	1.31	1.10	1.20	0.65	1.44	0.65	1.26	0.93	1.36	0.92
9a.38	0.60	0.13			1.18	0.10	1.18	0.60	1.08	0.17	1.29	0.17	1.13	0.41	1.25	0.42
9a.41	0.50	0.38			1.12	0.33	1.12	0.89	1.01	0.41	1.24	0.41	1.08	0.69	1.18	0.68
15a.2			1.94	0.73	1.17	0.67	1.17	1.19	1.01	0.73	1.32	0.75	1.08	1.07	1.23	1.06

15b.2	1.31	0.64	2.72	0.71	1.98	0.62	1.98	1.33			2.16	0.72	1.90	1.06		
15b.4	1.71	0.87			2.13	0.86	2.13	1.37	2.03	0.92	2.24	0.92	2.07	1.18	2.19	1.17
15c.1	0.79	0.73			1.22	0.69	1.22	1.13	1.10	0.76	1.35	0.75	1.19	1.03	1.30	1.03
22a.4			2.35	1.06	1.71	0.99	1.71	1.64	1.51	1.08	1.88	1.11			1.76	1.41
22a.13			2.62	0.77	1.91	0.73	1.91	1.38			2.06	0.84			2.02	1.24
22a.14			2.84	1.04	2.29	0.98	2.29	1.53			2.43	1.07			2.36	1.34
22b.1	1.03	0.70	2.40	0.70	1.77	0.65	1.77	1.41			1.92	0.75			1.80	1.14
22c.1	0.17	0.17			0.72	0.14	0.72	0.70	0.58	0.23	0.84	0.22	0.64	0.51	0.75	0.50
22c.3	0.12	0.25	1.25	0.26	0.66	0.22	0.66	0.75	0.52	0.29	0.79	0.30	0.60	0.55	0.71	0.55
22c.6	0.14	0.46	1.26	0.48	0.70	0.44	0.70	0.99	0.57	0.52	0.82	0.51	0.63	0.76	0.75	0.78
22c.8	0.35	0.30	1.04	0.30	0.71	0.27	0.71	0.63	0.65	0.32	0.77	0.32	0.67	0.48	0.74	0.49
22c.9	0.05	0.13			0.69	0.12	0.69	0.70	0.57	0.20			0.62	0.54	0.73	0.53
22c.10	0.08	0.40			0.68	0.39	0.68	0.93	0.54	0.46	0.83	0.47	0.62	0.78	0.73	0.77
22c.11			1.07	0.15	0.45	0.09	0.45	0.65			0.58	0.19	0.37	0.49	0.50	0.47
22c.12	0.18	0.37			0.78	0.35	0.78	0.93	0.61	0.44			0.70	0.77		
22c.13	0.16	0.17	1.18	0.17	0.67	0.13	0.67	0.63	0.55	0.21	0.77	0.21	0.62	0.46	0.72	0.48
22c.15	0.22	0.36	1.29	0.37	0.71	0.33	0.71	0.83	0.59	0.41	0.84	0.41	0.66	0.71	0.78	0.69
22c.17	0.12	0.53	1.15	0.52	0.62	0.48	0.62	0.96	0.51	0.56	0.73	0.56			0.66	0.83
22c.18	0.05	0.22	1.42	0.26	0.71	0.18	0.71	0.84	0.58	0.28			0.63	0.59	0.77	0.60
22c.21	1.27	0.94	2.32	0.93	1.81	0.90	1.81	1.41	1.69	0.99	1.93	0.98	1.76	1.24	1.86	1.24
22c.22			2.10	0.60	1.51	0.58	1.51	1.14	1.39	0.67			1.37	0.92	1.57	0.91
22c.23	1.34	1.09	2.66	1.09	2.00	1.04	2.00	1.70	1.86	1.13	2.17	1.15	1.94	1.45	2.06	1.48
22c.26			2.27	1.07	1.76	1.03	1.76	1.55	1.65	1.10	1.87	1.11	1.67	1.40	1.81	1.41
22c.29	0.90	0.74	2.28	0.74	1.60	0.69	1.60	1.49			1.77	0.78	1.53	1.08	1.66	1.10
22c.30	0.67	0.44	2.12	0.49	1.41	0.42	1.41	1.16			1.55	0.52	1.32	0.87	1.46	0.87
22c.31	0.96	0.71	1.92	0.75	1.45	0.70	1.45	1.13	1.34	0.75	1.55	0.76	1.37	0.97	1.48	0.97
22c.35			2.11	0.44	1.51	0.35	1.51	0.95	1.37	0.45	1.65	0.45	1.43	0.72	1.56	0.71

22c.37	0.79	0.66	1.64	0.67	1.23	0.64	1.23	1.04	1.13	0.70					1.27	0.90
22c.38	0.94	1.04	1.95	1.01	1.47	0.96	1.47	1.49	1.36	1.06					1.55	1.28
22c.40	0.52	0.64	1.71	0.62	1.10	0.59	1.10	1.20	0.95	0.68	1.26	0.68	1.02	1.03	1.16	1.02
23a.2	0.77	0.42	1.88	0.40	1.29	0.35	1.29	0.98	1.12	0.44	1.47	0.45	1.20	0.77	1.37	0.77
23a.4	0.70	0.65	1.86	0.66	1.25	0.58	1.25	1.18	1.09	0.69	1.41	0.69	1.21	1.01	1.30	1.03
23a.5	0.52	0.79	1.50	0.77	1.08	0.74	1.08	1.34	0.91	0.84	1.25	0.84	1.02	1.14	1.18	1.15
23a.15	0.71	0.84	1.79	0.83	1.25	0.80	1.25	1.42	1.11	0.89			1.17	1.23		
23a.16	0.73	0.82			1.32	0.74	1.32	1.44	1.17	0.87			1.27	1.23		
23a.18	0.59	0.86	1.88	0.87	1.24	0.82	1.24	1.41	1.10	0.89	1.40	0.90	1.18	1.17	1.31	1.17
23a.19	0.23	0.82			0.84	0.78	0.84	1.41	0.69	0.86	1.02	0.87	0.77	1.22	0.93	1.20
23a.20	0.44	0.46	1.98	0.52	1.21	0.41	1.21	1.21	1.05	0.51	1.37	0.51			1.26	0.91
23a.21	1.00	0.48			1.41	0.44	1.41	0.86	1.31	0.51			1.38	0.69		
23a.31	0.62	0.56	2.00	0.52	1.28	0.47	1.28	1.28	1.07	0.60	1.49	0.60	1.18	1.02	1.41	1.04
23a.32	0.76	1.24			1.27	1.20	1.27	1.73	1.15	1.27	1.39	1.27	1.22	1.57		
23a.33	0.49	0.73	1.85	0.67	1.15	0.62	1.15	1.35			1.33	0.71	1.07	1.09	1.25	1.09
23a.34			2.03	0.99	1.42	0.97	1.42	1.50			1.57	1.05			1.51	1.36
23a.35	0.79	0.49			1.35	0.45	1.35	1.13	1.20	0.54			1.28	0.86	1.41	0.84
23a.36	0.48	0.90	1.54	0.86	1.02	0.84	1.02	1.33	0.89	0.93	1.15	0.91			1.09	1.13
23a.40	0.25	0.39	1.53	0.44	0.88	0.33	0.88	1.09	0.65	0.46			0.80	0.85	0.97	0.84
23a.41	1.23	0.92	2.31	0.87	1.75	0.85	1.75	1.50			1.92	0.94			1.82	1.22
23a.42	0.22	0.29	1.44	0.32	0.86	0.26	0.86	0.88	0.69	0.38	1.02	0.37	0.77	0.72	0.93	0.71
23a.43	1.10	1.23	2.39	1.27	1.77	1.18	1.77	1.93	1.59	1.30	1.93	1.30	1.66	1.70		
23a.46	0.54	0.90	1.99	0.86	1.26	0.83	1.26	1.50	1.12	0.94	1.43	0.93	1.21	1.33	1.35	1.33
23a.48	0.60	0.67	1.75	0.67	1.18	0.61	1.18	1.28	1.02	0.71	1.34	0.70	1.11	1.05	1.26	1.05
23a.50	0.42	0.79			0.97	0.70	0.97	1.28	0.83	0.80	1.10	0.79	0.91	1.10	1.03	1.11
23a.51			1.74	0.64	1.14	0.61	1.14	1.23	0.97	0.71	1.32	0.72	1.07	1.09	1.21	1.09
23a.52	0.91	0.66			1.52	0.61	1.52	1.33	1.39	0.71			1.47	1.09		

23b.1			1.60	1.04	0.96	0.98	0.96	1.62	0.80	1.07	1.14	1.09	0.84	1.37	0.96	1.36
23b.2	0.60	0.67			1.15	0.63	1.15	1.12	1.04	0.70	1.27	0.69	1.12	0.90	1.20	0.90
23b.10	1.02	0.78			1.65	0.74	1.65	1.29	1.51	0.84			1.59	1.16		
23b.14			1.92	1.47	1.31	1.45	1.31	2.00			1.44	1.54	1.26	1.80		
23b.15			1.87	0.49	1.53	0.47	1.53	0.79			1.61	0.52	1.49	0.70		
23b.17	1.68	1.13	2.73	1.11	2.24	1.05	2.24	1.72	2.09	1.14	2.39	1.13	2.17	1.49	2.34	1.50
23b.19			2.50	1.02	1.96	1.00	1.96	1.52	1.84	1.09	2.08	1.06	1.93	1.39	2.06	1.38
23c.2	1.02	0.76			1.61	0.76	1.61	1.39	1.43	0.85			1.47	1.31		
23c.3	0.80	0.38			1.38	0.29	1.38	0.92	1.23	0.41			1.35	0.71		
23c.4	0.46	0.57			1.02	0.53	1.02	1.06	0.88	0.62	1.16	0.63	0.95	0.91	1.06	0.92
23c.7	0.61	1.07			1.23	1.00	1.23	1.69	1.06	1.11			1.17	1.44		
23d.1			1.50	1.12	1.10	1.07	1.10	1.47	0.99	1.12	1.21	1.12	1.06	1.31	1.13	1.32
23d.2	0.95	0.85			1.62	0.82	1.62	1.53	1.38	0.96			1.50	1.27	1.68	1.31
23d.18	0.77	0.35	1.90	0.44	1.32	0.37	1.32	0.90	1.20	0.45	1.43	0.46	1.28	0.69		
23e.2	0.49	0.85	2.06	0.84	1.27	0.78	1.27	1.48	1.11	0.89	1.44	0.90	1.21	1.25	1.35	1.25
24a.4	0.97	0.79	2.22	0.84	1.58	0.74	1.58	1.45	1.39	0.85	1.77	0.85	1.50	1.23	1.66	1.19
24a.5			1.93	0.73	1.23	0.66	1.23	1.32	1.02	0.77	1.41	0.78	1.13	1.10	1.30	1.11
24a.7	0.82	0.74			1.43	0.68	1.43	1.22	1.27	0.76	1.60	0.75	1.36	1.13		
24a.8			1.91	0.43	1.41	0.37	1.41	0.91	1.27	0.45	1.55	0.46	1.29	0.73	1.44	0.76
24b.3	1.13	0.92	2.29	0.95	1.67	0.89	1.67	1.56	1.52	0.99	1.81	1.00	1.57	1.31	1.73	1.33
24c.2	0.20	0.14			0.80	0.11	0.80	0.75	0.66	0.18					0.85	0.54
24e.2	0.94	0.96	2.56	1.01	1.72	0.95	1.72	1.65	1.52	1.06	1.91	1.07	1.62	1.43	1.73	1.43
24e.3			2.21	0.70	1.46	0.60	1.46	1.37	1.28	0.69	1.63	0.72	1.37	1.08	1.52	1.06
24e.4			2.54	1.23	2.04	1.19	2.04	1.66			2.17	1.27	1.97	1.57	2.10	1.57
24e.5	0.61	0.60	1.84	0.61	1.18	0.57	1.18	1.13	1.04	0.64	1.33	0.64	1.11	0.96	1.23	0.95
24e.7	1.06	1.32	2.34	1.27	1.69	1.23	1.69	1.89	1.55	1.33	1.87	1.33	1.66	1.60		
24e.8	0.82	0.58			1.53	0.48	1.53	1.21			1.74	0.63	1.45	0.97	1.59	0.98

24e.9			2.63	0.62	1.87	0.51	1.87	1.31	1.69	0.64	2.05	0.67	1.75	0.98	1.93	1.02
24e.10			2.46	0.52	1.61	0.46	1.61	1.29			1.84	0.59			1.68	0.97
24e.11	0.12	0.79			0.71	0.74	0.71	1.38	0.57	0.82	0.86	0.83	0.61	1.18		
24e.12	0.13	1.58	1.54	1.60	0.86	1.54	0.86	2.22	0.70	1.65	1.00	1.65	0.76	1.92	0.93	1.93
24e.16	0.88	0.86	2.12	0.86	1.48	0.82	1.48	1.43	1.34	0.91			1.42	1.17		
24e.18	0.64	0.80			1.27	0.76	1.27	1.36	1.12	0.85	1.42	0.87	1.18	1.15	1.32	1.16
24e.20			1.36	1.28	0.81	1.23	0.81	1.70			0.93	1.30	0.74	1.53		
24e.21			2.17	0.51	1.44	0.45	1.44	1.10	1.28	0.55	1.61	0.56	1.35	0.91		
24e.26	1.14	1.06	2.46	1.06	1.77	0.98	1.77	1.69	1.62	1.10	1.92	1.10	1.70	1.42	1.84	1.42
24e.27	1.65	1.09	3.04	1.01	2.37	0.99	2.37	1.65	2.18	1.11	2.55	1.10	2.32	1.41	2.46	1.41

APPENDIX B

Shape Coordinate/ Centroid Size Data for

Sowerbyella rugosa

Sample	Shape Coordinates (c-d Baseline)						Square root
	vab1	vab2	vef1	vef2	vgh1	vgh2	centroid size
0a.5	0.039	1.236	0.182	0.256	0.743	0.148	0.473
0a.6	0.080	1.114	0.155	0.222	0.736	0.113	0.660
0a.11	0.039	1.161	0.165	0.262	0.770	0.115	0.585
0a.16	0.031	1.181	0.156	0.223	0.675	0.139	0.520
0a.21	0.036	1.142	0.180	0.272	0.707	0.094	0.683
0a.25	0.083	1.183	0.132	0.239	0.776	0.159	0.441
0a.27	0.163	1.107	0.154	0.117	0.688	0.125	0.700
0a.40	0.102	1.083	0.172	0.258	0.693	0.098	0.674
0a.46	0.114	1.111	0.173	0.288	0.694	0.158	0.725
0a.47	0.189	1.010	0.172	0.260	0.705	0.116	0.581
0a.52	0.074	0.959	0.163	0.250	0.574	0.142	0.681
0a.53	0.073	1.128	0.148	0.263	0.592	0.136	0.709
0a.54	0.103	0.878	0.167	0.306	0.629	0.114	0.671
0b.1	0.057	1.117	0.153	0.239	0.553	0.107	0.578
0b.20	0.145	1.026	0.148	0.262	0.745	0.178	0.392
0b.23	0.084	0.989	0.096	0.198	0.586	0.109	0.707
0b.27	0.180	1.030	0.189	0.181	0.632	0.232	0.267
0b.28	0.099	1.214	0.141	0.256	0.622	0.179	0.587
0b.29	0.022	0.991	0.105	0.183	0.695	0.104	0.669
0b.30	0.053	0.972	0.121	0.208	0.628	0.142	0.545
0b.31	0.083	0.879	0.108	0.166	0.597	0.124	0.568
0b.33	0.081	1.072	0.134	0.220	0.639	0.127	0.814
0b.34	0.090	1.099	0.177	0.266	0.698	0.166	0.675
0b.37	0.077	0.930	0.126	0.225	0.624	0.095	0.735
0b.40	0.120	1.016	0.164	0.250	0.674	0.114	0.772
0b.41	0.060	1.089	0.146	0.232	0.698	0.156	0.632
0b.45	0.080	1.099	0.155	0.250	0.682	0.092	0.698
0b.48	0.058	1.050	0.108	0.223	0.668	0.117	0.701
0b.49	0.077	0.983	0.115	0.179	0.605	0.166	0.724
0b.52	0.112	1.043	0.149	0.222	0.791	0.139	0.542
0b.61	0.125	0.722	0.108	0.205	0.663	0.156	0.405
1a.9	0.161	0.907	0.173	0.242	0.677	0.056	0.615

1a.10	0.096	1.079	0.122	0.256	0.611	0.105	0.688
1a.15	0.103	1.072	0.158	0.221	0.569	0.172	0.601
1a.17	0.095	1.114	0.171	0.233	0.729	0.112	0.557
1a.19	0.052	0.935	0.133	0.197	0.738	0.159	0.714
1a.23	0.016	1.163	0.158	0.201	0.753	0.179	0.809
1a.26	0.087	0.949	0.156	0.216	0.639	0.113	0.567
1a.28	0.066	1.009	0.132	0.236	0.679	0.217	0.653
2a.1	0.103	1.179	0.182	0.244	0.689	0.123	0.522
2a.3	0.023	1.013	0.127	0.271	0.601	0.126	0.705
2a.10	0.183	0.899	0.139	0.239	0.680	0.109	0.641
2a.24	0.096	1.379	0.171	0.278	0.904	0.219	0.663
2a.28	0.117	1.212	0.201	0.258	0.682	0.092	0.694
2a.31	0.088	1.237	0.182	0.255	0.759	0.163	0.604
2a.34	0.054	1.241	0.172	0.261	0.738	0.134	0.636
2b.5	0.037	1.200	0.167	0.258	0.781	0.141	0.704
2b.13	0.087	1.331	0.173	0.257	0.757	0.134	0.629
2b.17	0.091	1.067	0.185	0.297	0.619	0.128	0.789
2b.18	0.109	1.154	0.177	0.233	0.608	0.184	0.721
2b.20	0.115	1.012	0.130	0.222	0.594	0.081	0.771
2b.24	0.071	1.204	0.155	0.250	0.687	0.138	0.747
3a.7	0.081	1.118	0.170	0.235	0.550	0.128	0.841
3a.8	0.100	1.190	0.157	0.252	0.708	0.109	0.681
3a.9	0.098	1.063	0.150	0.218	0.644	0.121	0.891
3a.10	0.116	0.965	0.137	0.222	0.574	0.094	0.785
3a.11	0.180	1.021	0.152	0.205	0.647	0.074	0.880
3a.14	0.071	1.027	0.114	0.253	0.672	0.133	0.837
3a.16	0.074	1.149	0.134	0.244	0.701	0.085	0.779
3a.17	0.122	0.959	0.140	0.203	0.655	0.124	0.729
3a.18	0.056	0.947	0.150	0.231	0.703	0.132	0.655
3a.20	0.038	1.101	0.102	0.207	0.612	0.121	0.633
3a.21	0.048	1.037	0.160	0.206	0.630	0.091	0.745
3a.22	0.102	1.061	0.149	0.226	0.644	0.098	0.700
3a.23	0.067	1.206	0.254	0.341	0.716	0.110	0.819
3a.25	0.071	0.979	0.141	0.190	0.636	0.109	0.751
3a.26	0.112	1.018	0.130	0.215	0.644	0.135	0.744
3a.27	0.117	0.872	0.122	0.209	0.598	0.107	0.977
3a.28	0.077	0.968	0.127	0.221	0.692	0.123	0.857
3a.35	0.094	0.986	0.153	0.234	0.649	0.125	0.783
3a.36	0.094	0.994	0.122	0.206	0.597	0.097	0.720
3a.37	0.024	1.138	0.139	0.233	0.682	0.098	0.740
3a.38	0.082	1.007	0.139	0.200	0.630	0.102	0.774

3a.39	0.105	0.920	0.169	0.247	0.672	0.158	0.920
3a.40	0.044	0.957	0.108	0.123	0.542	0.154	0.654
3a.42	0.091	0.906	0.140	0.236	0.667	0.088	0.942
3a.44	0.078	0.943	0.092	0.228	0.593	0.145	0.895
3a.46	0.164	0.904	0.151	0.204	0.619	0.151	0.584
3a.50	0.111	0.946	0.138	0.224	0.614	0.091	0.998
3b.3	0.069	1.096	0.152	0.221	0.650	0.111	0.957
3b.4	0.089	1.164	0.124	0.228	0.701	0.132	0.742
3b.5	0.078	0.856	0.121	0.191	0.569	0.096	0.675
3b.6	0.123	1.021	0.179	0.241	0.660	0.106	0.835
3b.7	0.092	1.122	0.137	0.202	0.649	0.070	0.609
3b.12	0.075	1.033	0.153	0.221	0.597	0.083	0.928
3b.13	0.105	0.880	0.145	0.229	0.765	0.120	0.950
3b.14	0.090	0.997	0.145	0.200	0.671	0.089	0.838
3b.18	0.095	0.953	0.132	0.208	0.704	0.129	0.720
3b.24	0.130	1.045	0.149	0.215	0.668	0.115	0.695
3b.29	0.039	1.039	0.137	0.221	0.658	0.047	0.882
3b.31	0.102	0.928	0.165	0.255	0.715	0.159	0.960
3b.32	0.112	1.067	0.161	0.270	0.667	0.094	0.831
3b.35	0.114	0.944	0.148	0.206	0.635	0.094	0.922
3b.36	0.086	1.111	0.147	0.218	0.632	0.090	0.678
3b.39	0.087	0.882	0.170	0.265	0.705	0.089	0.961
3b.40	0.173	1.115	0.151	0.238	0.738	0.116	0.715
3b.44	0.091	0.955	0.196	0.257	0.796	0.128	0.614
3b.47	0.139	1.035	0.153	0.201	0.575	0.103	0.740
3b.48	0.107	0.948	0.136	0.263	0.624	0.083	0.894
3c.1	0.049	1.022	0.183	0.268	0.924	0.103	0.668
3c.2	0.086	1.025	0.134	0.195	0.602	0.127	0.561
3c.3	0.098	0.966	0.148	0.228	0.787	0.106	0.845
3c.4	0.130	0.894	0.171	0.242	0.697	0.102	0.634
3c.5	0.066	1.052	0.148	0.207	0.694	0.115	0.416
3c.8	0.123	1.018	0.119	0.232	0.569	0.145	0.742
3c.10	0.087	0.974	0.155	0.211	0.603	0.094	0.911
3c.13	0.095	1.023	0.150	0.219	0.666	0.138	0.793
3c.15	0.102	0.883	0.156	0.241	0.726	0.096	0.753
3c.16	0.089	0.956	0.146	0.235	0.675	0.089	0.756
3c.20	0.067	1.043	0.151	0.220	0.631	0.106	0.574
3c.22	0.056	1.082	0.133	0.169	0.692	0.136	0.294
3c.28	0.103	0.954	0.181	0.268	0.723	0.120	0.832
3c.30	0.079	0.938	0.172	0.281	0.710	0.109	0.892
3c.39	0.122	0.997	0.191	0.288	0.855	0.175	0.753

3c.40	0.085	1.125	0.152	0.266	0.677	0.123	0.732
3d.1	0.048	1.202	0.116	0.229	0.687	0.135	0.768
3d.2	0.108	0.998	0.166	0.248	0.712	0.108	0.797
3d.3	0.096	0.855	0.119	0.216	0.571	0.090	0.856
3d.4	0.087	0.733	0.105	0.149	0.424	0.075	1.070
3d.5	0.065	1.041	0.143	0.233	0.593	0.118	0.732
3d.13	0.084	1.031	0.155	0.238	0.653	0.132	0.568
3d.14	0.083	1.055	0.159	0.248	0.635	0.176	0.985
3d.15	0.087	0.846	0.123	0.240	0.591	0.109	0.764
3d.17	0.101	1.162	0.151	0.219	0.615	0.131	0.773
3d.18	0.125	1.148	0.141	0.247	0.620	0.141	0.669
3d.19	0.087	1.017	0.166	0.264	0.710	0.154	0.685
3d.20	0.080	1.005	0.136	0.207	0.648	0.136	0.495
3d.23	0.149	0.984	0.187	0.297	0.745	0.163	0.830
3d.24	0.077	1.214	0.141	0.263	0.776	0.074	0.904
3d.26	0.093	0.947	0.173	0.242	0.730	0.125	0.858
3d.28	0.068	0.949	0.119	0.215	0.700	0.091	0.899
4b.2	0.114	1.090	0.145	0.212	0.631	0.165	0.564
4d.6	0.058	0.996	0.122	0.270	0.668	0.204	0.604
4d.16	0.096	0.965	0.153	0.218	0.682	0.146	0.717
5a.2	0.022	1.043	0.123	0.188	0.637	0.123	0.500
5a.3	-0.003	0.906	0.159	0.256	0.735	0.145	0.659
5a.5	0.108	1.085	0.162	0.228	0.626	0.139	0.703
5a.6	0.043	1.003	0.135	0.235	0.589	0.122	0.758
5a.7	0.076	1.074	0.144	0.218	0.683	0.119	0.703
5a.10	0.117	0.857	0.153	0.281	0.602	0.100	0.792
5a.11	0.065	1.023	0.148	0.265	0.730	0.134	0.730
5a.14	0.112	1.015	0.146	0.218	0.616	0.155	0.592
5a.17	0.067	1.065	0.150	0.243	0.704	0.129	0.829
5b.18	0.084	1.065	0.133	0.227	0.665	0.095	0.832
5b.24	0.063	1.043	0.139	0.202	0.642	0.123	0.628
5b.29	0.145	1.282	0.199	0.260	0.708	0.079	0.668
5b.31	0.095	0.910	0.159	0.236	0.693	0.110	0.941
5b.32	0.108	0.947	0.135	0.229	0.644	0.124	0.798
5b.33	0.073	1.077	0.142	0.230	0.686	0.146	0.599
5b.36	0.135	1.273	0.166	0.242	0.670	0.141	0.622
5b.37	0.089	0.951	0.160	0.242	0.373	0.080	0.811
5b.38	0.071	1.025	0.158	0.232	0.529	0.096	0.593
6a.4	0.080	1.108	0.156	0.304	0.720	0.136	0.722
6a.5	0.027	0.993	0.135	0.236	0.656	0.175	0.358
6a.7	0.068	0.981	0.146	0.246	0.690	0.140	0.595

6a.8	0.065	1.017	0.138	0.231	0.703	0.129	0.589
6b.7	0.024	1.146	0.097	0.162	0.618	0.129	0.466
6b.9	0.078	1.062	0.121	0.193	0.561	0.061	0.708
6b.11	0.067	1.048	0.110	0.206	0.564	0.174	0.588
6b.13	0.050	1.155	0.099	0.199	0.632	0.152	0.476
6b.14	0.060	0.987	0.111	0.198	0.610	0.151	0.465
6b.15	0.050	1.062	0.104	0.187	0.656	0.162	0.566
6b.19	0.058	1.053	0.101	0.149	0.628	0.122	0.510
6b.23	0.054	0.966	0.101	0.182	0.641	0.095	0.644
6b.28	0.053	1.003	0.119	0.191	0.578	0.119	0.429
6c.6	-0.005	1.128	0.123	0.271	0.791	0.158	0.639
6c.15	0.082	1.040	0.133	0.231	0.651	0.159	0.545
6d.1	0.040	1.241	0.131	0.232	0.655	0.129	0.953
6d.3	0.101	0.798	0.158	0.234	0.651	0.162	0.580
6d.4	0.099	1.064	0.165	0.243	0.702	0.118	0.967
6e.1	0.077	0.919	0.139	0.191	0.634	0.122	0.496
6e.3	0.102	0.903	0.105	0.232	0.676	0.145	0.441
6e.5	0.092	1.167	0.127	0.211	0.513	0.103	0.723
8b.3	0.122	0.995	0.169	0.243	0.436	0.098	0.804
8b.6	0.125	0.886	0.156	0.246	0.605	0.135	0.769
8b.7	0.076	1.148	0.195	0.305	0.818	0.149	0.774
8b.10	0.064	0.823	0.158	0.219	0.675	0.132	0.476
9a.7	0.196	0.993	0.169	0.254	0.675	0.101	0.712
9a.31	0.114	1.048	0.141	0.212	0.596	0.120	0.559
9a.33	0.090	0.962	0.165	0.225	0.667	0.084	0.639
9a.38	0.071	1.170	0.147	0.210	0.638	0.119	0.656
9a.41	0.078	1.123	0.143	0.208	0.622	0.088	0.715
15a.2	0.129	1.484	0.137	0.296	0.762	0.149	0.796
15b.2	0.071	0.996	0.138	0.256	0.620	0.125	0.844
15b.4	0.029	0.837	0.117	0.199	0.633	0.119	0.575
15c.1	0.091	0.980	0.144	0.281	0.763	0.126	0.536
22a.4	0.107	0.989	0.164	0.281	0.647	0.085	0.777
22a.13	0.069	1.095	0.168	0.234	0.780	0.178	0.843
22a.14	0.100	1.004	0.157	0.252	0.648	0.128	0.655
22b.1	0.073	0.899	0.132	0.201	0.649	0.045	0.883
22c.1	0.058	0.967	0.152	0.234	0.643	0.100	0.674
22c.3	0.062	1.063	0.141	0.250	0.618	0.104	0.664
22c.6	0.047	1.010	0.131	0.227	0.594	0.109	0.667
22c.8	0.084	0.975	0.142	0.169	0.605	0.099	0.420
22c.9	0.021	1.105	0.140	0.217	0.721	0.095	0.765
22c.10	0.030	1.097	0.146	0.257	0.719	0.101	0.709

22c.11	0.101	1.104	0.175	0.222	0.703	0.117	0.707
22c.12	0.043	1.039	0.161	0.287	0.728	0.129	0.722
22c.13	0.083	1.018	0.165	0.217	0.679	0.096	0.614
22c.15	0.072	1.073	0.158	0.242	0.744	0.127	0.632
22c.17	0.084	1.075	0.167	0.234	0.725	0.073	0.608
22c.18	0.091	1.041	0.158	0.208	0.627	0.104	0.807
22c.21	0.069	1.027	0.167	0.236	0.663	0.092	0.624
22c.22	0.046	1.053	0.168	0.217	0.607	0.179	0.684
22c.23	0.074	1.012	0.145	0.239	0.645	0.098	0.795
22c.26	0.093	0.989	0.145	0.215	0.732	0.132	0.631
22c.29	0.059	0.866	0.115	0.205	0.500	0.082	0.884
22c.30	0.056	0.990	0.129	0.201	0.617	0.098	0.884
22c.31	0.073	1.122	0.138	0.241	0.638	0.129	0.546
22c.35	0.149	0.993	0.163	0.236	0.596	0.110	0.707
22c.37	0.067	1.049	0.163	0.245	0.654	0.097	0.502
22c.38	0.118	0.952	0.175	0.195	0.598	0.151	0.608
22c.40	0.076	0.961	0.151	0.254	0.713	0.116	0.738
23a.2	0.096	0.875	0.148	0.271	0.663	0.135	0.717
23a.4	0.116	0.966	0.174	0.269	0.727	0.078	0.713
23a.5	0.065	0.820	0.160	0.286	0.667	0.130	0.664
23a.15	0.054	0.863	0.151	0.227	0.685	0.128	0.712
23a.16	0.115	0.845	0.184	0.226	0.696	0.069	0.782
23a.18	0.082	1.095	0.125	0.247	0.594	0.111	0.744
23a.19	0.058	0.969	0.137	0.261	0.676	0.123	0.760
23a.20	0.106	0.960	0.128	0.198	0.625	0.063	0.950
23a.21	0.083	0.965	0.149	0.222	0.579	0.072	0.490
23a.31	0.092	0.849	0.163	0.252	0.690	0.137	0.913
23a.32	0.082	0.955	0.143	0.235	0.710	0.090	0.635
23a.33	0.117	0.932	0.124	0.242	0.647	0.122	0.844
23a.34	0.044	1.143	0.159	0.275	0.733	0.163	0.693
23a.35	0.057	0.824	0.131	0.212	0.589	0.094	0.746
23a.36	0.077	1.077	0.163	0.260	0.590	0.137	0.605
23a.40	0.104	0.845	0.167	0.294	0.675	0.110	0.846
23a.41	0.073	0.826	0.131	0.259	0.567	0.103	0.710
23a.42	0.077	0.988	0.189	0.264	0.731	0.125	0.750
23a.43	0.092	0.862	0.157	0.232	0.689	0.134	0.842
23a.46	0.076	1.079	0.154	0.232	0.746	0.099	0.859
23a.48	0.089	0.846	0.143	0.238	0.658	0.105	0.757
23a.50	0.146	0.939	0.160	0.236	0.700	0.105	0.670
23a.51	0.050	0.973	0.176	0.284	0.772	0.115	0.759
23a.52	0.066	0.852	0.130	0.188	0.665	0.075	0.814

23b.1	0.100	0.989	0.164	0.259	0.596	0.096	0.765
23b.2	0.074	1.134	0.126	0.237	0.546	0.078	0.623
23b.10	0.067	1.160	0.168	0.252	0.760	0.111	0.724
23b.14	0.041	1.110	0.172	0.222	0.639	0.094	0.700
23b.15	0.071	1.045	0.144	0.244	0.706	0.121	0.400
23b.17	0.104	0.773	0.132	0.222	0.663	0.124	0.731
23b.19	0.046	1.025	0.154	0.232	0.743	0.118	0.656
23c.2	0.000	0.946	0.141	0.298	0.868	0.235	0.787
23c.3	0.145	0.936	0.180	0.238	0.666	0.038	0.720
23c.4	0.070	1.062	0.173	0.257	0.722	0.108	0.667
23c.7	0.108	0.901	0.165	0.245	0.639	0.079	0.784
23d.1	0.128	0.993	0.134	0.265	0.604	0.094	0.477
23d.2	0.039	0.960	0.196	0.350	0.661	0.127	0.835
23d.18	0.044	1.081	0.157	0.225	0.597	0.082	0.656
23e.2	0.085	1.128	0.154	0.234	0.667	0.102	0.900
24a.4	0.104	0.881	0.150	0.265	0.663	0.108	0.804
24a.5	0.113	1.069	0.175	0.296	0.677	0.125	0.818
24a.7	0.112	1.100	0.147	0.300	0.836	0.119	0.717
24a.8	0.116	0.930	0.162	0.263	0.703	0.133	0.628
24b.3	0.071	0.868	0.161	0.219	0.651	0.116	0.756
24c.2	0.051	0.948	0.112	0.227	0.679	0.071	0.765
24e.2	0.052	1.164	0.167	0.279	0.684	0.084	0.923
24e.3	0.126	0.981	0.133	0.225	0.604	0.097	0.907
24e.4	0.086	1.059	0.178	0.258	0.817	0.134	0.602
24e.5	0.071	1.096	0.138	0.254	0.687	0.108	0.719
24e.7	0.095	0.973	0.147	0.243	0.551	0.057	0.776
24e.8	0.135	0.968	0.195	0.292	0.678	0.099	0.850
24e.9	0.132	0.958	0.174	0.232	0.613	0.113	0.914
24e.10	0.070	1.029	0.158	0.289	0.622	0.089	1.007
24e.11	0.080	0.920	0.138	0.233	0.691	0.153	0.743
24e.12	0.075	1.027	0.162	0.223	0.560	0.122	0.823
24e.16	0.069	1.008	0.151	0.236	0.572	0.100	0.732
24e.18	0.063	1.039	0.161	0.248	0.647	0.114	0.738
24e.20	0.114	1.157	0.153	0.241	0.640	0.167	0.607
24e.21	0.097	1.116	0.170	0.255	0.707	0.143	0.833
24e.26	0.108	0.926	0.163	0.214	0.616	0.103	0.816
24e.27	0.093	1.052	0.178	0.279	0.643	0.105	0.810

APPENDIX C

Measurement error data for *Sowerbyella rugosa*

Sample	Replicate	Shape Coordinates (C-D Baseline)						Square root
		vab1	vab2	vef1	vef2	vgh1	vgh2	Centroid size
25a.4	1	0.061	1.117	0.139	0.218	0.568	0.120	0.347
	2	0.053	1.117	0.138	0.223	0.562	0.110	0.331
	3	0.057	1.117	0.153	0.239	0.553	0.107	0.327
	4	0.063	1.113	0.149	0.248	0.574	0.115	0.340
	5	0.057	1.120	0.153	0.241	0.566	0.106	0.326
0b.1	1	0.085	0.957	0.191	0.316	0.614	0.110	0.331
	2	0.082	0.959	0.209	0.312	0.597	0.112	0.334
	3	0.087	0.944	0.182	0.311	0.614	0.108	0.329
	4	0.081	0.954	0.212	0.325	0.610	0.120	0.346
	5	0.081	0.931	0.196	0.310	0.607	0.107	0.327
3a.3	1	0.119	1.153	0.197	0.250	0.704	0.129	0.359
	2	0.101	1.196	0.198	0.280	0.741	0.134	0.366
	3	0.115	1.155	0.197	0.249	0.780	0.128	0.357
	4	0.098	1.174	0.189	0.266	0.728	0.123	0.351
	5	0.094	1.191	0.176	0.251	0.704	0.131	0.362
9a.2	1	0.088	1.064	0.168	0.247	0.649	0.142	0.377
	2	0.093	1.094	0.171	0.252	0.664	0.146	0.383
	3	0.099	1.106	0.177	0.258	0.671	0.150	0.387
	4	0.094	1.108	0.172	0.256	0.672	0.148	0.385
	5	0.092	1.095	0.170	0.253	0.665	0.150	0.388
8a.1	1	0.080	1.117	0.137	0.207	0.678	0.104	0.322

2	0.078	1.123	0.146	0.208	0.739	0.103	0.321
3	0.082	1.111	0.144	0.207	0.643	0.107	0.327
4	0.085	1.111	0.151	0.206	0.672	0.117	0.342
5	0.073	1.129	0.135	0.209	0.658	0.114	0.338