Population Variation in Fossil Graptolites: a Quantitative Study Based on Single Species Assemblages

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Department: Geology
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Abstract

There are several different types of variation in populations of fossil organisms. These include intra-specific (population) variation, evolutionary variation (specimens on a slab accumulating over thousands of years), and preservational variation. An understanding of the extent and type of variation present in a population is fundamental to biological and paleontological studies. This study examines several populations of fossil graptolites from which population variation can be studied without the influence of the other types, and includes several types of morphometric analyses to examine population variation in several species of fossil graptolites. These analyses include isolating three dimensionally preserved specimens from limestone, and then photographing, digitizing, and measuring the specimens. Statistical measures such as standard deviation, coefficient of variance, modal distribution, and an index of dispersion (a similar test to the coefficient of variation, specifically meant for measuring count-based data sets as opposed to continuous data sets) will be used. We expect to gain an understanding of the range of biological variation in a number of morphologic characters in these taxa.

Acknowledgements

To my parents and my friends, for moral and caffeinated support. To the University of Dayton Honors Department, for all their support and understanding with the accelerated schedule of our project. To the University of Dayton Geology Department, for their flexibility in helping me balance classwork with my thesis work. And a heartfelt thank you to Dr. Daniel Goldman, for his patience, dedication, and direction. Dr. Goldman, I would not be the geologist I am today without your help, advice, and humor. Thank you.
# Table of Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Title Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abstract</td>
<td>Title Page</td>
</tr>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Methods</td>
<td>3</td>
</tr>
<tr>
<td>Results and Discussion</td>
<td>7</td>
</tr>
<tr>
<td>Conclusions</td>
<td>32</td>
</tr>
<tr>
<td>References</td>
<td>33</td>
</tr>
<tr>
<td>Data Appendix</td>
<td>34</td>
</tr>
</tbody>
</table>
Introduction

Graptolites were colonial, planktonic organisms that lived in the poorly-circulated Early Paleozoic oceans (Finney and Berry, 1997). Graptolites are a completely extinct group of animals that existed during the Middle Cambrian to the Lower Carboniferous (550-318Ma) (Palmer 1991). They are made of a fibrous, durable protein known as collagen (Palmer 1991) and are commonly well preserved because the low oxygen environment in which they were deposited did not support predatory or scavenger organisms. The graptolites in this study are Late Ordovician in age, about 455Ma.

Because graptolite fossils can be found in Early Paleozoic mud rocks worldwide, they are considered to be a significant index fossil for Ordovician and Silurian strata. Index fossils are fossil organisms that are especially good for ordering rock units into a superpositional sequence and making time correlations between units in different locations (Finney and Berry, 1997). The new Lower Paleozoic geologic timescale (Gradstein et al., 2012) is primarily based on the global succession of graptolite faunas.

A sequential arrangement of tube-like structures called thecae make up the rhabdosome, formed in a saw-tooth pattern along the length of the colony.

Figure 1: A specimen of G. typicalis, demonstrating the saw-tooth zooid arrangement characteristic of graptolites

These thecae held zooids, a common name for a single animal that is part of a larger colonial structure; bryozoans are a modern example of this. Graptolite morphology changed dramatically during their evolutionary history and hence, they are also textbook examples of organisms that exhibit evolutionary trends in the fossil record (e.g. Moore, Lalicker, and Fischer, 1952). The study of graptolites and their evolution is instrumental to the development of the geologic timescale and to our understanding of fossil zooplankton.

The central problem that we are addressing in this study is how to assess biological population variation in the fossil record. An understanding of population variation is essential to species identification, taxonomy, and evolution in both modern and fossil organisms. Examining variation in fossils can, however, be problematic. There are four main types of variation in fossilized remains, some of which can confound an assessment of actual population variation within a species. The types of variation are as follows.

Preservational variation is the most common cause of variation between specimens in a sample of fossils. Preservational deformation is due to the compressional and extensional stresses on the rock during deposition and lithification. Directional stresses that act on both the rock and the fossils contained within the rock can make cause one species to resemble two on a single bedding plane (Figure 2).
Figure 2: Preservational deformation in fossil graptolites—note the orientation of the rhabdosome changes the type of deformation it experiences

Graptolite fossils are most often preserved as flattened (and thus distorted) carbon films on black shales, a rock that commonly forms in deep water (again, see Figure 2). As a result, the shearing, compression, extension, or combination of these stresses at depth deforms the specimen or sample population in such a way that makes the measurement of true population variation between specimens difficult.

Graptolites can, however, be found preserved three-dimensionally in a type of rock called limestone. As limestone forms, the carbonate-rich sediment quickly lithifies, preventing the fossil from being crushed and preserving it without deformation. In this study we only examine graptolite populations that are preserved in limestone.

Evolutionary variation in a sample occurs when specimens are time-averaged on a bedding plane because of slow sedimentation rates. When the rate of deposition of sediments is almost always slower than the rate at which specimens die and are buried, specimens that may have existed thousands or millions of years apart can appear in a relatively thin section of sample. That is, evolutionary ancestors are found buried on the same bedding plane as their descendants, adding great uncertainty to the range of variation in a species at any one instance in time. Without an understanding of population variation it becomes difficult to answer the question “did the ancestor and descendant species coexist?”

In certain cases limestone beds were deposited in rapid storm events that are known as tempestites. Tempestites were usually deposited in shallow epicontinental seas that were swept by storm events such as hurricanes (Myrow 1996). Tempestites were thus deposited rapidly and are considered geologically instantaneous events. Hence, the presence of graptolites in tempestite indicates that a swarm was killed and rapidly deposited in a snapshot of geological time. We examined graptolite samples that, for independent sedimentological reasons, are thought to occur in tempestites.

Sedimentological indicators for limestone beds being deposited as tempestites include the disturbance of shallow-water organisms (Myrow 1996), as well as pot and gutter casts, rip-up clasts, current orientation of fossils, and coarse shell lags overlain by finer sediments. Gutter casts are formed when the unidirectional flow of an event causes channelization and deep, narrow scours in a muddy substrate (Myrow 1992). Rip-up clasts and other types of dislocated debris also indicate the presence of a sudden and violent event, most commonly interpreted as a storm event. The rapidity of the deposition
of tempestites both fills and surrounds the graptolite fossil with sediment during burial, three-dimensionally preserving the fossil within a single assemblage. Because tempestites formed in geologically instantaneous events, we can support the hypothesis of single-species assemblages deposited without time averaging as stated by Cope and Lacy (1995), a hypothesis which would otherwise be untenable.

Intraspecific variation, or variation within a species, is population variation. Variation within a species of graptolites translates to the range of variation that a certain character in a biological population exhibits that is statistically differentiable from the range of variation in a different species. Measuring intraspecific variation requires the examination of multiple samples of the same species in order to establish the range of variation. On the other hand, interspecific variation is the variation between different species. Separating intra- from interspecific variation is necessary for detecting the presence of multiple species in a given sample and for any accurate measurements of biodiversity.

Paleontological studies often neglect to take these different types of variation into account when defining fossil species. Because our graptolite samples consist of three-dimensional, undeformed, single species assemblages that were instantaneously buried, we can eliminate preservational and evolutionary variation so that we can more accurately examine true population variation. The quantification of graptolite size and shape allows us to compare species objectively, in a way not seen in many past studies.

We define true population variation as the presence of morphologic variation within a sample that is statistically differentiable from other samples and the result of adaptation to environmental and biological factors. As previously noted, variation comes in many forms, so we define “true population variation” as the component that is not preservational or evolutionary variation within a sample. Additionally, we want to make sure that whatever variation we do observe does not include human measurement, whatever [ideally small] error the act of measurement detects.

Material and Methods

Five samples from the late Sandbian and Early Katian stages (early Late Ordovician) were used in this study. These samples were collected from the uppermost portion of the Kope Formation, Maysville, KY [Geniculograptus typicalis]; the middle-upper Kope Formation, Covington, KY [Geniculograptus typicalis]; the middle Kope Formation, Covington, KY [Geniculograptus typicalis and Geniculograptus. pygmaeus]; the upper Bromide Formation, OK; [Amplexograptus maxwelli]; and the Lebanon Limestone Formation, Murphreesboro, TN [Amplexograptus perexcavatus].

The sampled strata represents a time during the Late Ordovician when a large inland sea dominated central North America. The mode of deposition for the samples is through the random and rapid storm events in which graptolite populations were swept out of the water column and buried, providing a sample without the time averaged accumulations of specimens commonly represented in fossil beds.

Three samples from different levels (uppermost Kope from Maysville KY, middle-upper Kope and middle Kope from Covington KY) in the Kope Formation were also examined for the possible coexistence of two species, an ancestor and descendant pair. The results from this are discussed later.
Image Pro software was used in conjunction with a digital camera and microscope to collect Cartesian coordinate data from landmarks (homologous morphologic character points; Bookstein, 1997) on each graptolite specimen (See Figure 3).

Figure 3: A sample of homologous point locations

These points were digitized and then exported to a Microsoft Excel data sheet for each that calculated linear morphologic measurements for each specimen.

Homologous points that could not be found due to a damaged or deformed specimen were placed in the far bottom right-hand corner of the image; this way, when measurement data was created using that particular point, the measurement would be an order of magnitude or larger than other similar measurements. Outliers caused by a missing homologous point were thus easy to spot. As a side note, specimens were aligned vertically in order to maintain consistency throughout the digitizing process.

Each specimen was digitized twice, with the two sets of measurements collected at least one week apart. This was a way to test for human error in the digitizing process. Thus, differences between measurements on a single specimen would be indicative of
human-introduced measurement variation – a source of error that would confound our 
evaluation of population variation. A comprehensive and complete record of microscope 
magnification settings, specimen specific notes, and other data during the imaging and 
digitization processes was crucial to maintaining reliable results. This point cannot be 
overstressed, especially when performing order-sensitive operations, as was the case with 
the data collection in this study. These measurements were averaged for each character 
and the means were compared using the T-test function of the PAST3 Program (Hammer 
et al., 2001). Comparisons of group means for morphologic characters measured twice 
were statistically indistinguishable indicating that human digitizing error was not a 
significant component of character variance. 

Morphometric data was primarily generated through the use of a simple distance 
formula using the Cartesian coordinates of digitized homologous points. The distance 
formula is

\[ LENGTH_{Theca} = \sqrt{(X_f - X_i)^2 + (Y_f - Y_i)^2} \]  

(Eq. 1)

Where \( X_f \) and \( X_i \) refer respectively to the final and initial x-components of the 
homologous point coordinate pairs. Likewise, \( Y_f \) and \( Y_i \) refer respectively to the final and 
initial y-components. The linear measurements were then copied to a master data sheet in 
Excel, where Intra- and interspecific variation for each character could be analyzed. 

Definitions of the common terms used in this project are given below.

**Characters** are defined in this study as the particular portion of graptolite morphology 
being measured.

The **rhabdosome** is the full structure of the colony. This is the graptolite as a whole, not 
just one theca or set of thecae.

A **theca** is the tube-like structure on the colony that housed the zooid during its lifetime.

**Zooids** were the colonial animals that lived in the rhabdosome.

The **aperture** is the opening in the rhabdosome that allows the zooid to feed and take in 
vital nutrients. There are apertures for each individual zooid.

**Samples** are the graptolite specimens that come from one bed of limestone.

**Two Theca Repeat Distances**, or **2TRDs**, are the distance from the bottom of one thecal 
aperture to the bottom of the second succeeding thecal aperture. This is the measurement 
from aperture one to aperture three, skipping the thecal aperture in between, with all 
theca in question on the same side.

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*Figure 4: Character measurements; A - Aperture Width, B - Thecal Length, C - Aperture 
Height, D - 2TRD, E - Enclosed Sicula Length, F - Rhabdosome Width*
The different measurements taken are indicated in Figure 4 above. The characters are aperture width (A), thecal length (B), aperture height (C), two theca repeat distance [2TRD] (D), enclosed sicula length (E), and rhabdosome width (F). We found that the point of enclosure of the sicula could be difficult to locate on many specimens, and as a result, the character measurement was not used in our analysis. In larger sample sizes or different sample sizes, this may not necessarily be the case, so it may be worth exploring in future studies.

Microsoft Excel was used for the bulk of the data generation and analysis. Plots were generated in Excel using the average values of each character measurement according to theca. Scatter plots for each digitized population were created to test for outliers, which would indicate either measurement error introduced by human measurement, or, in the case of a bimodal distribution, the presence of a second species in the sample. Outliers were primarily identified by looking for values that were outside 2 standard deviations about the mean. For example, the measurements for the thecal lengths of the G. typicalis population from the Kope Upper (Covington, KY) were averaging 0.500mm ± 0.050mm, the chosen value for flagging was 0.700mm or greater, at which point those points could be deleted; outliers will always be well over the flagging value because of where the missing homologous point was placed. Anomalous values were also produced when a homologous point was missed during the digitizing process, and that would in turn cause the measurement data fall well outside the normal range of variation. These outliers were rare; in larger sample sizes, there was at most one specimen (in only one case, two) outlier in a single set of measurements. Measurement reliability was also confirmed by comparing formula-generated values were compared to direct measurement (via the ruler tool on the ImagePro software).

Outliers that were clearly human-introduced were easily eliminated from the rest of the population measurement data. Additionally, plots of character measurements from individual specimens made spotting non-linear or erroneously large specimen measurements straightforward.

After removing the erroneous data, each character measurement from every specimen in each species was plotted on bivariate graphs to examine intraspecific variation. Intraspecific variation was also examined using a measure known as Coefficients of Variation (hereafter referred to as CoVs). The CoVs were calculated using the equation,

\[ CoV = \frac{s}{\bar{A}} \]  

(Eq. 2)

where “S” is the standard deviation for each character measurement at each theca and “A” is the mean value for the entire population at that theca. Donnelly et al. (1999) (508) noted

“When populations differ appreciably in their means, simple comparisons of their variances or standard deviations can be misleading since differences in absolute variation may reflect nothing more than differences in scale. The statistic that is most often used to quantify relative variation and test hypotheses of multiple species is the coefficient of variation (CV).”

In a study by Polly (1998) regarding CoVs in mammalian dentition, there exists the problem of the inverse relationship of CoVs to the mean measurement value. That is,
as the mean grows large, the CoV shrinks, making the coefficient of variation ineffective in describing the presence of variation. Polly stated (89),

“One negative correlation between the coefficient of variation and the mean may be found: (1) when measurement error is disproportionately large for smaller measurements, (2) when of a whole is compared to its parts, or (3) when a variable has a significant probability of a zero measurement. In the present study, however, the last two cases are not applicable. All variables are linear measurements of teeth with no probability of a zero measurement and no wholes are compared to constituent parts.”

This is important for three reasons. First, to reiterate, the comparisons we make in this study are between like character measurements of different species. Secondly, the measurements we make are all linear and like the mammalian dental measurements have zero probability of a zero measurement. Third, we are comparing parts of the graptolites, i.e. character measurements, to one another, thus eliminating the problem of large differences in scale or comparisons between the whole graptolite and its parts.

Finally, the average population values of each character across all samples were plotted to test for the range of interspecific variation.

**Results and Discussion**

T-tests were performed on the mean character values from the two sets of measurements to test for the distinguishability of group means. The T-test is a normalization test that measures the probability that the group means might be similar due to random chance. Large p values like those shown in Table 1 (p >> .05; Hammer 2001) indicate that the group means of the two sets of measurements are indistinguishable, which allowed us to rule out human introduced measurement error as an appreciable source of error in this study.
Table 1: P-values from T-tests show that the means are indistinguishable, based on the fact that the p>0.05

The plots of individual character measurements from all specimens in each sample displayed the range of variation that the character had at each individual theca within the population (see Figures 5-42 below). The thecal lengths for each population followed a slowly-increasing linear trend (even-numbered Figures after this statement), except for the plot of the thecae of the Upper Kope sample (Covington KY). This trend was different from the trends of the other populations.
Figure 5: Measurement error as seen between measurement trials. Range bars are one standard deviation about the mean. The orange and blue dots are means for each set of measurements taken on the same specimens.

Figure 6: The range of variation within a species is most conveniently demonstrated by this graphical representation, where all the specimens from the Upper Kope sample (Covington KY) were plotted to show the distribution of the entire population.
Figure 7: Aperture widths of the *G. typicalis* population from the Upper Kope sample showed relatively rapid growth as compared to other characters. Range bars are one standard deviation about the mean. Colored dots are character means for each set of measurements taken on the same specimens.

Figure 8: The aperture width and height data all showed a slowly increasing, linear trend, shown here. This was likely caused by the gradual growth of the zooids housed in the rhabdosome.
Figure 9: Rhabdosome widths were typically the largest measurements in this study, and had the greatest range of variation from the width at the proximal end to the largest width at the distal end of the colony.

Figure 10: 2TRD measurements proved to be the least variable, though the number of data points are small.

Aperture width, aperture height, and rhabdosome width also followed linear trends and showed similar CoVs. The CoVs will be discussed later in this section. Similar coefficients of variation within a species can be used as a form of differentiation between species.

Interestingly, in *G. typicalis* the two theca repeat distances (2TRDs) showed very little increase in size from one theca to the next. The exact range is not visible here, but it is clear that the 2TRDs are not growing nor shrinking rapidly. This is because the thecal lengths are actually decreasing distally (see Figures 5 and 6). Additionally, as we will see
at the end of this section, the coefficients of variation indicate low population variation in 2TRD measurements, a characteristic noted in other studies (Howe, 1983).

**Figure 11:** The thecal lengths for the Kope Maysville sample were more or less static

**Figure 12:** see figure 11 description
Figure 13: Variation increases with theca number in the aperture widths, which may suggest some type of nutrient variation for the zooids to grow differently.

Figure 14: see figure 13 description
**Figure 15:** Note the small variation throughout the theca

**Figure 16:** see figure 15 description
Figure 17: Rhabdosome widths did not vary much in the Kope Maysville sample.

Figure 18: Unfortunately, many of the specimens from the Kope Maysville were relatively short – we think that the 2TRDs would have maintained the same variation as intervals th. 1.1-3.1 and 4.1-6.1 – 1.1 refers to the side one theca 1.
Figure 19: Note the large range of variation in this sample. We interpret this to indicate that two species occur in this sample.

Figure 20: Note the set of specimens plotting above the main body—this broad data distribution supports the hypothesis of the existence of a second species, G. pygmaeus.
One of the ways that we could define the presence of two species within one bedding plane is to show the bimodal distribution of specimen measurements when the entire population was plotted at once. These distributions would be separated enough to be distinguishable.

**Figure 621**: Still more consistent growth – also, a good set of first and second trial comparisons

**Figure 22**: see figure 21 description
Figure 23: Slow growth in the aperture height of the Lower Kope; note the wide variation about thecae 4-8.

Figure 24: see figure 23 description.
Figure 25: the rhabdosome widths in the Kope Lower specimens showed small variation, based on how tightly packed the plots were.

Figure 26: from the samples that are larger, we see that the variation remains fairly small.
Figure 27: Variation shrinks after the 14th theca, which is likely a result of a shortage of large specimens

Figure 28: see figure 27 description
Figure 29: The variation that we see in the later thecae (16+) is due not to actual variation but from a large number of small specimens that did not have thecae past 16.1

Figure 30: Aperture widths varied widely, compared to the other character measurements of maxwelli.
Figure 31: Note, the first theca on graptolites of *A. maxwelli* has an anomalously large aperture. This could be measurement error as the margins could be difficult to define, with sloping aperture sides disguising the actual aperture edges.

Figure 32: The aperture heights in *A. maxwelli* grew rapidly then stabilized to a slower growth rate.
Figure 33: Interestingly, the colony width grows rapidly in the first five theca then the growth slows for the rest of the rhabdosome.

Figure 34: here we see consistently wide variation throughout the larger specimens.
Figure 35: Note the relatively slow growth of thecal length—other species exhibit greater growth rates than this.

Figure 36: Thecal lengths are fairly variable in A. perexcavatus—shrinking variation is actually a lack of large specimens, so the data for much of A. perexcavatus is truncated to ensure reliability.
Figure 37: Variation was consistent throughout the aperture widths here.

Lebanon Limestone *A. Perexcavatus* Average Aperture Width

Figure 38: see the description of figure 37

Lebanon Limestone *A. Perexcavatus* - Aperture Width
Figure 39: consistent variation and static aperture height growth – the zooids may have been in equilibrium with the supply of nutrients.

Figure 40: see figure 39 description
Figure 41: Among thecae 1-5, the rhabdosome widths showed very little variation, and the later thecae were not as useful because of small specimens.

Figure 42: the size of the perexcavatus specimens makes using the 2TRD measurements inadequate.
Figure 43: The clearest differentiation between populations is seen in this plot, where each population (G. typicalis – Upper Kope Covington, G. typicalis – Uppermost Kope Maysville, mixed G. typicalis – G. pygmaeus sample – Lower Kope Covington, AM – Amplexograptus maxwelli Bromide Fm., and LP – A. perexcavatus) is well-separated from the next.

Figures 43 – 47 illustrate the mean values for morphometric variables plotted from all five populations. The morphologies of the samples the same species are extremely similar to one another, but the measured variables of separate genera, as shown in Figure 43, are significantly different from one another. The populations of *Geniculograptus typicalis* from the Upper Kope Formation at Covington, KY and the uppermost Kope at Maysville have nearly identical mean thecal lengths (Fig. 43), and we think this might indicate some level of evolutionary stasis (Eldredge and Gould, 1972). However, specimens from the Lower Kope Formation at Covington have significantly smaller thecal lengths than the other two Kope Formation samples, (by more than 0.1mm). If the Lower Kope specimens were to follow the same pattern as the Upper Kope samples, we would expect to see all three plotting very close to one another. The difference between the Upper and Lower Kope samples either indicates significant evolutionary change through the interval of time represented by the Kope strata or supports the hypothesis of the existence of a second species in the sample. As discussed below, the CoV’s for this sample are high, which probably indicates a second species. Upon closer inspection we were able to identify specimens of *Geniculograptus pygmaeus*, the descendant of *G. typicalis*, in the sample.

The closely related *Amplexograptus* samples, *A. maxwelli* and *A. perexcavatus* had significantly different measurements from the *Geniculograptus* samples, and they also were easily differentiable from each other by much different thecal lengths. The *G. typicalis* samples from the Upper Kope and the *Amplexograptus* samples had much different thecal lengths (more than 0.15mm difference, in most cases). Hence, the two genera are easily distinguishable.
Figure 44: *Amplexograptus perexcavatus* is easily differentiable from *Geniculograptus typicalis*, but *Geniculograptus* and *A. maxwelli* have different aperture widths.

In the average aperture width graph, all three Kope samples plotted closely together, which is significant. The *Amplexograptus* populations both plot within about 0.02mm of each other, and within about 0.04mm of the *Geniculograptus* populations. In sum, the populations have similar but distinct aperture widths.

Figure 45: *Amplexograptus maxwelli* and *A. perexcavatus* are differentiated from the *Geniculograptus* populations, but the *Geniculograptus* samples plot close enough to each other to indicate similar aperture heights.

The average aperture heights of the Upper Kope samples plotted together and separate from the Lower Kope, but not by more than 0.02mm. The greatest divergence
can be seen is the middle part of the rhabdosome – thecae 4–9. The *Amplexograptus* populations both plot within about 0.04mm of each other, and have substantially greater aperture heights than *Geniculograptus*.. The clearest separation in this character is the separation between *A. perexcavatus* and *A. maxwellii*, which is greater than in the aperture width plots. The aperture height measurement averages had gentler overall slopes than the widths, suggesting simply that the apertures became deeper relative to their heights as the colonies grew. We do not know if this had a significance with respect to zooid feeding (or other ecological significance), but the trend is consistent across all populations, with some slight variation.

![Average Rhabdosome Widths - Testing for Interspecific Variation](image)

**Figure 46:** Note the separation of the samples in two two groups – rhabdosome widths were an effective character for species differentiation, especially looking at *A. maxwellii* and *A. perexcavatus* compared to the Kope samples.

Among all the character measurements, the rhabdosome width showed the greatest rate of growth in all populations. Similar to the aperture widths, the *Geniculograptus* samples all plotted right on top of each other, with well less than 0.0200mm difference distally between any of the populations. The *Amplexograptus* populations also plotted right on top of one another. This character is probably the clearest of all the measurements for generic comparisons, but it is speculation to say that it would always be the case with other genera. The two genera plotted consistently 0.1mm apart.
Figure 47: the variation is best viewed in the values of CoVs based on the small number of 2TRD intervals

Because there are few data points for the 2TRD plots, we can only say that the patterns for each species differ enough to be distinct. More information can be gleaned from examining the coefficients of variation (See Table 2).

Table 2: Coefficients of Variation values that show the range of intraspecific variation as well as the difference in variation between species. Note here that interspecific variation is greater than intraspecific variation, and that the large values for the Lower Kope in Thecal Length and Aperture Width suggest the presence of two species (See figures 15-22).

CoV values <10 are considered to be within normal population variation in modern species. A CoV >10 is considered to indicate more than one species in the sample (Simpson et al., 2003). In our fossil samples coefficients of variation for measured characters generally showed average values of CoV<10, or very slightly higher indicating normal biological population variation. Intraspecific variation was less than interspecific variation as indicated by the larger differences in CoV values between populations than within them. Specimens of different species and different genera are easily distinguishable in our morphometric analysis.
The coefficients of variation for measured characters from each population show that the greatest variation in each species took place in either thecal length or aperture width, which indicates the variation in zooid size living in the colonies. Because these characters are widely variable, their variation within the species may overlap with other species, so using the character for differentiation would be problematic. When comparing variation among samples the same species from the same formation, such as the Upper and Lower Kope Formation, we found that one sample had unusually large CoV’s (>>10). In addition to significantly higher coefficients of variation, the sample from the lower Kope Formation also had very different thecal measurements. This implies either significantly evolutionary change or the presence of two different species. We think that this sample contains two species, *G. typicalis* and its evolutionary descendant *G. pygmaeus*.

The two theca repeat distance varied the least within populations, and because of this, the 2TRD can be used as a stable index for comparison between species as previously noted by Howe (1983). Additionally, the rhabdosome widths exhibited low variability, but the rate at which they grew followed different patterns, between a rapid initial growth spurt followed by a stabilized more gradual growth period, a consistent but slow growth, or a very rapid growth cycle; in short, these two fields of comparison might aid in differentiation among many populations.

**Conclusions**

The graptolites examined in this study offer an important opportunity to examine biological variation in the fossil record. The preservation of specimens in limestone beds by storm deposition (called tempestites) allowed us to eliminate deformation and evolutionary time-averaging as sources of morphological variation. Thus, inter- and intraspecific variation could be evaluated and compared. Duplicate measurements taken from each morphologic character allowed for the evaluation of human measurement error, which was found to be negligible. Measurement reliability was also confirmed by comparing formula-generated values were compared to direct measurement (via the ruler tool on the ImagePro software).

The average values of character measurements were plotted and variation was represented by one standard deviation about the mean values. Variation was also evaluated using the Coefficient of Variation (CoV) statistic.

Interspecific vs. intraspecific population variation was clear in the plots of morphometric data (cite figures). Each genus is quantitatively [and thus graphically] distinct from the next, based on the thecal length and rhabdosome width measurements. Calculated Coefficients of Variation (CoVs) for each character and each population illustrated which character was the most variable in each population. Unusually high CoV’s indicate the presence of a second species, *Geniculograptus pygmaeus*, in the Lower Kope sample from Covington, KY., Measurements of thecal length and aperture height from this sample also plotted separately from the measurements of other samples from the same formation which are known to contain only *G. typicalis*.

Intraspecific variation was smaller than interspecific variation, as was demonstrated by the Coefficients of Variation. Two theca repeat distances (2TRDs) were
the least variable, which was consistent with the CoVs and is reflected in the work of (Howe1983). All plots showed species distributions that were distinct, though some characters were less variable than others, a result that may indicate some ecological significance.

Improvements to the accuracy and precision of the morphologic measurements on the graptolite specimens mentioned herein include: higher-resolution imaging, larger population sizes, and a greater breadth of sample locations to show possible geographic variation. To measure variation more accurately, it is suggested that the number of specimens in each sample population be increased so that the average measurement for each theca and character to better represent the species morphology.

Possible future studies could include geometric morphometrics (e.g., Bookstein, 1997), a method through which shape variation can be removed from size and analyzed separately.

References

Data Appendix
The data collected in this study is contained in the following eight sections. The
data was parsed by column sets; in other words, in order to re-represent the data in excel, each section is a set of columns running through multiple populations, as seen in Table 3.

Table 3: The division of the data set was essential in order to be able to fit it into this report.

All rows were copied for each section, such that each section contains nine (9) columns covering all rows. To reassemble the data set for the readers reference, simply place each section into excel side by side. The colors above represent which populations are present in each section. It is important to note here that spaces between populations MUST REMAIN BLANK in order for the transfer back to excel to be successful.

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**Measurement (mm)**

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- KUD1 - a: 0.500549
- KUD1 - b: 0.509979
- KUD1 - c: 0.500976
- KUD2 - y: 0.544941
- KUD2 - z: 0.424631
- KUD2 - a: 0.449473
- KUD2 - b: 0.500599
- KUD2 - c: 0.529551
- KUD2 - d: 0.489312

**Additional Measurements**

- 0.453394
- 0.373858
- 0.336753
- 0.414357
- 0.500061
- 0.380173
- 0.367521
- 0.413694

**More Measurements**

- 0.545144
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