The Pennsylvanian Cladid Crinoid *Erisocrinus:* Ontogeny and Systematics

by

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Abstract

Cladid crinoids have among the highest disarticulation rates of all Paleozoic crinoids, so the study of morphology and systematics has been hindered by a lack of available specimens. An unusually large collection of the genus *Erisocrinus* from numerous museum collections has been studied in order to determine the growth of the type species of the genus, as well as the systematics. Included in the collections were specimens from Lagerstätten deposits, including a complete growth series of *E. typus* from the Barnsdall Formation and a large number of relatively pristine specimens from the LaSalle Limestone.

A digital growth study using the complete growth series comprising eight crowns of *E. typus* collected from the Barnsdall Formation was performed using standard heads-up digitization methods in ArcGIS™. The sutures between all the plates of the crown were traced from high-resolution, two-dimensional photographs. Topological constraints that were put into effect prevented the digitized lines from overlapping and facilitated conversion into polygons. The perimeters, areas, and other measurements of these polygons, represented as individual plates, were automatically calculated by the software. A previous study of the ontogeny of this species concluded the growth of the cup to be isometric. However, results from this study concerning the relative rates at which plates changed size and shape show that *E. typus* grew anisometrically. The growth of the arm plates of the growth series appear to grow in three distinct stages, noted from the change in area in the arm plates of the growth series.

The systematics study of the genus *Erisocrinus* took into account the 36 proposed species since its naming in 1865. The species previously synonymized or reassigned were reevaluated. Those species still named within the genus *Erisocrinus* were evaluated on the basis of a new diagnosis of *Erisocrinus*. Over two hundred specimens comprising a variety of proposed species were measured (radial height and width, basal height and width, stem diameter, cup height) so that a Principal Component Analysis and further analyses could be run. Of the 18 species still named within the genus, only eight of them are considered valid: *E. typus* Meek and Worthen 1865, *E. propinquus* Weller 1909, *E. elevatus* Moore and Plummer 1940, *E. obovatus* Moore and Plummer 1940, *E. terminalis* Strimple 1962, *E. longwelli* Lane and Webster 1966, *E. mediator* Strimple and Watkins 1962, and *E. healdae* Pabian and Strimple 1974. This study redefines the temporal span of the genus as being present primarily during the Pennsylvanian, with two of the eight species surviving into the Early Permian. As re-defined in this study, *Erisocrinus* was restricted to the mid-continental United States.

Acknowledgments

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INTRODUCTION

Whereas crinoids are a major component of Paleozoic communities post-Cambrian (Sepkoski, 1981; Sims, 1999), complete specimens are rare. Crinoid skeletons are composed of many calcium-carbonate plates connected by muscles and ligaments; loss of the soft tissue causes the skeletal plates to be very prone to disarticulation after death. Actualistic studies have determined that, without burial, most modern-day echinoderms undergo disarticulation within a time frame of days to weeks (Meyer, 1971; Lewis, 1980; Donovan, 1991).

The rarity of well-preserved crinoid specimens in the fossil record hinders the study of their ontogeny and systematics. The genus *Erisocrinus* is no exception and more often than not, this genus is discovered with only the cup intact with the stem and arms often disarticulated (Fig. 1). Determining variation is even more difficult in this genus due to the fact that the simple cup of *Erisocrinus* is without ornamentation (Bowsher and Strimple, 1986).

The procedures that paleontologists follow concerning the study of crinoids have undergone dramatic changes since the class Crinoidea was named almost two hundred years ago (Miller, 1821). It was not uncommon to designate new genera and species of crinoid based on slight differences in characteristics or even similar specimens found in different localities. To further complicate the splitting of the class Crinoidea into minute categories, early authors did not commonly provide any images or measurements of the fossils that they named.

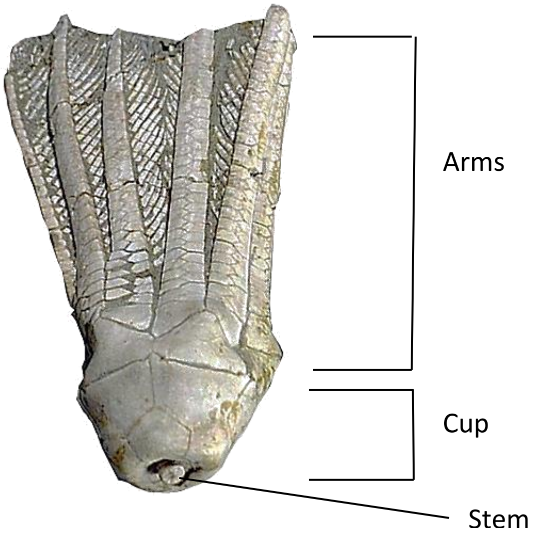

FIGURE 1-The three basic regions of a Paleozoic crinoid: arms, cups, and stem. Often, cladid crinoids disarticulate and are found as only cups. (*Erisocrinus typus*; photo credit: Humboldt State University)

Holotype specimens were not designated, and many genera were represented instead by syntypes, a practice no longer permitted by the International Code of Zoological Nomenclature (Stoll et al., 1964), nor did the authors provide information on where the fossils had been reposited. Even though these paleontological procedures are no longer in practice, the systematics of the class Crinoidea is quite tangled, and with the poor record keeping in earlier times, it can be difficult to determine important details about the genera and species that have been erected.

In the almost 150 years since the genus *Erisocrinus* was erected by Meek and Worthen (1865a), 37 species have been proposed as belonging to it. Many of these species have been synonymized in the intervening years and many others have been reassigned to other genera. Because no comprehensive examination of *Erisocrinus* has been undertaken, it is not clear how many valid species are within the genus.

The type species of the genus, *Erisocrinus typus,* has been found in unexpectedly large quantities in fossil Lagerstätten, defined as areas of exceptional fossil preservation, in the United States. With these larger collections, it is possible to determine the ontogenetic change that this species underwent. A complete growth series of the type species was discovered by Daniel Mosher in the Barnsdall Formation that shows the ontogenetic change during the lifespan of *Erisocrinus typus* quite well.

The research included in this study has utilized these collections of the nominal (type) species from crinoid Lagerstätten, such as the Barnsdall Formation, as well as other museum collections of *Erisocrinus* species, in order to study the range of intraspecific variability within the species and its mode of growth via both a non-traditional growth study in chapter one. A reappraisal of the systematics of the genus was also made possible by these large collections (chapter two). As crinoids are quite often not preserved in large numbers, the importance of studying these Lagerstätten collections of *Erisocrinus* cannot be overestimated.

The Ontogeny of *Erisocrinus typus*

Introduction

Typically, high disarticulation rates of cladid crinoids leave a rarity of complete skeletons in the fossil record, resulting in a lack of large collections from which to perform morphological studies. Arms and stems of cladid crinoids commonly disarticulate from the cup, leaving many taxa to be identified solely by the cup. This, of course, is true for the class Crinoidea as a whole, but it is particularly true for the subclass Cladida. The relative suturing of the plates of the calyx is different for each subclass of the crinoids. The camerates have tight suturing of the plates of the calyx, which results in a higher percentage of crown preservation. The cladids, in comparison, have relatively loose suturing of the plates of the calyx; this allows for the arms of the cladid to fall away from the cup soon after death (Ubaghs, 1978). Therefore, complete cladids are much scarcer in the fossil record compared with other subclasses of the class Crinoidea.

The lack of collections due to disarticulation prevents much from being known about cladid crinoids, especially Middle and Upper Pennsylvanian (Late Carboniferous) cladids (Ausich and Wood, 2012). Crinoid Lagerstätten can contain high numbers of crinoids that are unusually well-preserved. Defined as deposits of exceptional fossil preservation, commonly Lagerstätten can be a window into ancient communities that might not otherwise be seen (Seilacher, 1970). Two Lagerstätten that have been important in crinoid studies in the United States are the LaSalle Limestone, located in Illinois, and the Barnsdall Formation, exposed near Copan, Oklahoma.

While these deposits go far in alleviating the general lack of material with which to work, it is rare to find enough well-preserved specimens for a morphological study. Few papers have focused on the growth of Upper Paleozoic crinoids, with some exceptions (Peters and Lane, 1990; Ausich and Wood, 2012). These studies involved traditional growth studies of cladid crinoids using fairly large and well-preserved collections.

Peters and Lane (1990) found that the cups of the cladids they studied (*Erisocrinus typus, Apographiocrinus typicalis*) grow isometrically, or close to isometrically (*Apographiocrinus typicalis* growing with slight anisometric growth). The growth of *Erisocrinus* was determined based on a study of twenty-four cups and crowns from the LaSalle Limestone, with very few of the specimens being young juveniles. The study concluded that the growth of both the cup and the plates of the cup grow with virtually no change in shape. Ausich and Wood (2012) noted that *Hypselocrinus hoveyi*'s cup grew with a combination of growth: the basal and infrabasal plates grow allometrically, while the radial plates grow isometrically. All of the cladids from the studies show distinctly anisometric growth of the primibrachial plates. Other arms plates also expand in width as it grows, presumably for strength in the arms.

This study also focuses on the morphology of an Upper Paleozoic crinoid. However, the methods used to obtain the data for the growth study were nontraditional. This study, based on methods outlined by Zachos (2012), used ArcGIS© to create digital models of a growth series of *Erisocrinus typus* found in the Barnsdall

Formation (Fig. 2) in order to generate more accurate and more complete data. The results from this study were compared to the other known growth patterns of cladid crinoids.

Even though cladids have a relatively low preservation potential*, Erisocrinus* has a significantly higher preservation potential than expected. Its preservation has been evaluated in studies done at the genus level using bulk samples of the Wann (Lewis, 1986) and the Barnsdall Formation (Thomka et al., 2011). In these studies, radial plates were identified to genus and compared to data for the complete cups and crowns found within the unit to generate the Disarticulation Index (DI), defined as the percent of individuals that disarticulated. The results from the Barnsdall study are shown below (Fig. 3; Thomka et al., 2012). The Disarticulation Index of *Erisocrinus* is the lowest and is significantly lower than the next best-preserved cladid, *Apographiocrinus*. While the reasons for this are not fully understood, it is thought that the relatively thin nature of the radial plates of *Erisocrinus* might allow for the cup to stay articulated, even when being compacted by overlying sediment (Thomka, 2010; Thomka et al., 2011)(Thomka, 2010). This resulted in a large collection of *Erisocrinus typus*, including a full growth series ranging from 1.0cm-7.6cm (Fig. 4 and 5).

FIGURE 2-General location of the Barnsdall Formation within Washington County. Blue area represents Pennsylvanian Outcrop Belt; square represents Washington County. (Modified from Thomka et al., 2011).

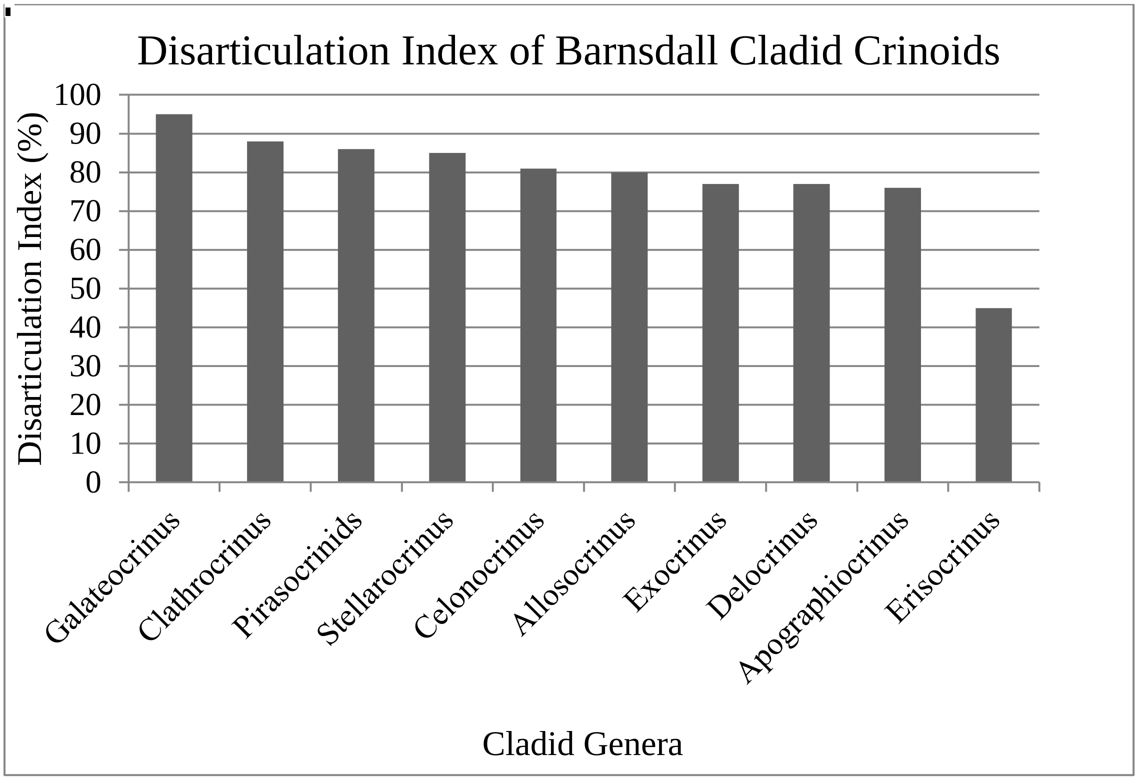

FIGURE 3-Disarticulation Index of cladids found in the Barnsdall Formation; note the extremely low Disarticulate Index of *Erisocrinus typus* (44%); meaning, 66% of the specimens belonging to *Erisocrinus* were found to be articulated. (From Thomka et al., 2011).

FIGURE 4-Barnsdall growth series specimens; 1. Youngest member of growth series; note rounded base of cup and uniserial arms. Growth series members 2-4 also represented. Scale bar in each photograph represents 1cm.

FIGURE 5-Barnsdall growth series specimens; growth series members 5-8 are represented here. Scale bar in each photograph represents 1cm.

Materials

A complete growth series of *Erisocrinus typus*, part of the 1,200 cups found in the area, collected by Daniel Mosher from the Barnsdall Formation was used for this study. The growth series (Fig. 4 and 5) comprises eight well preserved crowns representing the changes the species goes through from a juvenile to an adult stage. The size ranges from 1.0cm to 7.6cm in crown height.

Methods

Both sides of each specimen were photographed using a Nikon D-50 camera with a sigma macro-lens. Following the procedures outlined in Zachos (2012) the data for each specimen in the growth series were contained within a separate Personal Geodatabase within ArcGIS™10. Each database was subdivided into two Feature Datasets and each photograph for a crinoid specimen was contained within a Raster Dataset. The photographs were scaled to correct size using a scale bar in the photographs (Fig. 6a) and standard georeferencing methods.

The images were digitized using standard heads-up digitizing methods. The sutures between all of the plates on the crown were digitized as line features (Fig. 6b). Each of the lines was snapped to one another, with a 5-pixel error allowance. Five topological rules (no overlap, no self-overlap, no dangles, no intersection, no self-intersection) were enforced to ensure that the line features could be used to build valid polygons. The topology highlighted all of the areas in which these five rules were violated, so that they could be fixed to ensure that the digitized lines would not give inaccurate measurements.

The lines were converted into polygons that the program recognized as separate entities (Fig. 6c). Each polygon, or plate, had a separate area and perimeter that was calculated in centimeters.

The following measurements were extracted from ArcGIS©: cup height; crown height; radial height, width, and area; basal height, width, and area; primibrach height, width, and area; and brachial height, width and area. Statistical analyses of these measurements were performed using the software package PAST (Hammer et al., 2001; Hammer and Harper, 2006).

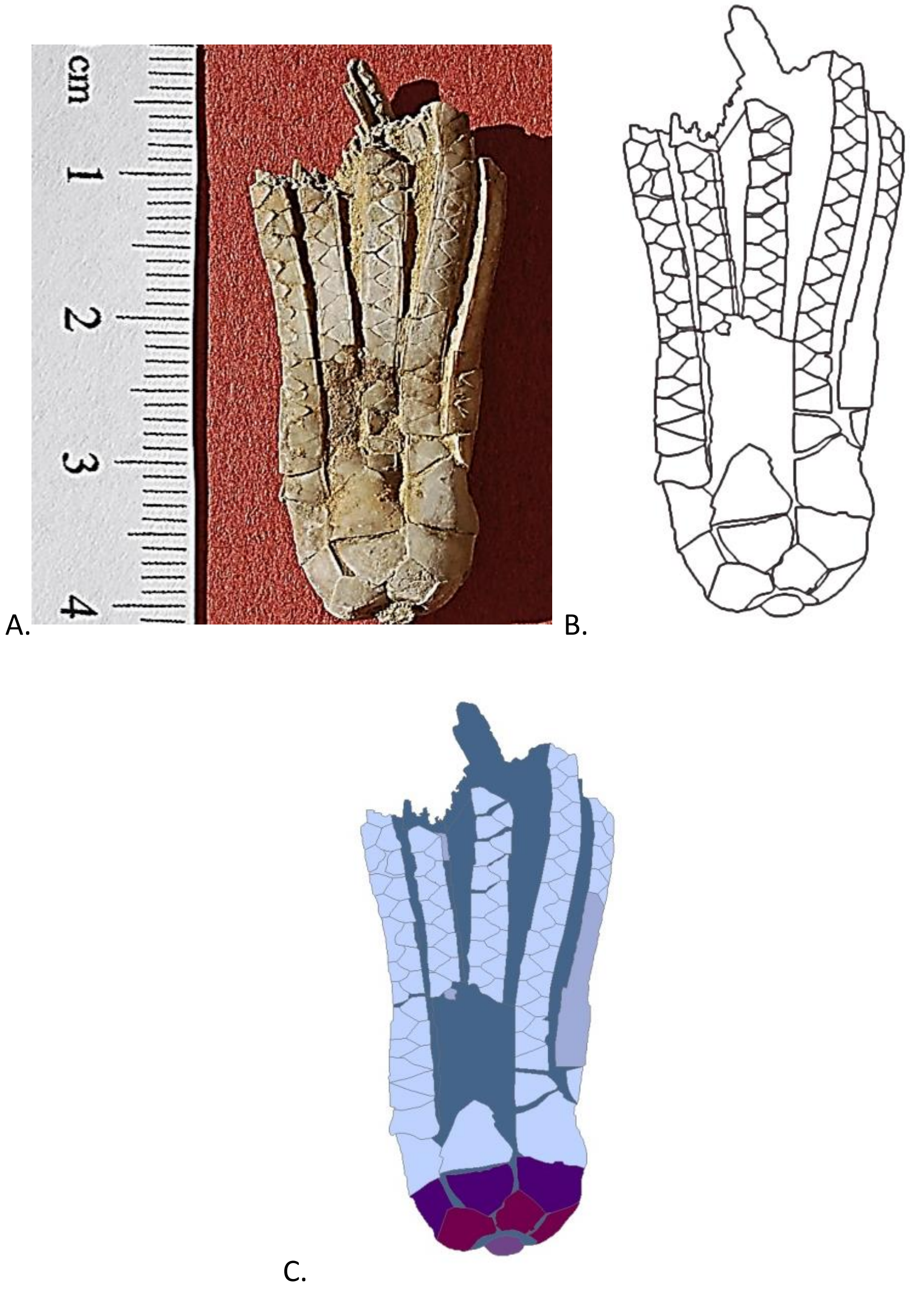

FIGURE 6-A. Photograph of GS #4 with scale bar in image. B. Line features digitized. C. Line features transformed into polygons.

Results

Complete data for the ontogenic study of the eight growth series specimens (Fig. 7) is presented in Appendix I; summary data is found in tables one and two. The data resulting from the ArcGIS™ growth study show that the growth of the plates of the cup was slightly anisometric. The radial plates' height, width, and area were compared to one another in bivariate plots (Fig. 8 and 9), as were the basal plates' height, width, and area (Fig. 10 and 11). The graphs depicting the changes in area are plotted as the square root of the area against the height of the plates (mm vs. mm) in order to equalize the units.

The arms (not including the primibrachial or first secundibrachials) of *Erisocrinus* begin in the juvenile stage as uniserial and change to biserial early in its life stages; in the growth series, we see that GS #1 is uniserial and GS #2 is biserial (Fig. 4 and Fig. 7). The change therefore happens in the juvenile stage. The primibrachials develop with strongly anisometric growth (Fig. 12 and 13). The juvenile plates are elongate and slender; as the crinoid ages, the primibrachials change shape to become wider than they are tall. The primibrachial in the A ray (presumably) is typically the longest in juvenile specimens, though the primibrachials become equal in height and width in later growth stages (Fig. 13).

The secundibrachials change from a wedge shape (i.e. cuneiform) in juvenile specimens and become biserial fairly early in its development.

FIGURE 77-Digitized growth series of *Erisocrinus typus*.

GS #	Basal Height (mm)	Basal Width (mm)	Basal Area (mm^2)
GS #1	0.979	1.20	0.939
GS #2	1.85	2.68	3.08
GS #3	1.89	2.84	2.65
GS #4	3.01	3.56	7.49
GS #5[1]	N/A	N/A	N/A
GS #6	3.47	5.17	10.7
GS #7	5.46	7.08	29.2
GS #8	6.29	9.02	37.6

TABLE 1-Basal plate data for growth series of *Erisocrinus typus*. The data is an average of the 22 available undistorted basal plates of the specimens (complete data is listed in Appendix I).

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[1] The cup of GS#5 is very compacted; unfortunately, no basal plats measurements were able to be taken with confidence.

GS #	Radial Height (mm)	Radial Width (mm)	Radial Area (mm^2)
GS #1	1.40	2.37	16.2
GS #2	2.50	3.49	28.1
GS #3	2.79	4.24	35.5
GS #4	3.26	4.69	37.4
GS #5	3.63	4.12	50.1
GS #6	4.49	7.47	66.5
GS #7	6.25	8.48	79.1
GS #8	6.87	14.41	87.7

TABLE 2-Radial plate data for growth series of *Erisocrinus typus*. The data is an average of the 20-23 available undistorted radial plates of the specimens (complete data is listed in Appendix I).

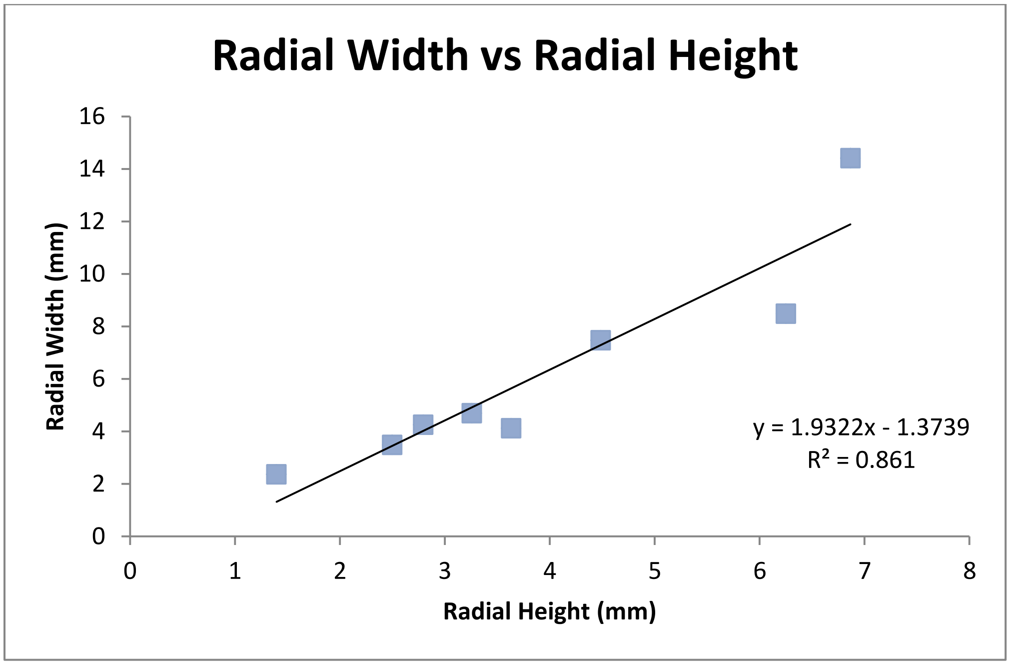


FIGURE 8- Slightly allometric growth of radial plates' width versus height.

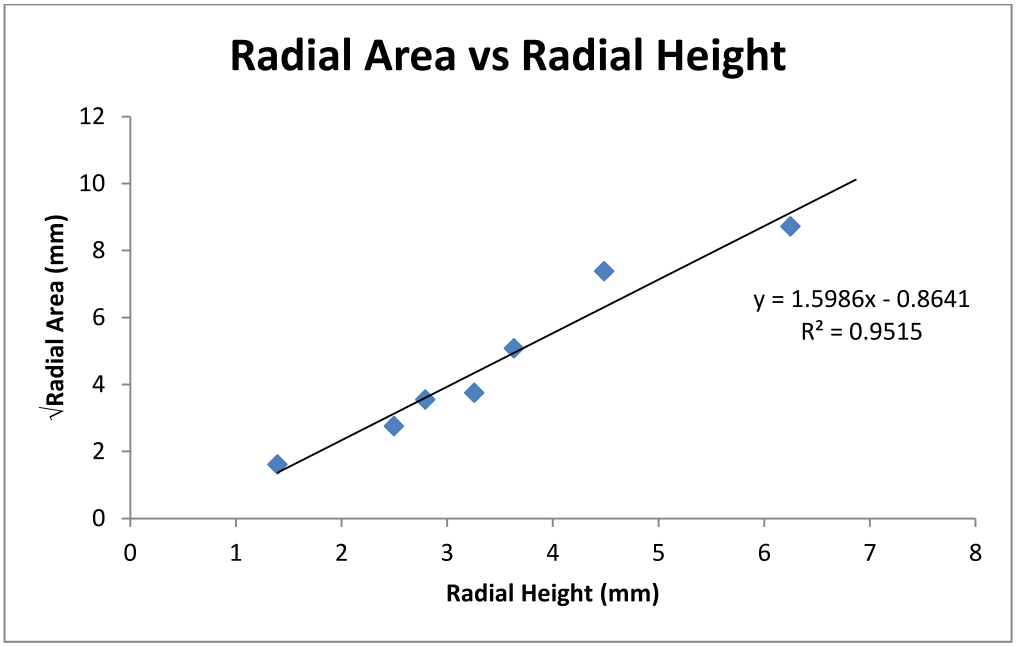


FIGURE 9-Slightly allometric growth of versus radial area radial height.

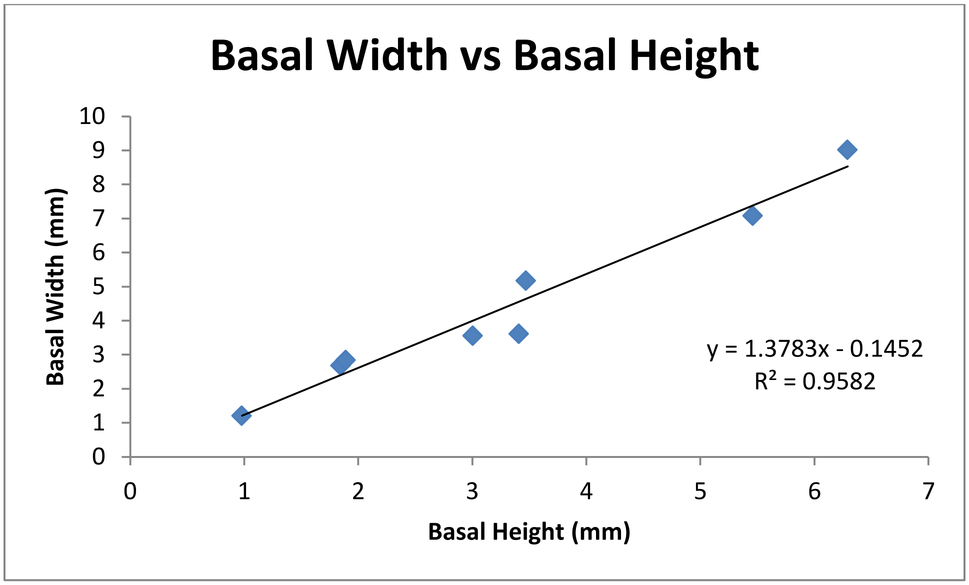


FIGURE 10-Slightly anisometric growth of basal plates' width versus height.

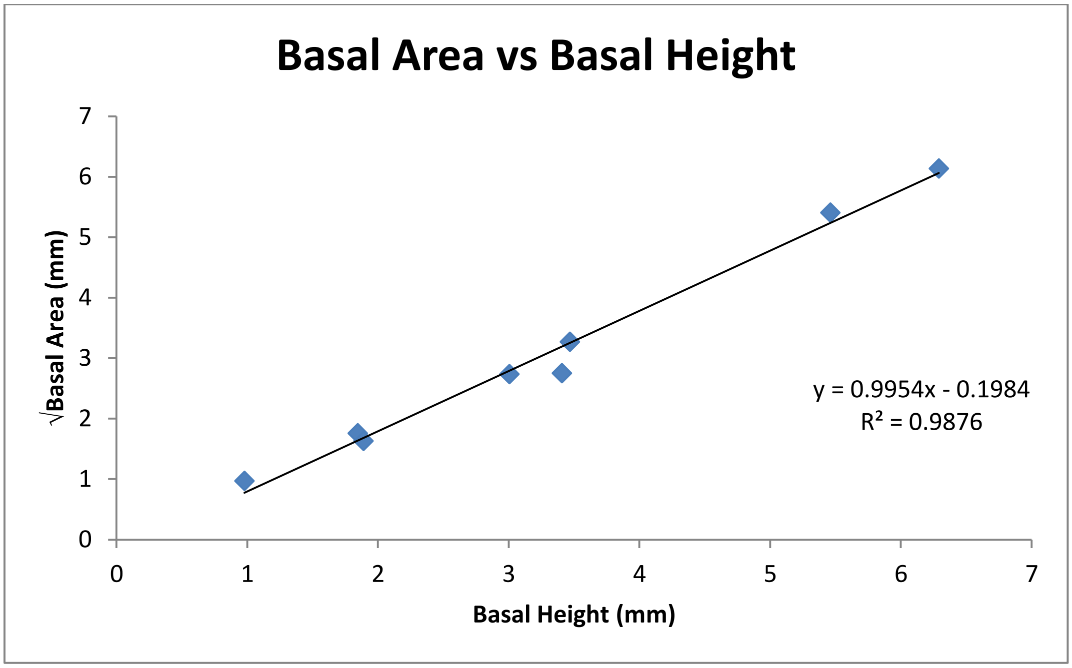


FIGURE 11-Slightly allometric growth of basal plate area versus height.

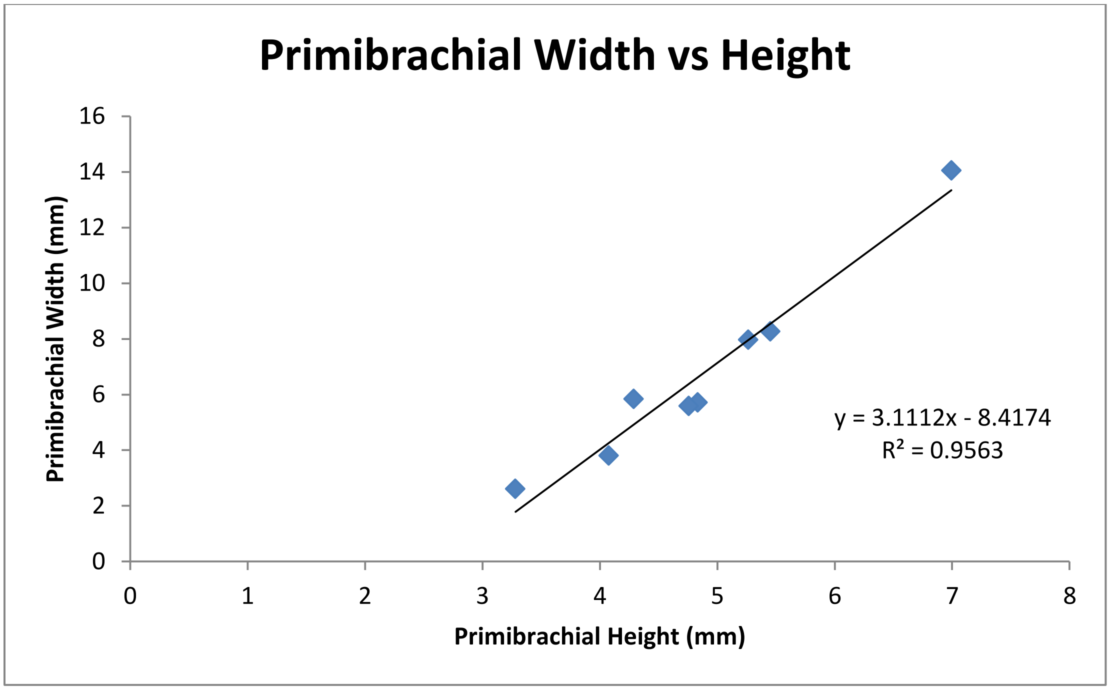


FIGURE 12-Anisometric growth of primibrachial plates (width versus height).

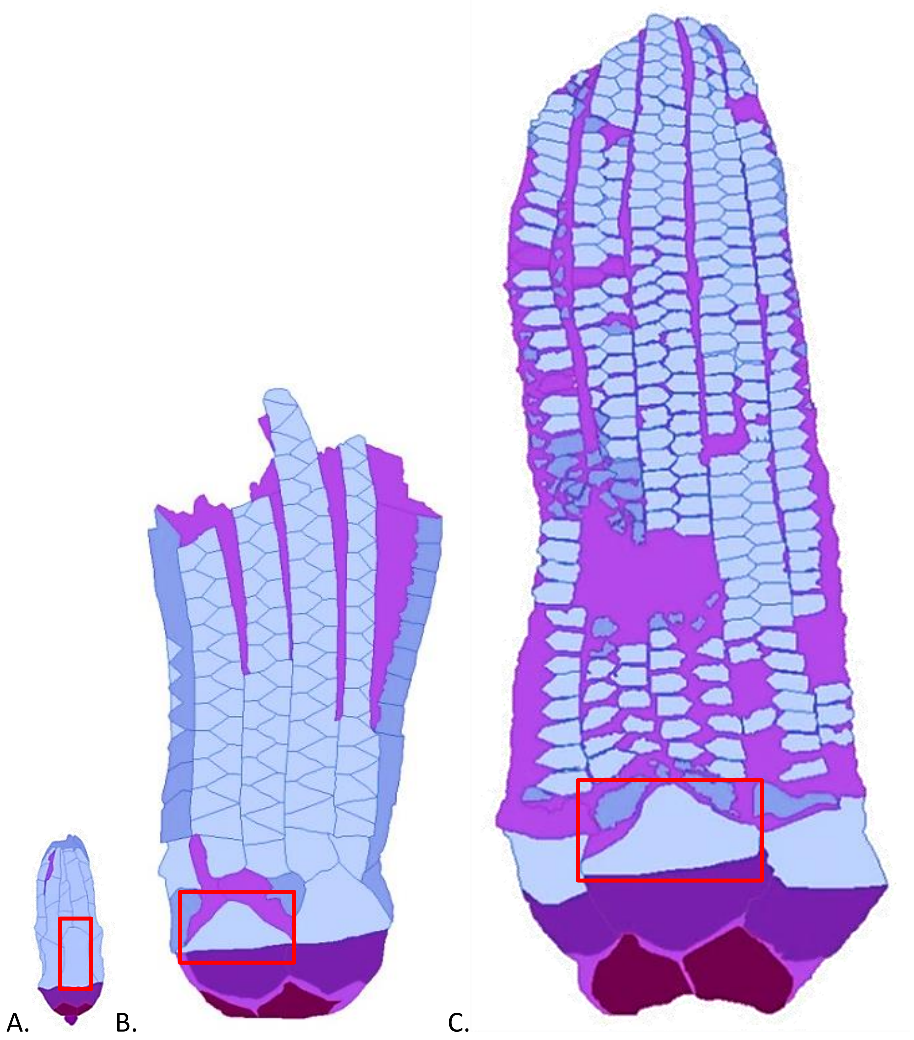


FIGURE 13-The primibrachials begin as uniserial (A) and change to a cuneiform-biserial arrangement (B and C).

Statistical analyses were performed to differentiate between allometric and isometric growth, as in Ausich and Wood (2012). The measurements and statistics were calculated using the software program PAST (Hammer et al., 2001; Hammer and Harper, 2006). The allometric measurements and following statistics were based on the Reduced Major Axis (RMA) model. RMA is a common method in paleontology for calculating allometric measurements; the model takes into account the errors in the x and y direction. The following statistics were calculated: r^2, correlation coefficient, the probability of no correlation (p), and p a=1 (the probability that the slope (a) equals one.

The statistical methods applied here are used to determine whether the growth of the plates of the cup is isometric or allometric. The allometric equation, $y=bx^a$ (where a and b are constants), was linearized by log transformation for this study and became log(y)=alog(b), with the slope being ‘a’ and the y-intercept being ‘b’. The ‘a’ constant determines whether or not the growth of the specimen is isometric: if a=1, the growth is considered isometric; if a>1, the growth exhibits positive allometry; and if a<1, the growth is showing negative allometry. The constants a and b were estimated by using the log-transformed cup plate data in PAST.

The data for the cup plate height, width, and area is provided in tables one (basal) and two (radial). All measurements are provided in millimeters (mm). The data for the statistical tests for each of the allometric growth tests are included in table 3.

The data give reasonably high r^2 values for the allometric growth statistics performed on the log-transformed growth data for the *Erisocrinus typus* growth series.

The data show a slope (a) that is less than a=1 consistently for all of the measurements. The slope for measurements of the primibrachial plates are much less than 1, whereas measurements involving plates of the cup (area, height, and width) are much closer to 1. The probability that a=1 is much higher in measurements involving plates of the cup than those involving measurements of the primibrachials.

X-axis	Y-axis	Slope (a)	Y-intercept (b)	r^2	Probability a=1
Basal Height	Basal Width	0.986	1.01	0.956	0.384
Basal Height	Basal Area	0.995	1.01	0.987	0.807
Cup Height	Basal Height	0.885	1.12	0.986	0.04
Cup Height	Basal Width	0.873	1.13	.963	0.26
Radial Height	Radial Width	0.946	1.05	0.862	0.141
Radial Height	Radial Area	0.985	1.05	0.954	0.406
Cup Height	Radial Height	0.973	1.03	0.938	0.136
Cup Height	Radial Width	0.919	1.08	0.934	0.95
Primibrach Height	Primibrach Width	0.646	1.40	0.956	.0260
Cup Height	Primibrach Area	0.807	1.19	0.931	0.007

TABLE 3-Allometric growth statistics for log-transformed growth data for *Erisocrinus typus*.

As is easily seen from a casual glance at an *E. typus* crown, the brachials decrease in size from the primibrachial at the base to the tips of the arms. The brachials seem to decrease in area in a specific pattern, a trend that is seen throughout all the growth stages of *Erisocrinus typus.* The primibrachs are significantly larger than the rest of the brachials; the first secundibrachs also are larger on average than the remaining secundibrachials. The brachials decrease in size until the plates reach a minimum and then stabilize and remain approximately consistent for the uppermost portion of the arm.

Graphs depicting the changing area of brachials are shown below (Fig. 14-17). Figures 18-21 plot the normalized data of the brachial areas for the eight specimens of the growth series against its nth-tile. The data was normalized by subtracting the mean area from the actual area of each brachial, and then dividing it by the standard deviation. By normalizing the data, we were able to remove the visual bias that occurs when larger crinoids with a significantly larger number of brachials are plotted against younger specimens with few brachials. The normalized data represents the area of each plate as it compares to the average plate size of each member of the growth series. The nth-tile represents the position of the percentile of brachials; meaning, each mark along the x-axis shows the percentage of brachials that are present.

The graphs showing these trends are not a representation of every brachial. As seen in the digital models of the growth series, a number of the plates have been disarticulated from the crown. A large percentage of the arm plates have also distorted.

Only plates that were not damaged noticeably were included in the arm area data to avoid the skewing of data. A slight outlier is seen concerning the area of the third specimen of the growth series (Fig. 15). The plates in the middle of the arms have been disarticulated, so the arm plates between the larger and smaller are missing; therefore, the trend in the third specimen's arm plate area is biased towards the larger brachials closer to the base of the arm. The eighth specimen of the growth series also has an interesting trend (Fig. 17). The graph shows a decrease in the percentage of brachial area that decreases further than is seen in the other specimens' trends. This is explained by the fact that the growth series specimens 5, 6, and 7 are missing the uppermost portion of the arm plates.

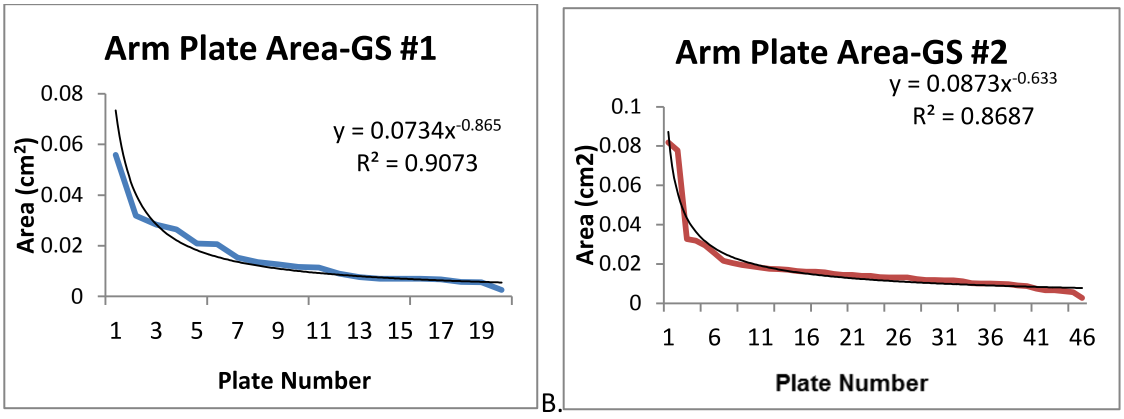


FIGURE 14-Arm Plate Data for GS #1 (A) and GS #2 (B)

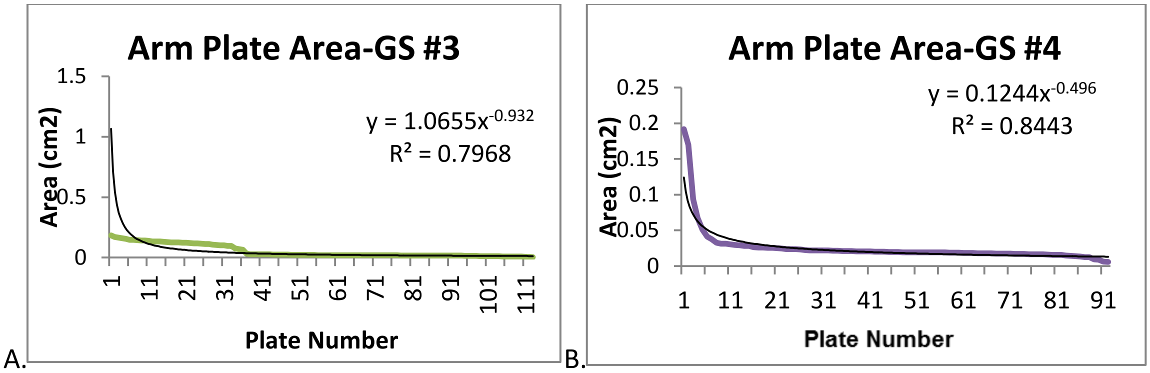


FIGURE 15-Arm Plate Area Data for GS# 3 (A) and GS#4 (B)

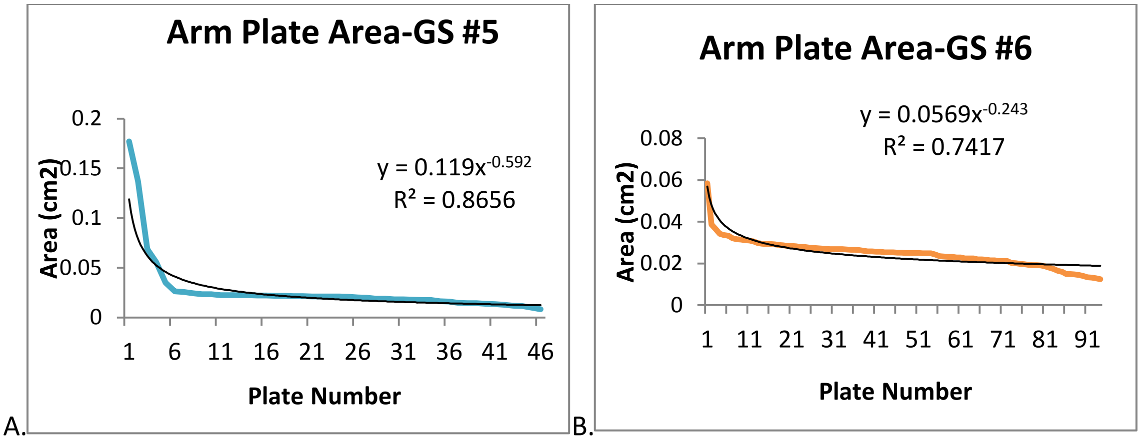


FIGURE 16-Arm Plate Area Data for GS# 5 (A) and GS#6 (B)

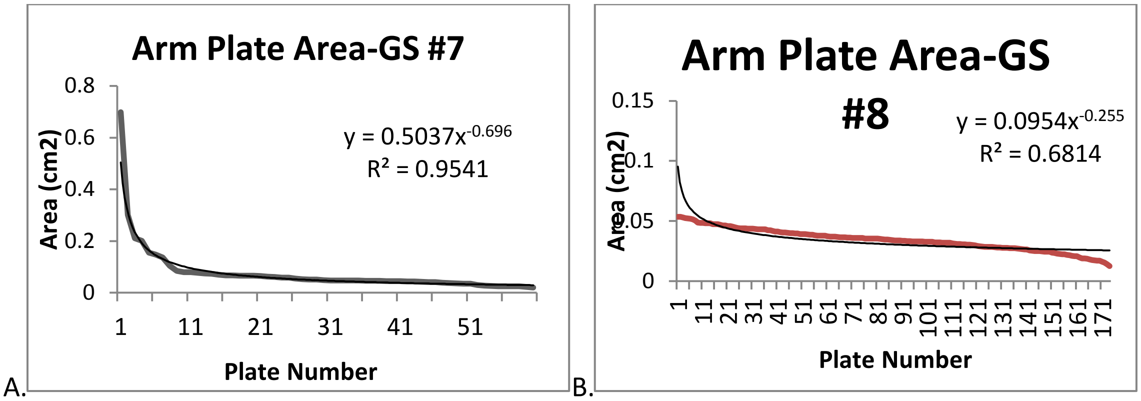
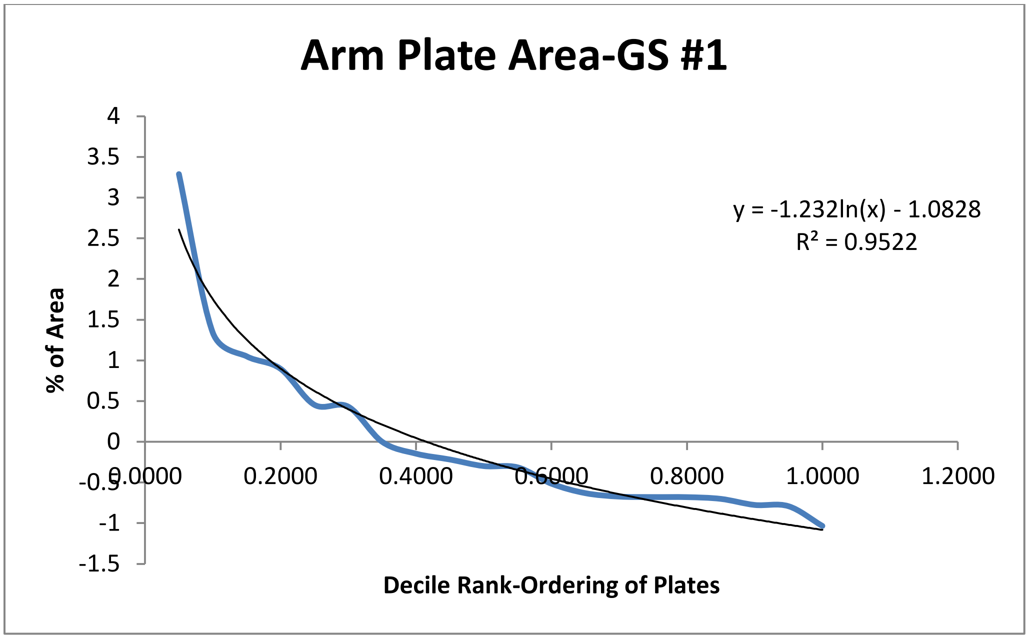


FIGURE 17-Arm Plate Area Data for GS#7 (A) and GS#8 (B)



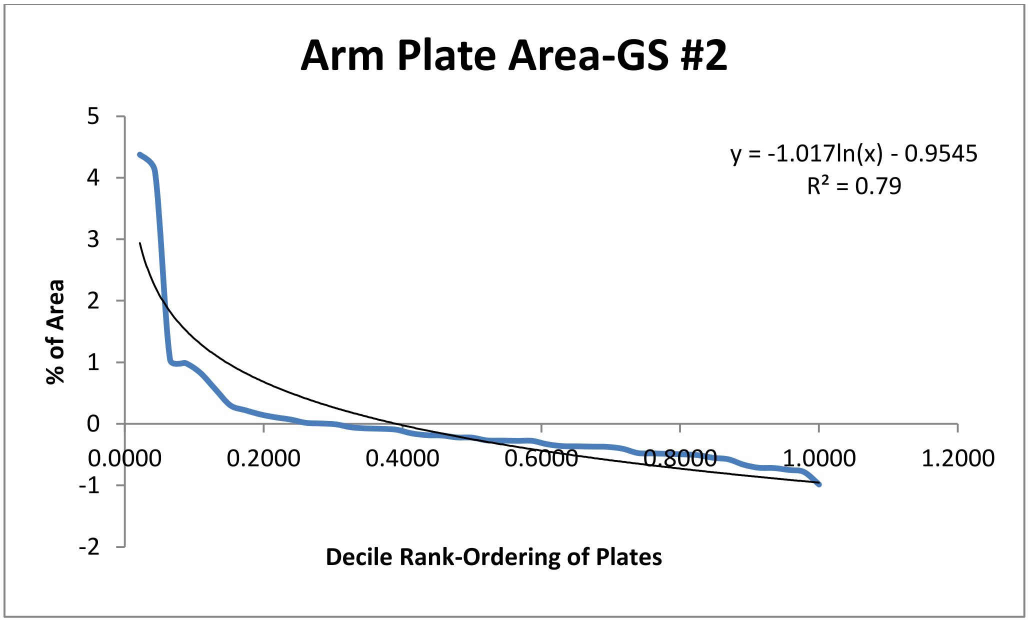
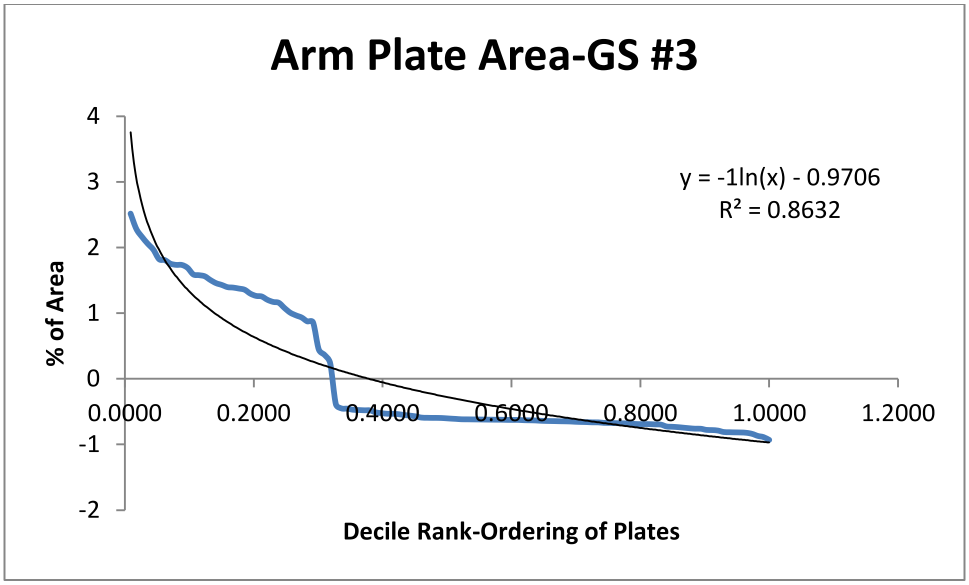


FIGURE 18-Arm Plate Data for GS #1 (top) and GS #2 (bottom).



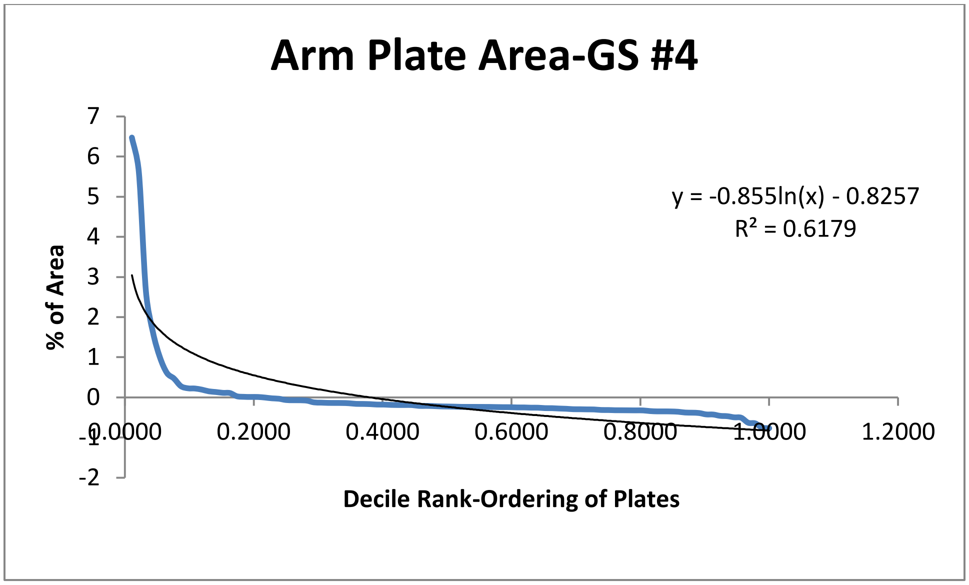
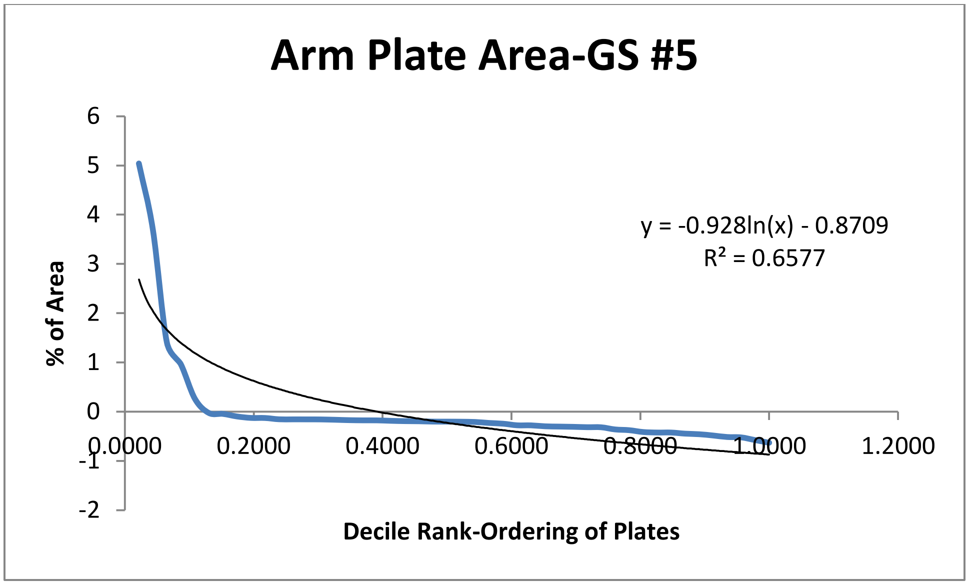


FIGURE 19-Arm Plate Area Data for GS# 3 (top) and GS#4 (bottom).



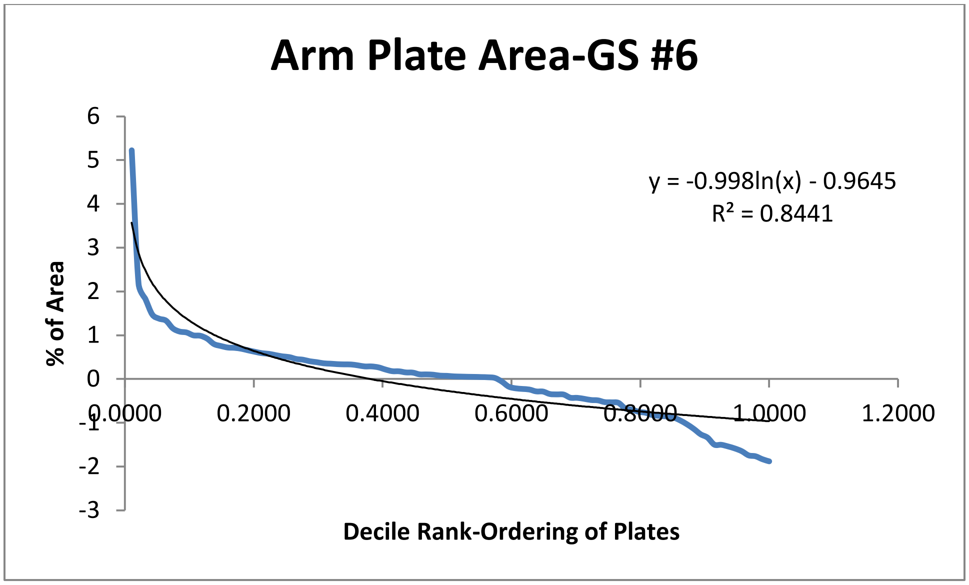
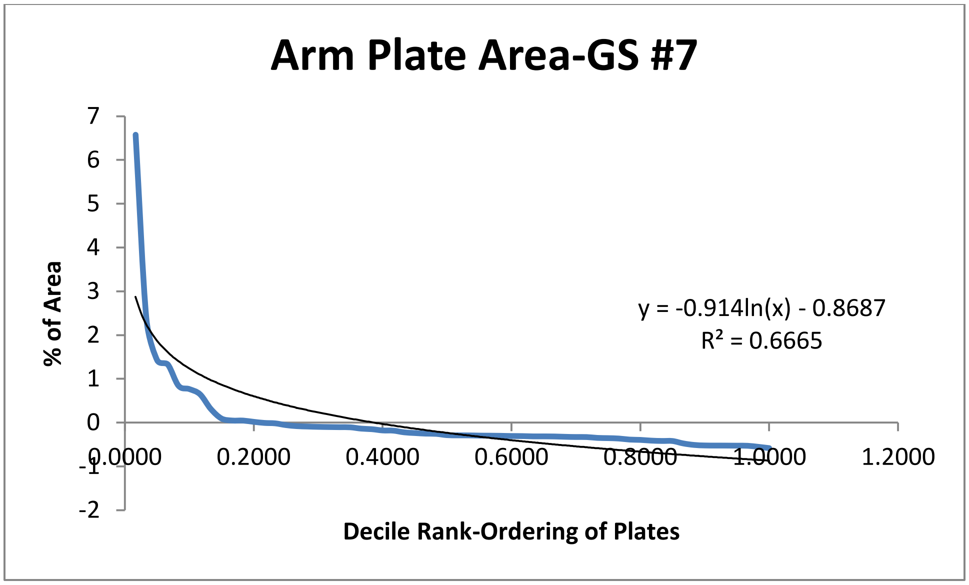


FIGURE 20--Arm Plate Area Data for GS# 5 (top) and GS#6 (bottom).



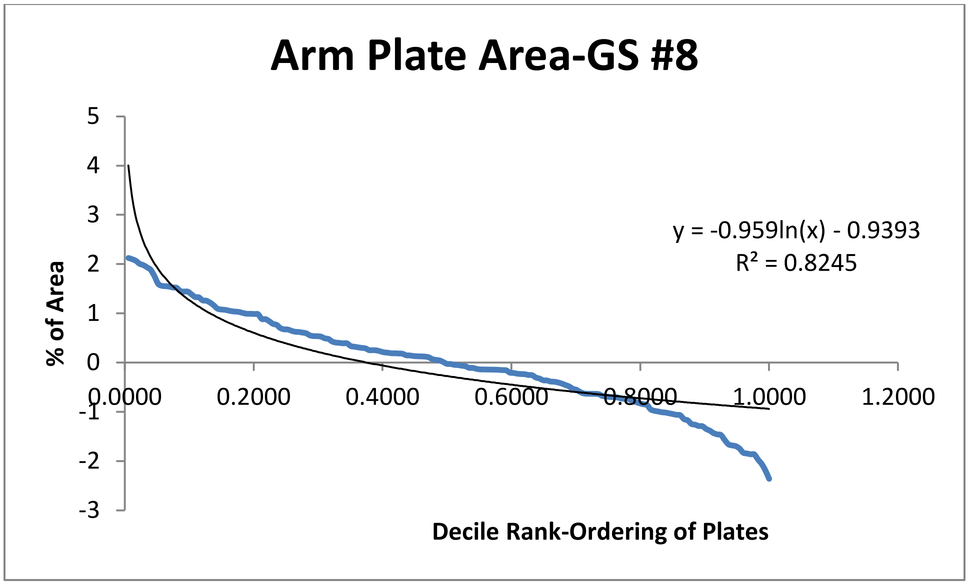


FIGURE 21-Arm Plate Area Data for GS#7 (top) and GS#8 (bottom).

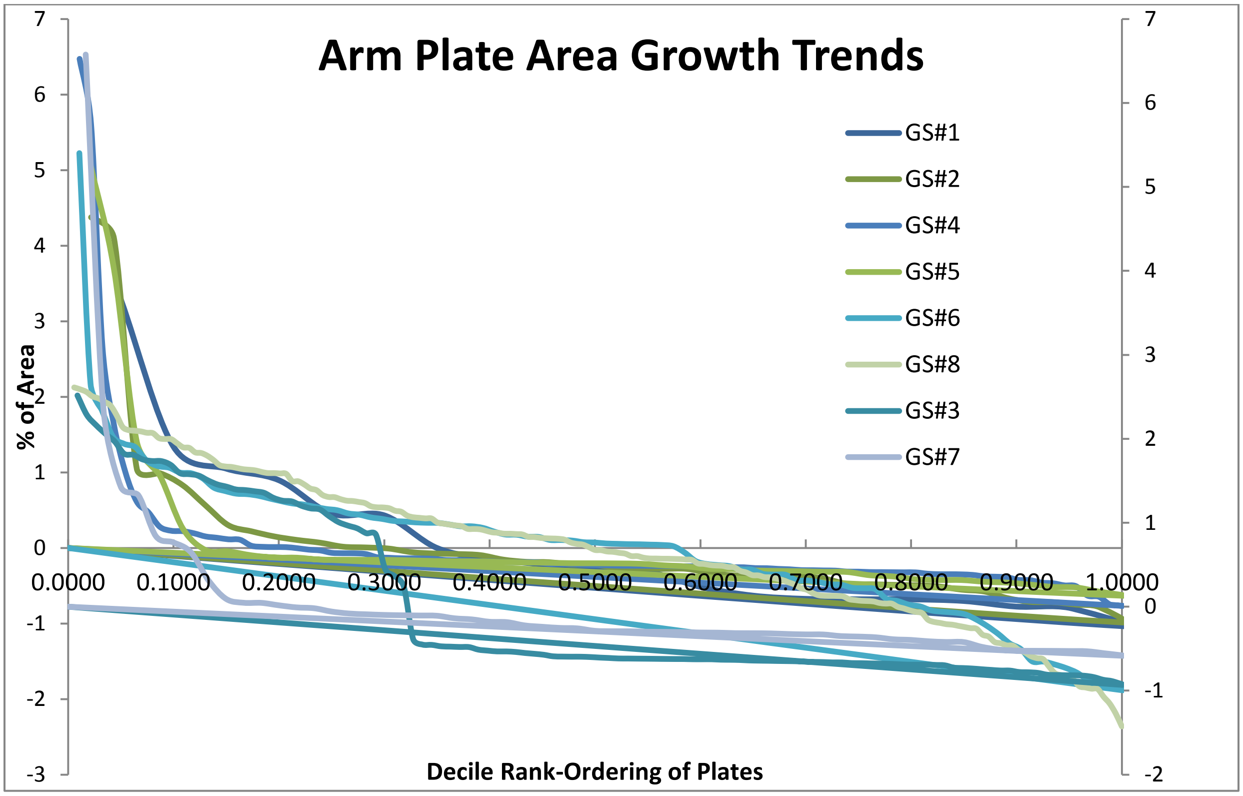


FIGURE 22-Arm Plate Areas for all specimens of the *E. typus* growth series.

Discussion

The growth measurements were plotted against both cup height and plate height, both used as indicators of age in this study. Because of common shale compaction of cup height, radial and basal plate height were also used in order to ensure that an accurate age indicator was used. The null hypothesis that was tested is that $a \neq 1$.

The plates of the cup show a strongly isometric trend. However, the data does show that $a \neq 1$ in any of the tests performed. The slope is consistently less than 1 in the measurements, even if it is by a small margin. This indicates that the growth of the crinoid is not isometric, but more closely aligned to negative allometric growth. The probability of the slope equaling one ($a=1$) is statistically significant. This pattern holds true for the basal plate and radial plate bivariate plots of height versus width, as well as radial plate and basal plate areas plotted against their respective heights. The probability that the basal plate growth is isometric ranges from a 4% (cup height versus basal height) to an 80% (basal height versus basal area) probability that the growth is isometric. The probability that the radial plate growth is isometric ranges from a 14% (cup height versus radial height) to 95% (cup height versus radial width). These numbers show that the probability of isometric growth of the plates of the cup should not be ignored during a discussion of *Erisocrinus'* methods of growth. Thus, the null hypothesis ($a \neq 1$) cannot be rejected.

In the primibrachial plates, the statistical tests indicate that the method of growth was strongly anisometric; more specifically, the method of growth was negatively allometric (a<1). Both the r^2 value and the probability that a=1 lend credence to this statement, values for primibrach height versus primibrach width are 95.5% (r^2) and 2.6% (a=1) and cup height versus primibrach area is 93.1% (r^2) and 0.07% (a=1). The measurements and statistical analysis reinforce what can be visually seen in the changes of the primibrachials from a juvenile to adult stage. The null hypothesis cannot be rejected here either, even though the probability that a=1 is much lower in the measurements of the primibrachials than it is the plates of the cup.

A study of *Erisocrinus typus'* growth previously stated that the growth of both the plates of the cup and the shape of the cup grew isometrically, with virtually no change in the shape of either (Peters and Lane, 1990). However, there were very few juvenile specimens used in this study and none as young as the first specimen in the Barnsdall Formation growth series. The statistical analyses performed in this study concerning the plates of the cup show that the plates of the cup grow closely isometrically, though there is a small factor of negative allometric growth involved, seen from the data from the growth study (Table 3). The fact that *Erisocrinus typus* grows with slightly anisometric growth appears to follow the trend of other cladid crinoids' growth, shown by other studies (Peters and Lane, 1990; Ausich and Wood, 2012). These studies have shown that *Apographiocrinus typicalis* grows with slight anisometric growth in the plates of the cup, and striking anisometric growth in the growth of the primibrachial plates (Peters and Lane, 1990). The ontogeny of *Hypselocrinus hoveyi* seems to have developed in a similar pattern: the plates of the cup grow slightly allometrically, whereas the primibrachial plates develop with strong anisometric behavior (Ausich and

Wood, 2012). *Erisocrinus typus* also follows suit in the growth trends of the plates of the cup and the primibrachial plates, in slight contrast to the original publication of the growth of this genus (Peters and Lane, 1990). This highlights the importance of using juvenile specimens in a study of growth; dramatic changes of the cup can occur with age.

It should be noted while the plates of the cup grow with only slight anisometry, the cup itself changes shape quite noticeably from a juvenile to adult stage (refer to Fig. 7). The juvenile stage of *Erisocrinus typus* does not have downflared infrabasals; therefore, the shape of the cup is quite rounded. This shape changes very early in ontogeny. No quantitative analysis has been performed on the anisometric development of the cup. However, if it is noted that the basal and radial plates form with closely isometric growth, than the change in cup shape more than likely lies within the downflaring of the infrabasal plates.

A further look at the change in growth of the plates should be done to better determine the reasons for the anisometry of the growth of the cup. The plates of the cup are not entirely planar; therefore, it is entirely possible that the change in the curvature of the plates as the crinoid ages could be anisometric; if this were true, it could mean that the plates themselves do not grow closely isometrically as the current view holds. While this aspect of the study is in its preliminary stages, it should be noted that the LaSalle Formation and other collections of crinoids are being used in this to make sure that the curvature of the basal plates being measured is not merely preservational.

The primibrachial plates grow with a strongly anisometric trend, something that has been noticed in other cladid crinoid growth studies (Peters and Lane, 1990; Ausich and Wood, 2012). The data show that the likelihood of rejecting anisometric growth of the primibrachial plate growth is isometric ranges from 0.07% (cup height versus primibrach area) to 2.6% (primibrach height versus width). The anisometric growth trend of the primibrachial plates enables the food capturing capacity function of the arms to grow with the expanding cup. The food capturing capacity has been shown in crinoid ontogenetic studies to increase substantially with larger crown volumes (Brower, 2006; Ausich and Wood, 2012). The trends of arm growth also show that the decrease in the size of the plates is more dramatic closer to the primibrachials and becomes less dramatic towards the tip of the arms.

The brachials of the arms also change dramatically throughout the growth series of the crinoid. As seen from the graphs previously shown (Fig. 14-22), the primibrachs are the largest plates by a large margin and the plates decrease in size after that. The trend of the percentage of area plotted against the decile-rank ordering of the plates, the trend shows a dramatic change in size of the plates in three stages: at the 0.1, 0.3, and the 0.6 decile rank order. This perhaps indicates that there are three distinct episodes of plate growth in the crinoid arms. There are no studies yet that have measured the change in area of arm plates, so more analysis will be needed to conclude the reasons as to why the arms seem to reflect three stages of growth.

Conclusions

This study of the morphology of *Erisocrinus typus* using ArcGIS™ showed some results that were expected and some that were unexpected from what is currently known about the growth of cladid crinoids. The reevaluation of the growth of *Erisocrinus typus*, evaluated using ArcGIS10™, showed results that differed from Peters and Lane's (1990) original interpretation. They concluded that the plates of the cup grow with isometry. However, data from this study show that the growth is only close to isometric: the plates of the cup do grow with slightly negative allometric growth. The near isometric growth is seen in other cladids on which ontogenetic studies were performed. The growth study also shows that the primibrachial plates grow with noticeable anisometric behavior, something else that is seen in other cladid crinoids.

We also conclude that the growth of the cup itself grows with allometric behavior, noted in the change in shape from a juvenile to an adult stage. The amount of allometric growth was not determined in this study and will be evaluated in the future by measuring the degree of curvature in the basal and radial plates in *Erisocrinus typus.*

The area of the brachials of the cladid crinoid decrease noticeably after the primibrachials. The brachials seem to decrease in size in three separate stages, which could indicate three episodes of growth. More analysis is required in order to determine if there are in fact three distinct episodes of growth.

Systematics of the genus *Erisocrinus*

Introduction

The arms and stems of cladid crinoids often disarticulate from the cup, leaving many taxa to be identified solely by the cup or loose plates of the cup. This, of course, can sometimes be an issue for the class Crinoidea as a whole, but it is particularly true for the subclass Cladida. *Erisocrinus* is no exception; the large majority of the species within the genus are known only from the cup.

Erisocrinus is found quite commonly in the mid-continental United States (New Mexico, Texas, Oklahoma, Kansas, Iowa, Indiana) in Upper Carboniferous (Pennsylvanian) and Lower Permian strata, although a number of species proposed have been found exclusively in South America (Katzer, 1903), Europe (Yakovlev, 1934; Yakovlev and Faas, 1938; Wright, 1939, 1945), and Asia (Wanner, 1916, 1921). The fact that many of these species were erected from one or two cups presents some difficulty in determining the variability within the different species of the genus. Species have been erected based on slight variations from *Erisocrinus typus*, the type species (Meek and Worthen, 1865a). Variations such as a slight difference in the relative height of the cup or the width of the stem facet have been used to split the genus into numerous species (Meek and Worthen, 1868; White, 1870; Strimple and Watkins, 1969; Strimple, 1975)**.** The splitting of species based on slight differences is not an unusual concept in the history of crinoid paleontology. Other paleontologists have written about this common trend of splitting genera into more species than were warranted, and crinoid systematics have to be revised periodically to fit more modern species concepts (Meyer and Ausich, 1997). Specifically, other researchers have acknowledged the unreliability of the certain characteristics that presently determine the differences between the *Erisocrinus* species (Bowsher and Strimple, 1986).

This study examines which morphological features contribute to variability and which variations appear to be contributed by ontogenetic features by analyzing all proposed species of *Erisocrinus*. The first phase of this project was to research the literature from 1865 to 2003, the time span from the first to the most recent publication concerning the genus (Meek and Worthen, 1865a; Pabian and Rushlau, 2003) and to locate all original species descriptions. This was followed by corresponding with museums and universities where the literature reported that specimens were reposited (see Appendix II for museum holdings). The second phase of the research was to critically analyze those species currently considered valid according to the literature: that is, those that have not been synonymized or reassigned to another genus. In part one, those species that did not conform to the genus diagnosis is discussed; and, in part two, the remaining species were analyzed to determine which species are valid according to modern paleobiological standards.

Phase One: Literature Review

Over thirty-five species of *Erisocrinus* have been proposed to date; Table 4 lists the species described, along with the location and age of the original material studied (the hypodigm) and its location at present. A number of these species proposed have been found to be the same, but were discovered by paleontologists that had no information of others working on the genus. Other species were erected over the slight change in the height of the aboral cup or a slight enlargement of the cicatrix diameter (Meek and Worthen, 1865b; Strimple, 1975).

Due to the fact that so many paleontologists over the last 150 years have made attempts to redefine both the genus and the species contained within it, many different diagnoses and species lists have been circulated throughout the paleontological literature (Moore and Plummer, 1940; Strimple, 1951; Moore and Teichert, 1978). The literature review for this study has, therefore, been quite extensive in determining how many of these proposed species are still considered to be contained within the genus. All the publications concerning *Erisocrinus* were gathered, and using these, we were able to determine which of the species of *Erisocrinus* had been previously synonymized or reassigned to another genus (a full description of each species that has been previously synonymized is included in Appendix III). We were also able to use the publications, as well as online databases, to locate the museums where many of the specimens are currently located. Many of the museums were able to loan the specimens in their collections to us to complete the study. Those that were not able to loan their collections provided photographs.

Species and Author		**Formation/ Location**	**Age**	**Hypodigm/ Location**
1. *Erisocrinus typus*	Meek and Worthen, 1865a	Coal measures; Springfield, Illinois	Pennsylvanian (Missourian)	2 cups; missing
2. *E. nebrascensis*	Meek and Worthen, 1865a	Coal measures; Bellevue, Nebraska	Pennsylvanian (Missourian)	1 cup ; missing
3. *E. pelvis*	Meek and Worthen, 1865b	Coal measures; Springfield, Illinois	Pennsylvanian (Missourian)	1 cup; missing
4. E. conoideus	Meek and Worthen, 1865b	Coal measures; Springfield, Illinois	Pennsylvanian (Missourian)	1 cup; missing
5. *E. inflexus*	Geinitz, 1866	Morton, Nebraska	Pennsylvanian	1-2 cups; UNSM
6. *E. cernuus*	Trautschold, 1867	Myachkowo Quarry; Moscow, Russia	Pennsylvanian (Moscovian Kasimovian)	1 cup; 1 crown; Berlin
7. *E. tuberculatus*	Meek and Worthen, 1865b	Upper coal measures; Sangamon CO, Illinois	Pennsylvanian (Missourian)	Detached Plates; missing
8. *E. cognatus*	Wachsmuth and Springer, 1886	Burlington Group; Burlington, Iowa	Mississippian (Early Carboniferous)	1-2 cups; UNSM

9. *E. antiquus*	Meek and Worthen 1868	Coal measures; Bellevue, Nebraska	Mississippian (Early Carboniferous)	1 cup; Harvard University
10. *E. whitei*	Meek and Worthen, 1869	Burlington Group; Burlington, Iowa	Mississippian (Early Carboniferous)	1 crown; Harvard University
11. *E. planus*	White, 1870	Upper coal measures; Humboldt, Kansas	Pennsylvanian	1-2 cups; UNSM
12. *E. cognatus*	Wachsmuth and Springer, 1886	Burlington Group; Burlington, Iowa	Mississippian	1-2 cups; missing
13. *E. megalobrachius*	Beede, 1899	Upper coal measures; Topeka, Kansas	Pennsylvanian (Missourian)	1 crown; missing
14. *E. toddanus*[2]	Butts, 1899	Unable to locate	Middle Pennsylvanian	Unable to locate
15. *E. loczyi*	Katzer, 1903	Lower Amazon; Brazil	Early Permian	3 partial crowns; Natural History Museum of Bosnia-Herzegovinia[3]
16. *E. propinquus*	Weller, 1909	Cibolo Limestone; Presidio Co, Texas	Early Permian (Wolfcampian)	1 cup; Field Museum
17. *E. trinodus*	Weller, 1909	Cibolo Limestone; Presidio Co, Texas	Early Permian	1 partial cup; Field Museum
18. *E. granulatus*	Wanner, 1916	Basleo, Timor	Permian	1 cup; missing
19. *E. malaianus*	Wanner, 1916	Basleo, Timor	Permian	3 cups; missing
20. *E. obliquus*	Wanner, 1916	Baucau, Timor	Permian	21 cups; Peabody Museum

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[2] The reference for this paper was not correctly cited, and has therefore been difficult to locate (Moore and Plummer, 1940; Webster, 2003)

[3] The location of this fossil has not been confirmed; sources at the University of San Paulo and University of California-Los Angeles believe that *E. loczyi* has been reposited in Bosnia-Herzegovinia.

21. *E. lutana*	Boos, 1929	Luta Limestone; Winfield, Kansas	Early Permian (Wolfcampian)	Partial crown; missing
22. *E. araxensis*	Yakovlev, 1933; Yakovlev and Ivanon, 1956	Aras River, near Iranian Border	Permian	1-3 cups; missing
23. *E. stefaninii*	Yakovlev, 1934	Valle Del F. Sosio; Palmero, Italy	Permian	Cups; University of Pisa
24. *E. pentangulatus*	Yakovlev and Faas, 1938	Pietra la Salomone; Pisa, Italy	Permian	Cups; University of Palmero
25. *E. carlopensis*	Wright, 1939	Lower Limestone Group; Carlops, Peebleshire, England	Pennsylvanian (Stage Unknown)	3 cups, 1 partial crown; Natural History Museum, London
26. *E. elevatus*	Moore and Plummer, 1940	Palo Pinto Limestone; Palo Pinto Co, Texas	Pennsylvanian (Missourian)	1-2 cups; Texas Memorial Museum
27. *E. erectus*	Moore and Plummer, 1940	Mineral Wells Formation; Palo Pinto Co, Texas	Pennsylvanian (Missourian)	1-2 cups; Texas Memorial Museum
28. *E. obovatus*	Moore and Plummer, 1940	Graford Formation; Palo Pinto Co, Texas	Pennsylvanian (Missourian)	1-2 cups; Texas Memorial Museum
29. *E. scoticus*	Wright, 1942	Lower Limestone Group; Carlops, Peebleshire, England	Pennsylvanian (Stage Unknown)	3 cups, 1 partial crown; Natural History Museum, London
30. *E. lustrum*	Strimple, 1951	Iola Limestone; Iola, Kansas	Pennsylvanian (Missourian)	5-6 cups; UNSM

31. *E. wapunucka*	Strimple, 1961	Wapunucka Formation; Pontotoc Co, Oklahoma	Pennsylvanian (Atokan)	1 cup; Sam Noble Museum
32. *E. mediator*	Strimple, 1962	Oologah Formation, Tulsa, Oklahoma	Pennsylvanian (Desmoinesian)	Cups; Sam Noble Museum
33. *E. terminalis*	Strimple, 1962	Oologah Formation, Tulsa, Oklahoma	Pennsylvanian (Desmoinesian)	Cups; Sam Noble Museum
34. *E. longwelli*	Lane, N.G., Webster, 1966	Bird Spring Formation, Clark Co, Nevada	Early Permian (Wolfcampian)	Cups, partial crowns; UNSM
35. *E. georgeae*	Strimple and Watkins, 1969	Big Saline Formation, Mason Co, Texas	Pennsylvanian (Atokan)	2 cups; missing
36. *E. healdae*	Pabian and Strimple, 1974	Ervine Creek Limestone, Nebraska	Pennsylvanian (Virgillian)	1 cup; missing
37. *E. knoxvillensis*	Strimple, 1975	Unnamed Limestone, Knoxville, Iowa	Pennsylvanian (Desmoinesian)	1 cup; University of Iowa

TABLE 4-List of all proposed *Erisocrinus* species and authors. Included are the localities in which the holotypes were found, hypodigms, and current location of holotypes (if known).

History of Research on *Erisocrinus*

Meek and Worthen (1865a) erected the genus *Erisocrinus* based on isolated cups found in the "Upper Coal Measures" of Illinois and Nebraska. *Erisocrinus typus* was represented by two cups[4] from Springfield, Illinois, and *E. nebrascensis* from a single cup found in the Coal Measures at Bellevue, Nebraska. The two were differentiated by the proportionally larger radial plates in *E. nebrascensis.* As is common with systematic descriptions from this time period, neither images of the fossils nor were measurements of them included with the paper. Neither species was designated as the type species nor was either specimen of *E. typus* chosen as the holotype specimen, both procedures that are required in current taxonomic practice (Stoll et al., 1964).

Meek and Worthen were also responsible for naming a few other species within *Erisocrinus*: *E. pelvis* and *E. conoideus* from the Coal Measures at Springfield, Illinois and *E. tuberculatus* from New Jersey (Meek and Worthen, 1865b). *E. antiquus* was discovered soon after, also in the Coal Measures at Springfield and also based on one cup (Meek and Worthen, 1865b).

Moore and Plummer (1940) designated *E. typus* as the type species for the genus (Fig. 23). Two of the above species were eventually synonymized with *E. typus. E. nebrascensis* was synonymized with *E. typus* by Pabian and Strimple (1980), and *E. pelvis* was synonymized by Pabian and Rushlau (2003). *E. tuberculatus* was reassigned out of

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[4] The current location of these cups is unknown. The holotypes were reposited at the UNSM, but they are no longer within the collection. I visited the UNSM and the original hypodigm was not within the *Erisocrinus* collection.

the genus: Moore and Plummer (1940) reassigned it to *Ethelocrinus tuberculatus* Meek and Worthen due to its distinctive plate ornamentation. *E. antiquus* was synonymized with *Natocrinus antiquus* by Kirk (1947) due to its Early Carboniferous (Mississippian) age and uniserial arms.

The shape of the base of the cup at the point of stem attachment is often used as a diagnostic indicator in cladid systematics. Upflaring infrabasals produce a conical shape; downflaring infrabasals form a basal concavity that may result in a bowl-shaped profile. Species within *Erisocrinus* have been differentiated based on their differing concavities (White, 1870; Strimple, 1975).

Many species of *Erisocrinus* that were named in the late 1800's and early 1900's exhibited a deep basal concavity in contrast to the relatively flat base of *E. typus*. *Erisocrinus planus* White 1880 is one such example: the species exhibits a deep concavity and rounded cup shape. Ten years later, a new genus, *Delocrinus*, was erected to which *Erisocrinus planus* more closely belonged (Miller and Gurley, 1890). *Delocrinus* differs from *Erisocrinus* due to its rounded cup shape and pronounced basal concavity (as compared with *Erisocrinus'* strikingly pentagonal shape and more shallow basal concavity; Fig. 24). As more crinoid paleontologists began to use basal concavity to determine systematic relationships, more specimens of *Erisocrinus* were reassigned to *Delocrinus*: *Erisocrinus whitei* Meek and Worthen 1860, and *E. cognatus* Wachsmuth and Springer 1886 were synonymized with *Erisocrinus planus* White, 1880, which was then reassigned to *Delocrinus* by Moore and Plummer (1940). *E. megalobrachius* Beede

1900 was reassigned to *Delocrinus* and *E. malainus* Wanner 1916 became *Delocrinus malainus* (Moore and Plummer, 1940). *E. inflexus* Geinitz 1866*,* after numerous systematic revisions, was renamed as *D. inflexus* (Pabian and Rushlau, 2002).

Because a large majority of these species have been erected on the basis of a single cup (refer to table 4), information about the arms and different growth stages are commonly lacking. The history of *Erisocrinus* provides an excellent example of how crinoid systematics can become unclear without such vital information. *Erisocrinus trinodus* (Weller, 1909) was erected on finding a partial cup near Presido County, Texas. However, another specimen of *E. trinodus* was discovered as a partial crown, and the crown did not have biserial arms. As the definition of *Erisocrinus* includes biserial arms, Moore and Plummer (1940) tentatively reassigned this species to *Spaniocrinus.*

Without knowing the growth stages of a species of crinoid, it is quite possible to inaccurately assign juvenile specimens, which can often look quite different from their adult counterparts, to the wrong genus. Such is the case with *Erisocrinus carlopsensis* (Wright 1939). Wright believed he had found the first representative of the genus *Erisocrinus* from northern Europe based on a single cup he discovered in Scotland. However, it was determined much later that the cup in question was a juvenile specimen of *Exaetocrinus* (Fig. 26; Kammer and Ausich, 2008).

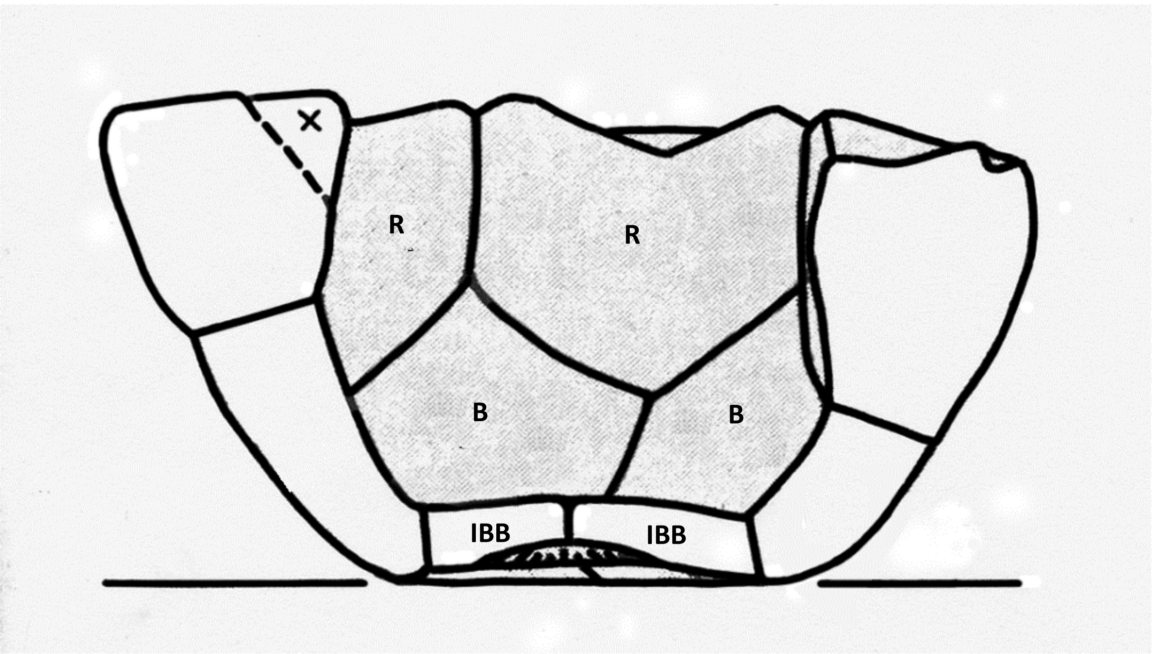

FIGURE 23--*Erisocrinus typus*; note the mild basal concavity shown where the infrabasal plates (IBB) are tucked into the concavity formed by the basal plates (B). Anal plate (x). (Modified from Moore and Plummer, 1940).

FIGURE 24-*Delocrinus* (A); note the deep, narrow basal concavity and roundness of the cup, as compared with *Erisocrinus*' pentagonal shape and mild basal concavity (B). (From Moore et al., 1978).

Strimple named two species of *Erisocrinus* in his 1962 paper based on his studies of the Oologah Formation, each containing three or four cups within their hypodigms: *E. terminalis* and *E. mediator.* Both of the species were determined to be a different from others previously named due to the abnormally low nature of the cup (calculated by a height to width ratio). *E. mediator* was considered by Strimple to be very similar to *E. typus,* except for the outward flare of the radials that the type species lacks. In 1969, Knapp moved both of these species into another genus, *Libratocrinus*. The genera *Libratocrinus, Parerisocrinus, and Pontotocrinus,* however, were synonymized with *Erisocrinus* (Moore and Teichert, 1978). Thus, both *E. mediator* and *E. terminalis* are still considered to be valid species within the genus *Erisocrinus.*

Erisocrinus belongs to the family Erisocrinidae Wachsmuth and Springer 1886, along with two other genera: *Sinocrinus* Tien 1926 and *Exaetocrinus* Strimple and Watkins 1969. The three are differentiated primarily by the differing size of the infrabasal plates, the orientation of the infrabasals (upflaring or downflaring), and the cup shape (Fig. 25-27).

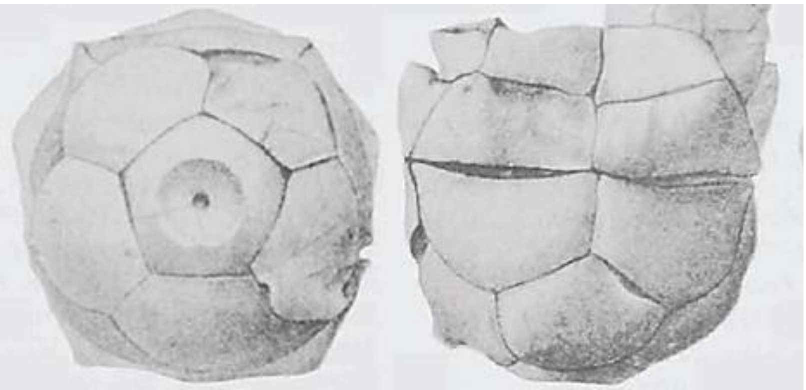

FIGURE 25-*Sinocrinus*, showing its slightly rounded cup, a circular lumen, and downflared infrabasals. Note bulbous nature of basal and radial plates. (From Moore et al., 1978).

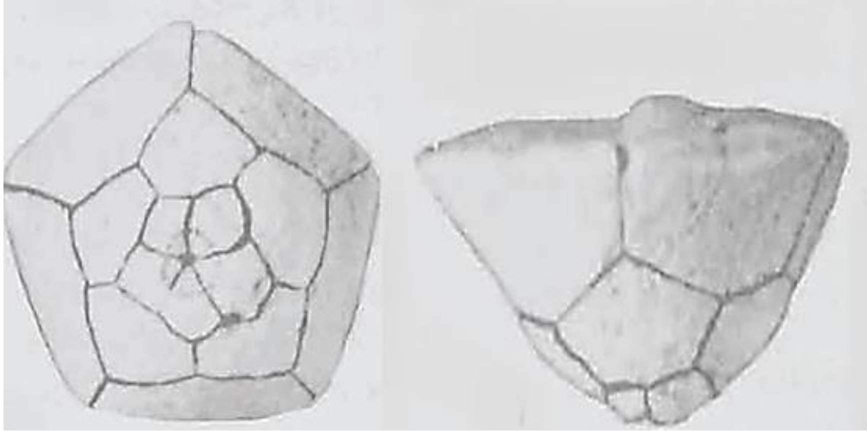

FIGURE 26-*Exaetocrinus*, with its pentagonal cone-shaped cup and upflared infrabasals. (Moore et al., 1978).

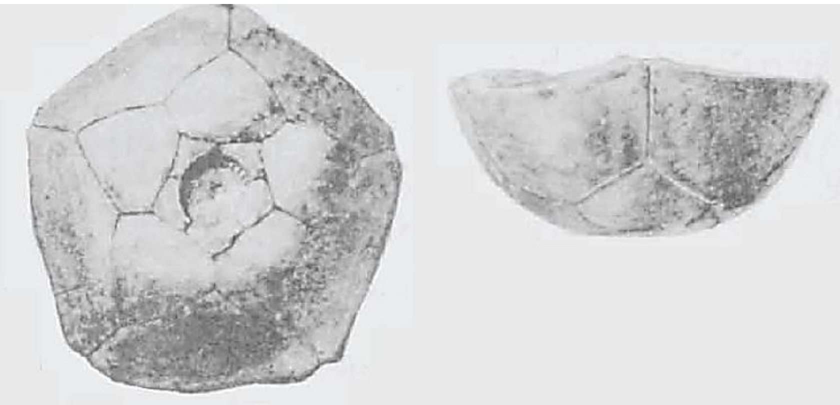

FIGURE 27-*Erisocrinus*, with its pentagonal cup and downflared infrabasals. Cup profile in side view is truncated cone to bowl shaped. (Moore et al., 1978).

The current list of the twenty *Erisocrinus* species that have not been either synonymized or reassigned to other genera are given below:

- *E. araxensis* Yakovlev 1933
- *E. cernuus* Trautschold 1867
- *E. conoideus* Meek and Worthen 1865b
- *E. elevatus* Moore and Plummer 1940
- *E. erectus* Moore and Plummer 1940
- *E. georgeae* Strimple and Watkins 1969
- *E. granulatus* Wanner 1916
- *E. healdae* Pabian and Strimple 1974
- *E. knoxvillensis* Strimple 1975
- *E. loczyi* Katzer 1903
- *E. longwelli* Lane and Webster 1986
- *E. mediator* Strimple 1962
- *E. obliquus* Wanner 1916
- *E. obovatus* Moore and Plummer 1940
- *E. pentagulatus* Yakovlev 1938
- *E. propinquus* Weller 1909
- *E. stefaninii* Yakovlev 1934
- *E. terminalis* Strimple 1962
- *E. typus* Meek and Worthen 1865a
- *E. wapunucka* Strimple 1961

Phase Two: Reappraisal of Currently Accepted Species

Materials

This study is based on a collection of *Erisocrinus* specimens from various localities. The specimens were borrowed from the National Museum of Natural History (USNM), the Cincinnati Museum Center, Indiana University at Bloomington, Auburn University, Sam Noble Museum of Natural History, University of Nebraska, and the Yale Peabody Museum (Appendix II). The total number of specimens collected for this project totals over 200.

Methods: Part One

The first portion of this part of the study was to critically analyze all of the proposed species against the *Erisocrinus* diagnosis. All of the species that did not agree with the diagnosis were analyzed further to determine if a reassignment into another genus was possible.

Methods: Part Two

Even though a large collection of specimens was available, many of the specimens' measurements were unobtainable due to incomplete preservation and compaction. The following measurements were taken using calipers: cup height, radial height, radial width, basal height, basal width, infrabasal height, infrabasal width, stem facet width, and primibrach height (if present).

The measurements of cup width were not taken for this study as they are in other growth studies (Peters and Lane, 1990) because of the severe compaction that affected the cup width of a majority of the specimens. Instead, cup height was used to represent an age indicator, and measurements of the radial, basal, infrabasal, and primibrach plates were compared to it. Meaning, the plate measurements were divided by their respective cup height to obtain a ratio. Only plates that showed no evidence of compaction or other distortion were used in the study. The remaining ratios of measurements divided by cup height were averaged to determine one standard ratio of radial height and width, basal height and width, and stem diameter per species (only measurements that could be found on every species were used; therefore, the infrabasal plate and primibrachial plate measurements could not be used in this study).

As there was a large collection of *E. typus* (upwards of one hundred specimens), and very small collections of others (*E. propinquus, E. mediator, E. erectus, E. elevatus, E. wapunucka, E. georgeae,* and *E. healdae* are only represented by one or two specimens each), the measurements were averaged in the larger collections. Principal Component Analysis (PCA) was used to determine which of these five variables that may or may not be causing the variability within the genus. The PCA data was compared with other analyses: a cluster analysis and k-means clustering in order to help determine the number of valid species that were present within the genus along with examining relative position of the different species based on the shape of the entire cup. The cluster analysis determines how far removed in terms of the proportional sizes of the radial plate, basal plate, and stem diameter each species is compared with one another. The k-means cluster was to determine which species would likely group together, if the data were forced into a certain number of pre-determined clusters.

Results of Revised Systematics: Part One

The species discussed below do not fit within the description of the genus *Erisocrinus*. These species have been reassigned to other genera, if possible. A detailed diagnosis of the genus is given below. Re

Subclass CLADIDA Moore and Laudon, 1943

Order DENDROCRINIDA Bather, 1889

Superfamily ERISOCRINACEA Wachsmuth and Springer, 1886

Family ERISOCRINIDAE Wachsmuth and Springer, 1886

Genus *Erisocrinus* Meek and Worthen, 1865

Diagnosis: Cup medium to low truncate cone. Cup outline strongly pentagonal in oral and aboral view. Radial plates 5, forming majority of lateral walls of the cup; basal and infrabasal plates 5 each, varying in relative size. Radials straight or flared outward in side view and relatively thin. Basal concavity mild to moderate, resulting from slightly downflared infrabasals. Arms 10, biserial after first secundibrach in all rays. Anal plate missing or confined to notch between radial facets. Surface of the cup plates smooth. Stem impression circular and proportionally small.

Erisocrinus conoideus Meek and Worthen 1865b

Meek and Worthen differentiated this species from *E. typus* by the higher and more conical cup shape (Fig. 28). No specimens were found to study for this project, but the original authors included a line drawing of the cup found in Illinois, as well as a plate diagram of the cup (Fig. 29). Meek and Worthen describes the specimen as having plates of the cup that have a smooth surface and depressed sutures. The plates are also not convex; meaning there is no tumidity.

E. conoideus was included as a species of *Erisocrinus* in Moore and Plummer's (1940) species list, which was the first compiled list of *Erisocrinus* taxa. However, I do not consider this species to belong to *Erisocrinus* due to the presence of upflared infrabasals (Fig. 28). The features that the species does exhibit are more closely aligned with the description of *Exaetocrinus*. The shape of the cup, lack of tumidity, and depressed sutures would place it within the genus *Exaetocrinus,* as opposed to the other genera within the family Erisocrinidae, *Erisocrinus* and *Sinocrinus.*

Therefore, the following reassignment is proposed:

Exaetocrinus [*Erisocrinus*] *conoideus* (Meek and Worthen, 1865)

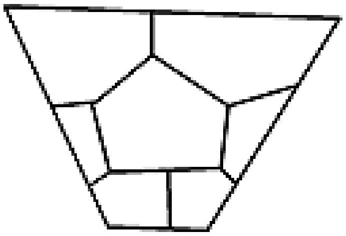

FIGURE 28-Line drawing of *Erisocrinus conoideus*; note upflared infrabasals, causing a high-conical cup shape. (From Meek and Worthen, 1865b).

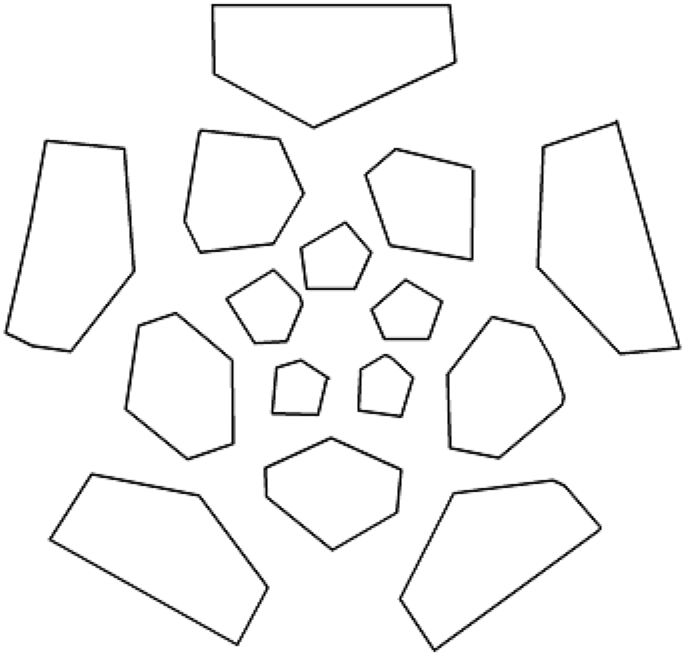

FIGURE 29-Line drawing of plates of the cup of *Erisocrinus conoideus*. (Modified from Meek and Worthen, 1865b).

Erisocrinus cernuus Trautschold 1867

This species was originally named as *Stemmatocrinus cernuus* from Pennsylvanian strata near Moscow, Russia. However, the genus *Stemmatocrinus* was synonymized with the genus *Erisocrinus* (Moore and Teichert, 1978). The holotype of this specimen was lost some time ago, but there is an existing crown in the Museum of Natural History in Berlin, Germany (Fig. 30 and 31) as well as a cast of the same crown at the UNSM. This analysis is based on recent images of the crown, taken by Dr. Christian Neumann, head curator for the Institute of Evolution and Biodiversity Research at the Museum of Natural History in Berlin, as well as images and text translations provided by Gera Mirantsev, a researcher at the Paleontological Institute at the Russian Academy of Sciences based in Moscow, Russia.

The medium bowl-shaped cup is quite round from an aboral view (Fig. 31). The cup exhibits proportionally larger basal plates than *Erisocrinus* does and has infrabasal plates of unequal size. An important feature that can be seen clearly in the photographs following are the presence of impressed plate sutures, a feature that is not seen in *Erisocrinus*. The specimen currently representing the species has a coarsely granular cup-plate sculpture, as do the primibrachs and secundibrachs. This is in contrast to the smooth cup plate and arm plate sculpture in *Erisocrinus*.

Based on these characteristics, I do not consider *Erisocrinus cernuus* Trautschold 1867 to be a part of the genus *Erisocrinus*. This particular species should be reassigned to *Sinocrinus* Tien 1926.

Designation: *Sinocrinus* [*Erisocrinus*] *cernuus* (Trautschold, 1867)

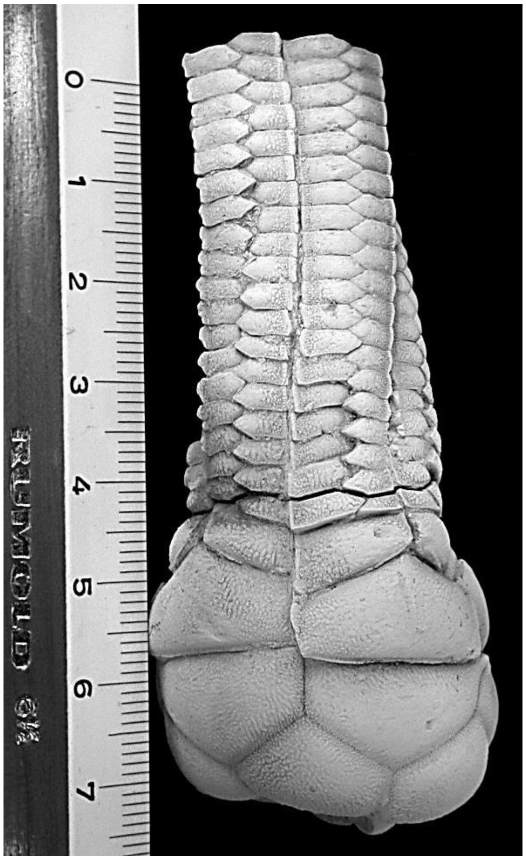

FIGURE 30-Partial crown of *Erisocrinus cernuus*. Note the bulbous plates with impressed sutures, and the coarsely granular ornamentation on cup and arm plates. (Photo credit: Christian Neumann).

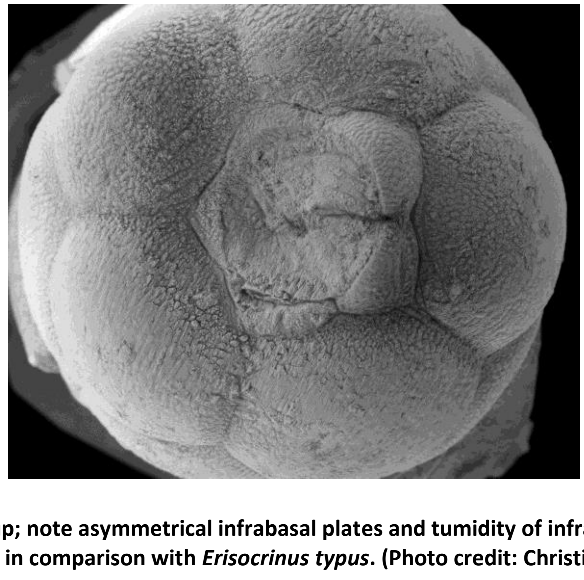

FIGURE 31-Aboral view of cup; note asymmetrical infrabasal plates and tumidity of infrabasal plates, as well as the largeness of the basal plates in comparison with *Erisocrinus typus*. (Photo credit: Christian Neumann).

Erisocrinus loczyi Katzer 1903

This specimen was named from partial crowns and cups found in Permian strata of Brazil. It has been re-examined at least once previously (Lane and Webster, 1969), but has only been seen in photographs since the original naming. The location of the holotype is not currently known, though researchers at San Paulo University and UCLA are fairly certain that the specimen currently resides in the Natural History Museum of Bosnia-Herzegovinia; the curators of the museum were not able to be contacted.

The original description states that the cup of *E. loczyi* has strictly pentagonal plates, as well as proportionally large basal plates. The basal and radial plates have slight to moderate tumidity (not able to be seen from the images provided). It was differentiated from *Erisocrinus typus* by the bowl shape of the cup of *E. loczyi.*

I do not consider this species to belong to the genus *Erisocrinus.* The cup is pentagonal, but much more rounded than an *Erisocrinus* specimen. The cup is bowl-shaped in the lower half but is constricted distally to produce a vase-like lateral outline. The radial plates have a pentagonal shape that does not fit the radial plates of the genus *Erisocrinus* in that the widest part of the plate measures much lower than than would be expected (Fig. 32)

While some of the features resemble those of the genus *Sinocrinus*, the shape of the cup and the unique shape of the radial plates do not match with a description within the family Erisocrinidae. I cannot confidently reassign this species to a genus at this time; however, I am confident that it does not belong to the genus *Erisocrinus*.

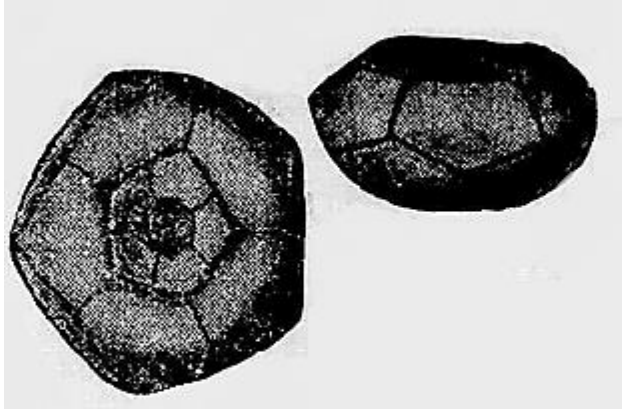

FIGURE 32-*Erisocrinus loczyi*; note the shape of the radial plates of the cup, as well as the rounded bowl shape of the cup and its constriction above. (Modified from Katzer, 1903).

Erisocrinus obliquus Wanner 1916

This species was also described from Permian strata of Timor. A single specimen from the Yale Peabody Museum was studied in this project, along with the original paper from which *E. obliquus* was described.

The original description provided photographs of three different specimens of *E. obliquus.* However, after carefully studying the images and the associated text, I believe that there are two different crinoid genera being grouped together as *Erisocrinus.* One image, Wanner's "example E" (Fig. 33) shows a tall cone-shaped cup with upflared infrabasals[5]. Example C in Wanner's paper is the specimen currently on loan from the Yale Peabody Museum (Fig. 34a and b). This specimen (C) shows pronounced tumidity of the radial and basal plates. The cup is a low bowl shape. The plates of the cup are smooth. The infrabasals are downflared, with a slight basal concavity. The stem attachment scar is proportionally large, with a round lumen.

The specimen of *Erisocrinus obliquus* on loan from the Yale Peabody Museum does not represent *Erisocrinus*, based on the characteristics listed above. The characteristics that this species embodies more closely align itself with the genus *Sinocrinus*. Therefore, the following reassignment is proposed:

Sinocrinus [*Erisocrinus*] *obliquus* (Wanner 1916)

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[5] This specimen was not reassigned during this study; it does not belong to the genus *Erisocrinus*. It does have characteristics (cup shape, upflared infrabasals) that mirror features seen in *Exaetocrinus*. More study of this specimen would be needed to reassign it, however.

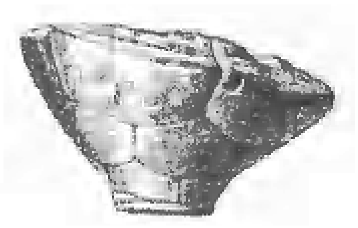


FIGURE 33-*Erisocrinus* obliquus: Example E provided by Wanner; tall cone shaped cup with upflared infrabasals. (Wanner 1916).

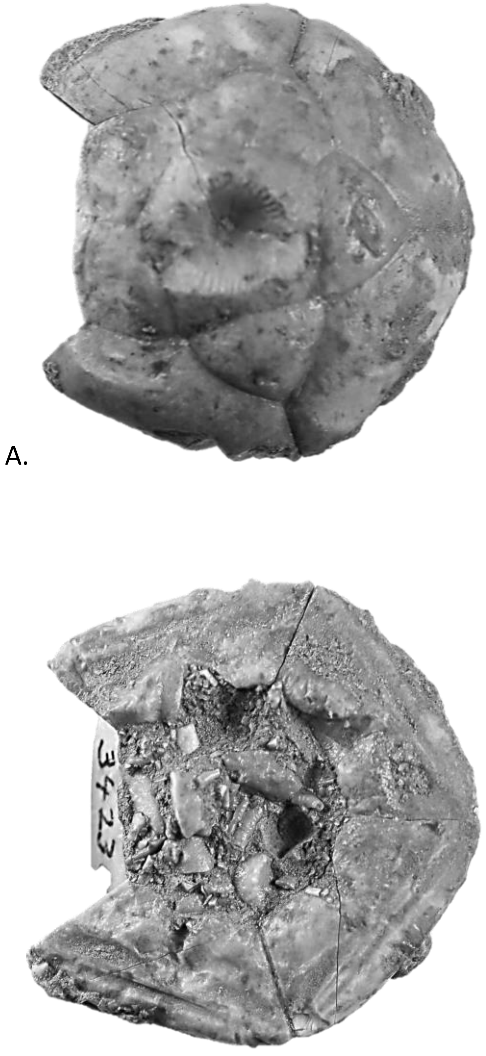


FIGURE 34-*Erisocrinus obliquus* (Yale 34239); **note rounded and large stem scar diameter, bulbous basal plates, and roundness of the cup.**

Erisocrinus granulatus Wanner 1916

E. granulatus is named from specimens only found in Permian strata near Basleo, Timor. No specimens of this species were available for analysis. The analysis is based on the photographs and descriptions published in Wanner's 1916 and 1924 papers that describe *E. granulatus* and two other species of *Erisocrinus*.

E. granulatus exhibits some interesting characteristics. The oral view of the cup presents a strongly rounded shape. The plates of the cup are quite nodose and tumid, deviating from the traditionally smooth and flat features that one would associate with the genus *Erisocrinus.* The radial plates from the aboral view are quite thick (Fig. 35a). The down-flared infrabasal plates, not visible in side-view, are mostly obscured by the stem attachment. The stem attachment is proportionally larger than expected in an *Erisocrinus* specimen, with a circular lumen contained within it (Fig. 35b).

Based on the characteristics present in the figures of the holotype specimen, provided in Wanner's 1916 paper, I do not believe that *E. granulatus* should remain within the genus *Erisocrinus*. The characteristics closely align with that of the genus *Sinocrinus* Tien 1926. Therefore, the following reassignment is proposed

Sinocrinus [*Erisocrinus*] *granulatus* (Wanner, 1916).

FIGURE 35-*Erisocrinus granulatus* holotype; A. Note rounded shape. B. Note tumidity of plates, circular lumen; Band C. Nodose texture of the plates of the cup. (From Wanner, 1916).

Erisocrinus stefaninii Yakovlev 1934

This species was described from cups discovered in Permian strata near Pisa, Italy. The holotype was reposited at the University of Pisa. *E. stefaninii* is a low to medium truncate bowl shaped cladid with proportionally large basals, compared to other species of *Erisocrinus.* The tumidity of the basal plates should be mentioned (Fig. 36a). While tumidity is not necessarily a measurable feature of cladid crinoids, and is not part of the diagnosis, the high tumidity seen in the specimen is not seen in other *Erisocrinus* species.

The shape and outline of the cup do not fit the diagnosis of *Erisocrinus*. The outline of the cup is decidedly circular, whereas *Erisocrinus* is pentagonal. The cup shape of *E. stefaninii* is a rounded bowl shape (Fig. 36b and c). Further, the radial plates of *E. stefaninii,* seen in an oral view in Fig. 6, show a thickness that is not a part of the *Erisocrinus* genus definition.

Based on these characteristics, I do not consider *E. stefaninii* Yakovlev 1934 to be a part of the genus *Erisocrinus*. After careful review, *E. stefaninii* aligns with the characteristics of *Sinocrinus* Tien 1926.Thus, the following reassignment is

Sinocrinus [*Erisocrinus*] *stefaninii* (Yakovlev, 1934).

FIGURE 36-*Erisocrinus stefaninii*; A. the tumidity of the basals and proportionally large size of the basals that extend B. Roundness of cup in aboral view. C. Roundness of cup and thickness of radial plates. (Photo Credit: Chiara Sorbini).

Erisocrinus pentangulatus Yakovlev and Faas 1938

This species is only known from Permian strata near Palmero, Italy. The specimen was described by the original author as having a cone-shaped cup with a strong outward flare caused by the radial plates. The cup outline is pentagonal in oral and aboral view. The plates of the cup have a fine granulation covering the surface; the sutures of the plates are mineralized over, and thus difficult for the original author to obtain accurate measurements. It should be noted that the basal plates are proportionally large when compared with the radial plates. The radial plates are also thick in oral view. The stem scar is proportionally quite large, is somewhat pentagonal in shape, and has coarse crenulations (Fig. 37).

Based on these characteristics, I do not consider *E. pentangulatus* to be a part of the genus *Erisocrinus.* Due to the poor photographs and lack of available material from which to study, a reassignment to another genus is not currently possible.

FIGURE 37-*Erisocrinus pentangulatus*; height of the cup 4.5mm, width of the cup 7.5mm. (From Yakovlev and Faas, 1938).

Erisocrinus araxensis Yakovlev 1933

The original paper, published in the USSR in 1933, was not located for this study. However, *E. araxensis* was re-described in a later paper discussing the hypodigm material found close to the Aras River in the region of Caucasus (Yakovlev and Ivanon, 1956) in Permian shale. The location of both the holotype and the hypodigm is currently unknown. This analysis is based on the photographs that Yakovlev included in his 1956 paper (Fig. 38).

With the diagnosis of *Erisocrinus* in mind (above), there are some pertinent features present in *E. araxensis* that deviate from a typical *Erisocrinus* specimen. The cup does exhibit a cone shape, but it is a high truncate cone, as opposed to a medium to low. This is caused by the infrabasal plates being visible in side view, as opposed to *Erisocrinus*, whose infrabasal plates are not visible in side view. The radial plate thickness is much thicker than *Erisocrinus'* radial plates are; the radial facets are also much wider than in any *Erisocrinus* specimen. I consider thin radial plates with narrow articular facets to be important diagnostic characteristics for the genus *Erisocrinus.*

Based on these characteristics, I do not consider *Erisocrinus araxensis* Yakovlev 1933 to be a part of the genus. After careful analysis, this particular species should be reassigned to *Exaetocrinus* Strimple and Watkins 1969.

Designation: *Exaetocrinus* [*Erisocrinus*] *araxensis* (Yakovlev, 1933).

FIGURE 38-*Erisocrinus araxensis*; rounded cup outline (left), thick radial plates and radial facets (left); infrabasals visible in side view (center). The stem scar is proportionally large (right). (Yakovlev and Ivanon, 1956).

In summary, the following taxa were removed from Erisocrinus and re-assigned to *Exaetocrinus* because of the upflared infrabasals and high cone-shape cup:

- *Erisocrinus conoideus* Meek and Worthen 1865b; Pennsylvanian (“Coal Measures”)
- *Erisocrinus araxensis* Yakovlev 1933; Permian strata near Aras River, Iranian border

Because of their tumid plates, impressed sutures, and ornamentation, the following taxa were transferred to the genus *Sinocrinus*:

- *Erisocrinus cernuus* Trautschold 1867; Pennsylvanian strata of Moscow, Russia
- *Erisocrinus granulatus* Wanner 1916; Permian strata in Timor
- *Erisocrinus obliquus* Wanner 1916; Permian strata in Timor
- *Erisocrinus stefaninii* Yakovlev 1934; Permian strata near Pisa, Italy

The following were recognized as not belonging to the genus *Erisocrinus* or to the family Erisocrinidae;

- *Erisocrinus loczyi* Katzer 1903; Permian strata in Brazil
- *Erisocrinus pentangulatus* Yakovlev 1938; Permian strata near Palmero, Italy

Results of Analysis of species within *Erisocrinus:* Part Two

The PCA analysis of the twelve species still considered to be within the genus *Erisocrinus* showed that out of the five characteristics used in the study (radial height, radial width, basal height, basal width, and stem diameter), only radial height and width play a major role in the variability of *Erisocrinus* species. The percentage variance of the five principal components is shown below (Table 5).

The percentage variance shows that the first principal component comprises 65.6% of the variance between the species. The second component makes up 23.8% of the variation. Thus, the first and second principal components account for 89.4% of the variance in the *Erisocrinus* species. In the first two components, radial height and width contribute the most to the variation (Table 6). Basal height and width play a larger role in variability in the second to fifth principal components. The stem diameter contributes very little to the variation of the species, comprising only a significant amount of variance in the fifth principal component (1.53% of the variance).

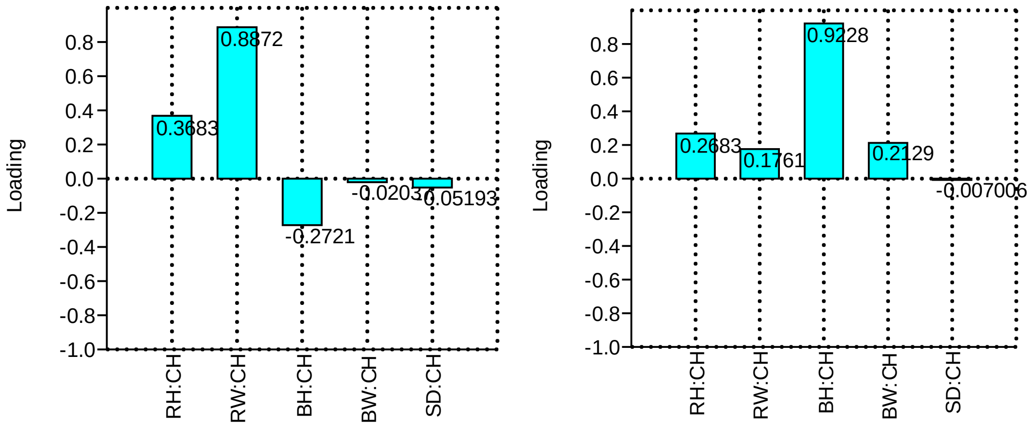
The scatterplot (Fig. 40) shows that there is a large amount of similarity between *E. typus, E. erectus,* and *E. wapunucka.* Both *E. longwelli* and *E. propinquus* also plot closely to these three species. *E. mediator* and *E. georgeae* plot closely to one another as well, as do *E. knoxvillensis* and *E. terminalis. E. obovatus, E. elevatus,* and *E. healdae* do not plot closely to the other species.

Principal Component	Eigenvalue	Percent Variance
1	0.151	65.6
2	0.059	23.8
3	0.162	7.01
4	0.007	3.03
5	0.001	0.601

TABLE 5-Percentage variance of principal components.

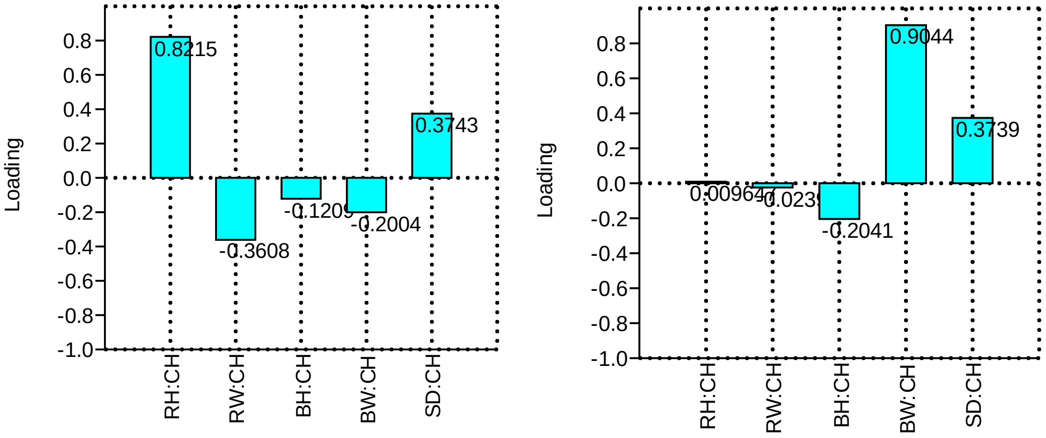
Variables	Component 1	Component 2	Component 3	Component 4	Component 5
Radial Height	0.368	0.268	0.822	0.010	-0.343
Radial Width	0.887	0.176	-0.361	-0.023	0.226
Basal Height	-0.272	0.922	-0.120	-0.204	0.135
Basal Width	-0.020	0.213	-0.200	0.904	-0.310
Stem Diameter	-0.052	-0.007	0.374	0.374	0.847

TABLE 6-Loadings for Principal Component Analysis.



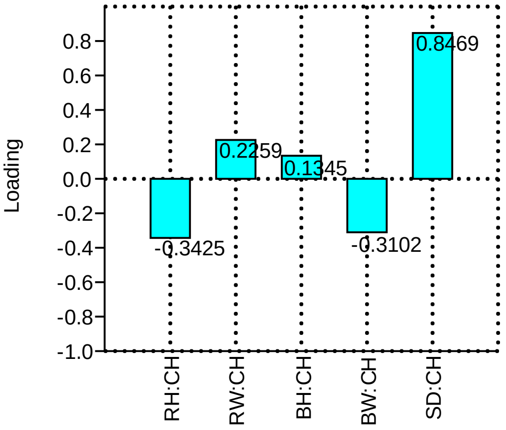
A. Component 1

B. Component 2



C. Component 3

D. Component 5



E. Component 5

FIGURE 39-Graphical representation of loadings for each principal component.

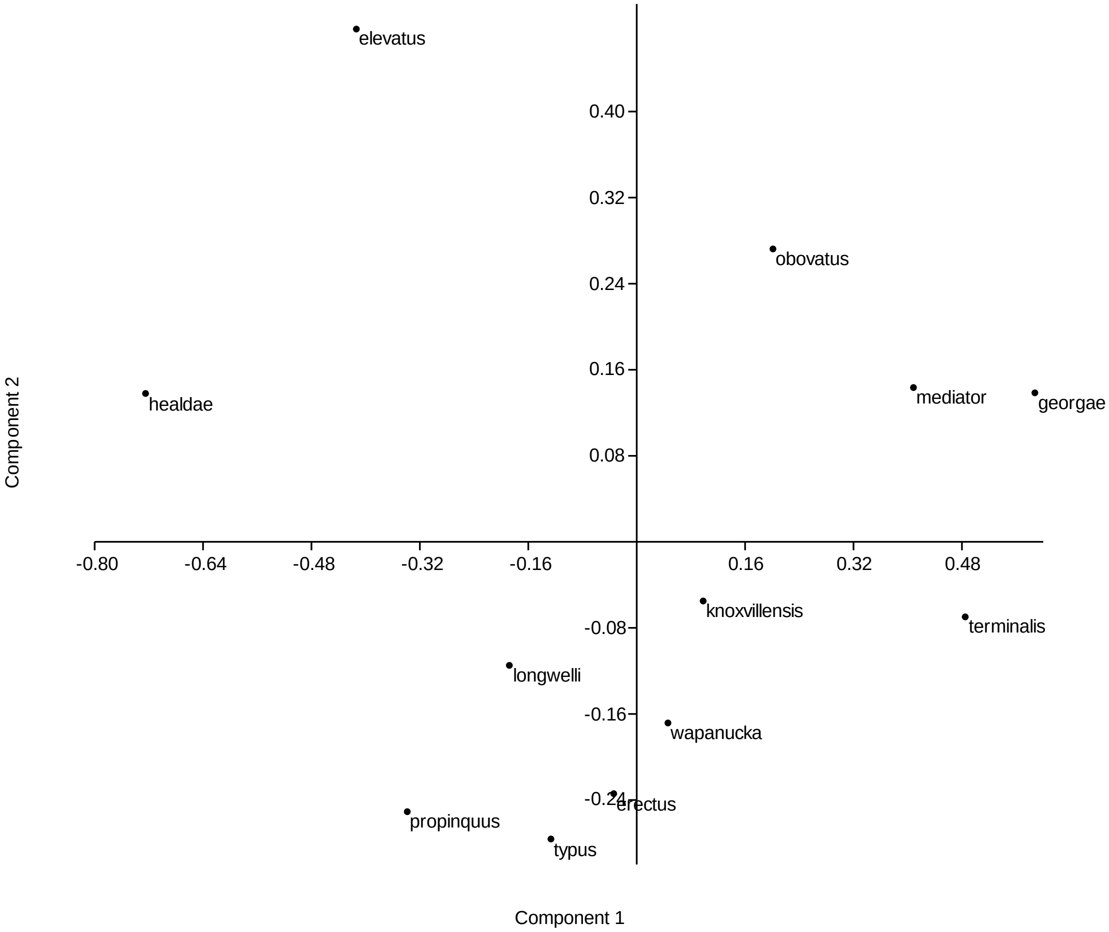


FIGURE 40-Scatterplot of the principal component analysis showing the 12 species analyzed.

The species data were run through a cluster analysis and K-means clustering to determine if any of the species were similar enough to be synonymized with one another. The cluster analysis was projected in Mahalanobis distance so that the co-variances between the species were taken into account (Fig. 41).

The cluster analysis projects *E. healdae* and *E. elevatus* as being the furthest removed from the rest of the species of *Erisocrinus*, something that the scatterplot (Fig. 40) also shows. *E. obovatus* also shows high levels of variation. A tight cluster is shown towards the middle of the cluster analysis diagram, comprising *E. wapunucka, E. propinquus, E. longwelli, E. typus,* and *E. erectus*. *E. knoxvillensis* and *E. terminalis* are clustered closely together, as are *E. georgeae* and *E. mediator* which represents a heightened amount of similarity in their radial and basal plate height and width.

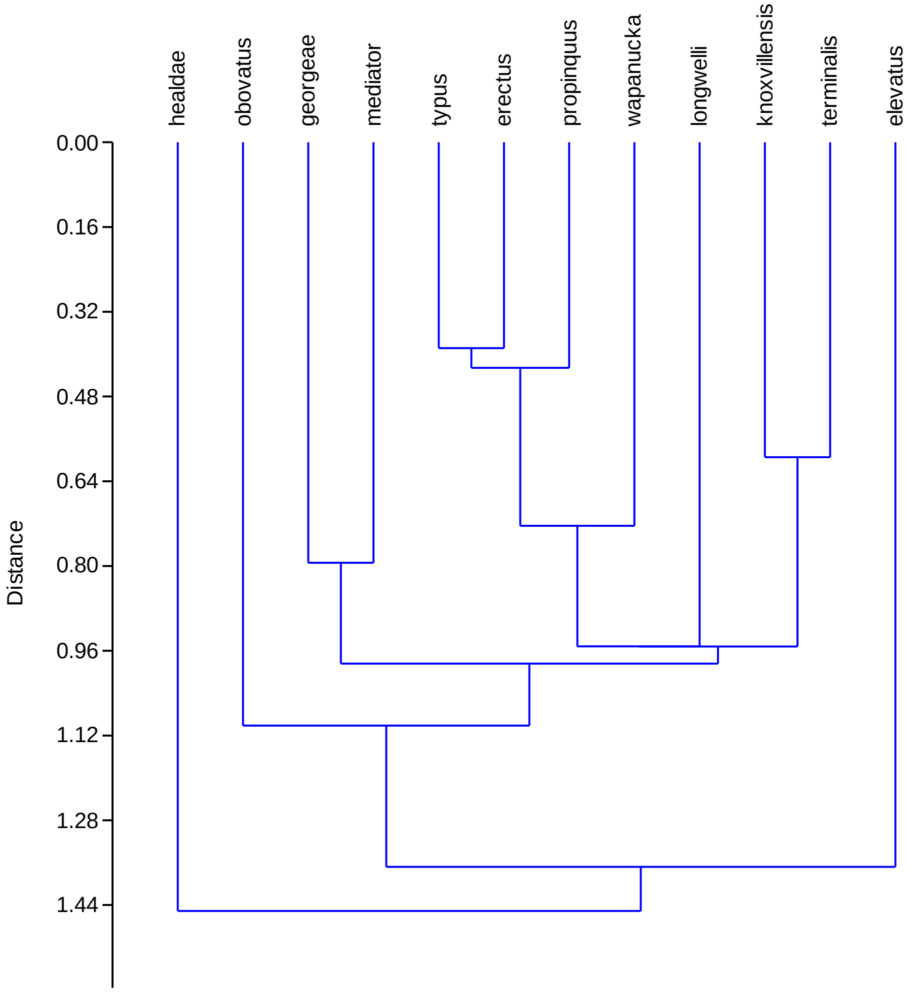


FIGURE 41-Cluster analysis of species data projected in Mahalanobis distance.

The k-means cluster analysis was performed in order to determine which species should be grouped together and synonymized, out of the eleven proposed species used in this portion of the study. The k-means cluster uses a pre-determined number of clusters and determines which species are similar to one another. The number of clusters can be changed. The number was varied many times in order to determine which number of clusters best agreed with the data shown in the scatterplot (Fig. 40) and the cluster analysis (Fig. 41). Table 7 shows the proposed groupings of the species of *Erisocrinus*, based on varying number of clusters (2-8 clusters).

The k-means cluster analysis shows certain trends as it expands into a higher number of clusters. The general trend shows that *Erisocrinus typus* consistently groups with two to three other species in higher order clusters (*E. erectus* and *E. wapunucka*). It also shows that there are a few species, namely *E. healdae, E. obovatus,* and *E. elevatus* that quite commonly present as the two groups that are the farthest removed from the rest of the species. The k-means cluster shows that *E. georgeae* and *E. mediator* plot together when there are a higher number of clusters, as do *E. terminalis* and *E. knoxvillensis.*

Species	n=2	n=3	n=4	n=5	n=6	n=7	n=8
E. longwelli	1	3	4	2	4	1	3
E. knoxvillensis	1	3	4	2	4	3	5
E. terminalis	2	2	2	4	1	6	6
E. typus	1	3	4	2	4	4	3
E. georgeae	2	2	2	5	2	2	6
E. erectus	1	3	4	2	4	4	3
E. elevatus	1	1	1	1	3	5	2
E. obovatus	2	1	3	3	5	6	4
E. wapunucka	1	2	4	2	4	4	3
E. healdae	1	1	1	1	3	5	1
E. propinquus	1	3	4	2	4	4	7
E. mediator	2	2	2	3	6	6	6

TABLE 7-K means cluster analysis for species of *Erisocrinus;* n=2-n=8 shown.

Discussion

The reevaluation of the systematics of *Erisocrinus* reveals that the geographic range of these crinoids is contained entirely within the mid-continental United States. The species that were named in other continents- *E. cernuus, E. loczyi, E. granulatus, E. obliquus, E. malainus, E. stefaninii, E. pentangulatus, E. scoticus, E. carlopsensis,* and *E. araxensis*-have been shown, either through previous synonomies or ones made during the course of this study-to not be within the genus. A majority of those that proved not to be *Erisocrinus* were transferred to closely related genera, within the family (*Sinocrinus* Tien 1926, *Exaetocrinus* 1969), with only two exceptions: *E. loczyi,* and *E. araxensis*. The results of this study show that *Sinocrinus* and *Exaetocrinus* are more globally widespread than *Erisocrinus* was.

It should also be noted that a large majority of the Permian-age species do not belong to the genus *Erisocrinus*, as they were originally assigned. The species- *E. loczyi, E. propinquus, E. granulatus, E. obliquus, E. malainus, E. stefaninii, E. pentangulatus, E. araxensis, E. longwelli*-were found to be in Lower to Middle Permian strata. Of those named from Permian strata, only *E. longwelli* and *E. propinquus* is considered to be within the genus *Erisocrinus.* The range of this genus must be clarified; while it proliferated in the Pennsylvanian, it appears to have been much less common during the Permian than previously thought, and even then existing only into Early Permian.

The PCA analysis shows that only the first two components contribute to the variability within the genus. The loadings of the components show that the radial height and width contribute to the majority of the variation of the loadings, although the basal plates do contribute a significant amount of the variation. Therefore, the relative sizes of the radial plates of *Erisocrinus* are the main feature that distinguishes species from one another (as opposed to the basal plate size or stem attachment diameter).

The PCA analysis, cluster analysis, and k-means clustering of the species still considered to be within the genus *Erisocrinus* showed that some of the species within the genus are indistinguishable from one another. Both the scatterplot and the neighboring cluster analysis show that based on the amount of variation from the species, some of the species within the genus *Erisocrinus* should be synonymized.

To determine which species were valid within the genus, a K-means clustering technique was applied. The test was run seven times and each test was run with a different number of allowed clusters. When the k-means analysis is divided into two clusters, it is obvious that there are not enough clusters to show the variability within the genus; therefore, the k-means analysis needed to be forced into a higher number of clusters.

The results indicate that the K-means clustering data, when compared with the cluster analysis and the scatterplot, best matches when the data is clustered into seven or eight different species. It is obvious from the cluster analysis (Fig. 41) that both *E. healdae* and *E. elevatus* are separate species due to the fact that they are the furthest removed from the other species. *E. obovatus* is also separated by a large distance from the rest of the species.

There is a large cluster of very similar species in the center of the graph, joining *E. typus, E. erectus* and*, E. wapunucka* together. The measurements of *E. propinquus* consistently ally themselves closely with those of *E. typus.* However, an analysis of the holotype of this specimen shows a steeper bend in its basal plates, slightly pentagonal stem, thicker radial plates, and proportionally larger basal and radial plates from *E. typus*. *E. propinquus* has only been found in Permian strata, whereas *E. typus* is not. I theorize that *E. propinquus* is a Permian descendent of *E. typus,* and therefore a closely related, but distinct, species. A cladistics analysis of the genus *Erisocrinus* would have to be performed in the future in order to analyze the validity of this idea.

E. wapunucka Strimple 1961 is shown to be indistinguishable from *Erisocrinus typus.* The holotype for *E. wapunucka,* reposited at the Sam Noble Museum in Oklahoma, is a juvenile specimen of *E. typus.* This truly highlights the importance of including juvenile specimens in systematic studies. A very young juvenile of *E. typus* was not found for more than two decades (from the Barnsdall Formation) after *E. wapunucka* was erected (Strimple, 1961). Without knowing the juvenile stages of a species of crinoid can cause confusion when dealing with its systematics. Also synonymized with *E. typus* is *E. erectus* Moore and Plummer 1940; while I was not able to study the holotype in person, both the photograph of the holotype and the measurements provided in the original description used in the PCA analysis and following analyses show that it represents *Erisocrinus typus.* Both *E. wapunucka* and *E. erectus* should be synonymized with *E. typus.*

E. longwelli and *E. obovatus* each presented some difficulty in determining whether or not they represented valid species. The two species showed a significant amount of distance from other species due to variation in the cluster analysis, but the scatterplot did not show a significant amount of distance represented (Fig. 40). *E. longwelli*, an exclusively Permian species, will be considered a separate species due to the distance plotted by the cluster analysis. Both a quantitative and qualitative analysis was undertaken. The *E. longwelli* specimens that were analyzed are considerably larger than even the largest of the *E. typus* crowns or cups. Proportionally, the *E. longwelli* crown is over 1.5 times as large as *E. typus*, which is why it earned a place in the genus as a separate species by Lane and Webster (1966). This species is also one of the only *Erisocrinus* groups that have been found in the Permian. *E. obovatus* plots closely to *E. longwelli* on the cluster analysis, but it does not plot closely on the scatterplot. Therefore, *E. obovatus* will still be considered a separate species.

Erisocrinus terminalis and *E. knoxvillensis* plot closely to one another on the scatterplot and in the neighborhood cluster analysis and appear to represent the same species. Therefore, *E. knoxvillensis* Strimple 1975 will be synonymized with *E. terminalis* Strimple 1962.

E. georgeae and *E. mediator* appear to be nearly indistinguishable in the scatterplot and cluster analysis as well. They also group together often in the k-means analysis. Therefore, *E. georgeae* Strimple and Watkins 1969 will be synonymized with *E. mediator* Strimple 1962.

Using a combination of the K-means cluster, the cluster analysis, and the scatterplot of the data of the currently proposed species of *Erisocrinus*, it would seem that there are eight valid species within the genus: *Erisocrinus typus*, *E. propinquus, E. elevatus, E. obovatus, E. terminalis, E. longwelli, E. mediator,* and *E. healdae.* Future work will include a phylogenetic study in order to strengthen this study's conclusion that the intraspecific variability within *Erisocrinus* amounts to eight valid species. It should also be mentioned that as some of these species above (namely, *E. obovatus, E. elevatus,* and *E. healdae*) were erected based on very few specimens. It may be the case that once more specimens of these species are found, another reclassification of the species within the genus *Erisocrinus* might be necessary.

The following brief descriptions of the valid species of *Erisocrinus* are given as indicators as to how each differs from the type species. Photographs are provided in Figures 46-51.

1. *Erisocrinus typus* Meek and Worthen 1865 (type species). Cup medium to low truncate cone. Cup outline strongly pentagonal in oral and aboral view. Radial plates form majority of lateral walls of the cup. Anal plate rarely found, but confined to notch between radial plates when present. Basal concavity often mild. Stem impression circular and proportionally small (Fig. 42-44).
2. *Erisocrinus propinquus* Weller 1909. Walls of the cup bend at a proportionally sharper angle. Radial plates proportionally thicker. Stem impression slightly pentagonal. Proportional sides of radial and basal plates and stem attachment

comparable to type species, but can be differentiated by proportionally thicker radial plates, sharper bend in basal plates, and pentagonal shape of stem impression (description amended from Moore and Plummer, 1940; Fig. 45).

3. *Erisocrinus elevatus* Moore and Plummer 1940. Sharp bend between base and nearly perpendicular sides. Radial plates proportionally large and make up majority of cup walls. Small anal plate confined to notch between radial facets in holotype. Differentiated from type species by sharp bend from the flat base to perpendicular walls (description amended from Moore and Plummer, 1940; Fig. 46).
4. *Erisocrinus obovatus* Moore and Plummer 1940. Proportionally large radial plates that form majority of walls of the cup. Moderate basal concavity seen in all specimens. Proportionally large stem scar impression. Differentiated from type species by more pronounced basal concavity (description amended from Moore and Plummer, 1940; Fig. 47).
5. *Erisocrinus terminalis* Strimple 1962. Cup low truncate cone shape. Cup proportionally wider than *E. typus*. Basal plate sutures proportionally shorter. Presence of anal plate common. Differentiated from type species by low, wide cup shape and shorter sutures between basal plates (description amended from Strimple, 1962; Fig. 48)

6. *Erisocrinus longwelli* Lane and Webster 1966. Cup very large, truncate cone shape. Basal plates proportionally large and sharply convex on sides of the cup. Differentiated from type species by proportionally larger basal plates and

unusually large cup and crown size (description amended from Lane and Webster, 1966; Fig. 49)

7. *Erisocrinus mediator* Strimple 1962. Cup medium to low truncate cone shape. Basal plates slightly tumid. Photos of previously named *E. georgeae* do not show radial, basal sutures clearly; little can be said about them. Proportionally large stem cicatrix diameter. Differentiated from type species by proportionally taller cup and proportionally larger stem cicatrix diameter (description amended from Pabian and Strimple, 1974 and Strimple and Watkins, 1969; Fig. 50).
8. *Erisocrinus healdae* Pabian and Strimple 1974. Cup medium to low truncate cone. Cup outline less pentagonal than most species within *Erisocrinus.* Proportionally large stem cicatrix diameter. Radial plates flare slightly outwards of the cup. Radial facets are proportionally narrower than *E. typus*. Differentiated from type species by proportionally larger stem cicatrix diameter, less pentagonal outline of the cup, proportionally narrower radial facets, and slightly flared walls of the cup (description amended from Pabian and Strimple 1974; Fig. 51)

FIGURE 42-*Erisocrinus erectus* (Holotype P4732); *E. erectus* Moore and Plummer 1940 is rejected as the junior synonym of *Erisocrinus typus.* (Photo Credit: Texas Memorial Museum)

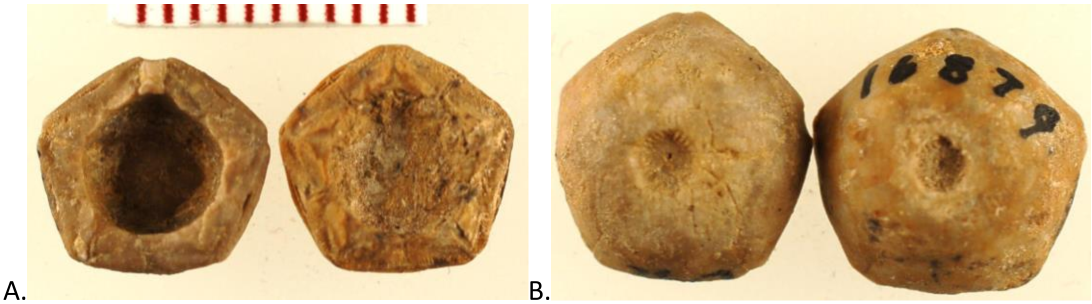


FIGURE 43-A. Oral view of *Erisocrinus wapunucka* (L) and juvenile *Erisocrinus typus* (R). B. Aboral view of *Erisocrinus wapunucka* (L) and juvenile *Erisocrinus typus* (R). Scale bar represents 1cm. (*E. wapunucka* holotype: Sam Noble Museum 7517; *E. typus* Peabody Museum 16879). *E wapunucka* Strimple 1961 is rejected as the junior synonym.

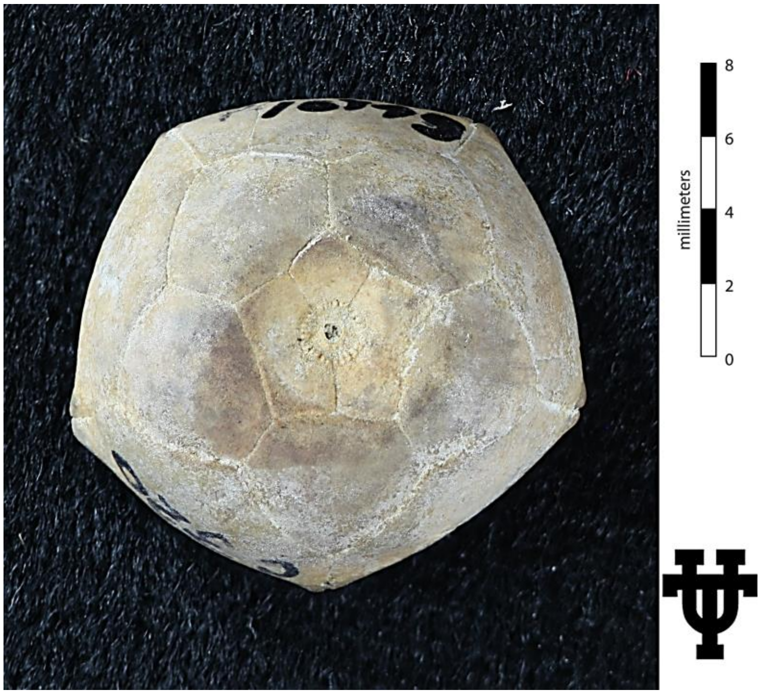


FIGURE 44-*Erisocrinus typus* (P10749). (Photo credit: Texas Memorial Museum).

FIGURE 45-*Erisocrinus propinquus* holotype (UC 13367). A. Aboral view; note pentagonal stem attachment. B. Oral view; note proportionally thicker radial plates. (Photo credit A.: Paul Mayer).

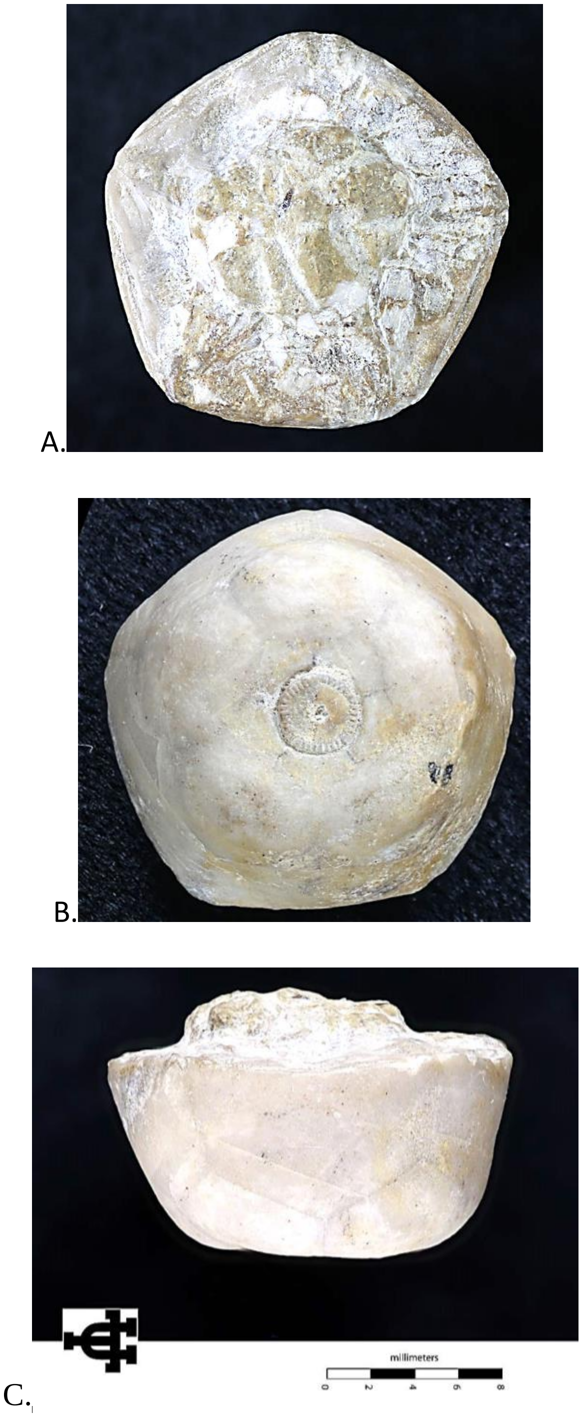


FIGURE 46-*Erisocrinus elevatus* (holotype); A. Oral view ofcup. B. Aboral view of cup. C. Side view; note erect sides. (Photo credit: Texas Memorial Museum)


A.


B.


C.

FIGURE 47-*Erisocrinus obovatus* (holotype; P-10737). A (oral view) and B (aboral view) distinguished from the type species by a more pronounced basal concavity; proportionally thick radial plates. (Photo credit: Texas Memorial Museum)

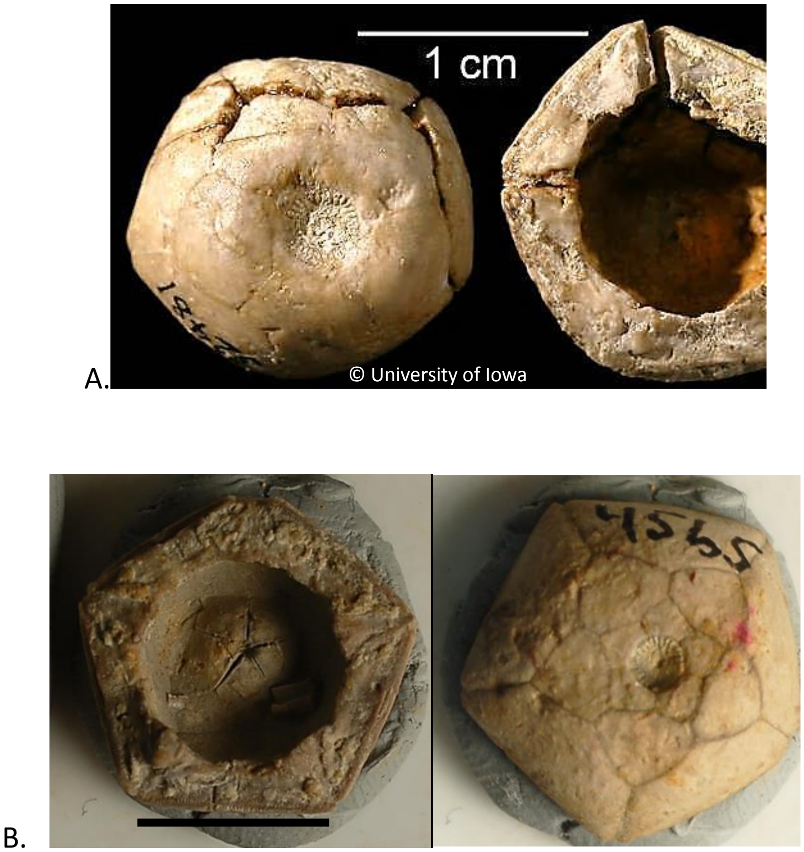


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FIGURE 48-*Erisocrinus terminalis* Strimple 1962. A. *E. knoxvillensis* (Holotype; SUI 32481). B. *Erisocrinus terminalis* (Sam Noble Museum 4565; scale bar represents 1cm). These two species are synonymized with *E. knoxvillensis* rejected as the junior synonym.

FIGURE 49-*Erisocrinus longwelli* (UNSM 529117); scale bar represents 1cm.

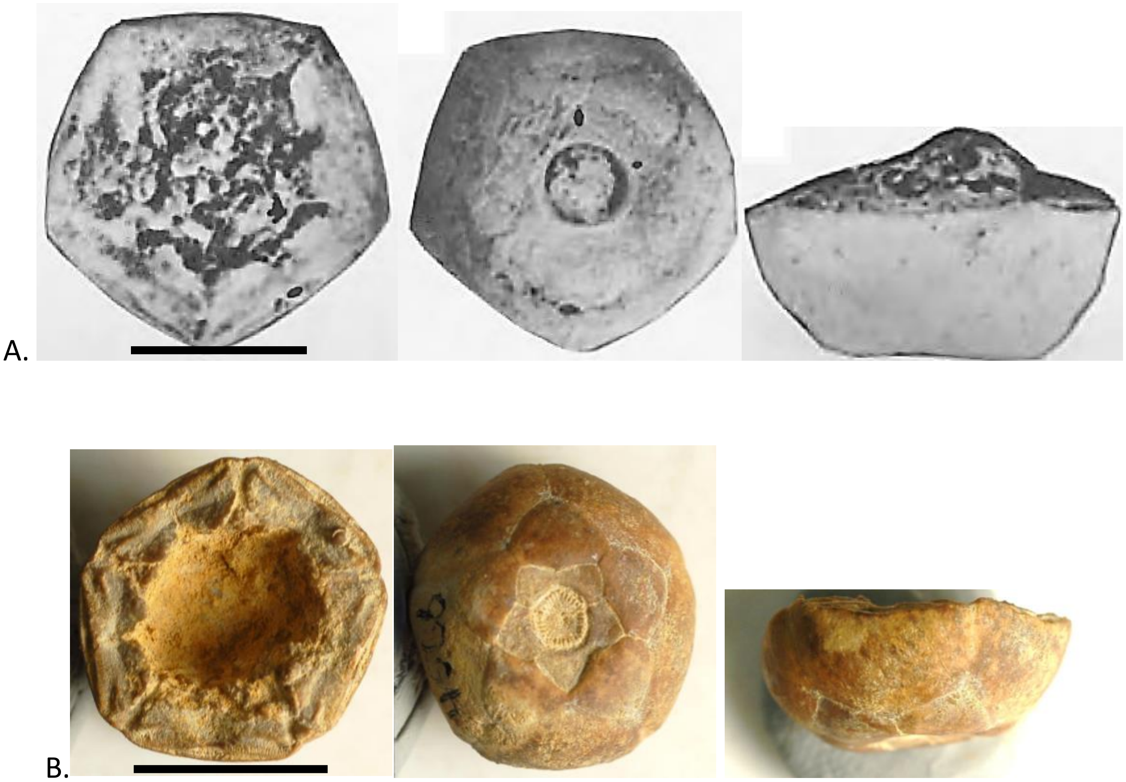

FIGURE 50-*Erisocrinus mediator*; A. *E. georgeae.* (Pabian and Strimple, 1974). B. *Erisocrinus mediator* (holotype: Sam Noble Museum 4566); *E. georgeae* is rejected as the junior synonym. Scale bar represents 1cm.

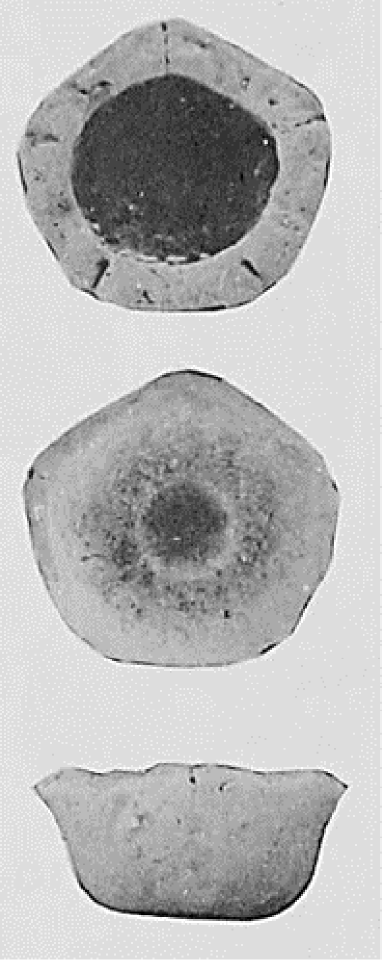

FIGURE 51-*Erisocrinus healdae*; only known from Big Saline Formation of Texas. (Pabian and Strimple, 1974).

Conclusions

Of the 37 species proposed as being within in the genus *Erisocrinus*, a large majority do not belong within the genus, based on the amended diagnosis of the genus:

Cup medium to low truncate cone. Cup outline strongly pentagonal in oral and aboral view. Radial plates 5, forming majority of lateral walls of the cup; basal and infrabasal plates 5, varying in size. Radials straight or flared outward in side view and relatively thin. Basal concavity mild to moderate. Arms 10, equibiserial, branching after first secundibrach in all rays. Anal plate missing or confined to notch between radial facets. Surface of the cup plates smooth. Stem impression circular and proportionally small.

The geographic range of *Erisocrinus* is restricted to the mid-continental United States; all species proposed on other continents do not belong within the genus, and almost all have been reassigned to genera within the family Erisocrinidae. A large majority of those species named within the Permian age have also been reassigned to other genera; only *E. longwelli* Lane and Webster 1966 and *E. propinquus* Weller 1909 are still considered to be a valid species within *Erisocrinus.* The range of *Erisocrinus* would appear to be restricted to the Pennsylvanian through Early Permian, specifically the Wolfcampian (within the presently named Cisuralian)

Through a thorough reevaluation of the genus *Erisocrinus* using a principal component analysis, cluster analysis, and k-means clustering test, this study shows that there are eight valid species within the genus: *E. typus* Meek and Worthen 1865, *E. propinquus* Weller 1909, *E. elevatus* Moore and Plummer 1940, *E. obovatus* Moore and Plummer 1940, *E. terminalis* Strimple 1962, *E. longwelli* Lane and Webster 1966, *E. mediator* Strimple 1962, and *E. healdae* Pabian and Strimple 1974.

Summary

A thorough analysis of the growth and systematics of this genus has provided a different insight from what has been published previously about *Erisocrinus,* as well as information that has not previously been studied.

The cup of *Erisocrinus* grew anisometrically as it changed from a juvenile to an adult, which deviates from what was originally published (Peters and Lane, 1990). The plates of the cup grow close to isometrically, as did other cladid crinoids (Peters and Lane, 1990; Ausich and Wood, 2012). The arm plates of *Erisocrinus* decrease in size in three separate stages, which may indicate three episodes of growth.

This study has highlighted the importance of including juvenile specimens in these studies. Growth of the cup of *Erisocrinus* is noticeably anisometric when juvenile specimens are included in the study. The study of juvenile specimens of this genus has also allowed for a more accurate analysis of the systematics; *E. wapunucka* was erected from a juvenile specimen of *Erisocrinus typus* (Strimple, 1961).

The systematics study shows that *Erisocrinus'* geographic range is restricted to the mid-continental United States. All of the species named outside of this region have been reassigned out of *Erisocrinus.* The age range of *Erisocrinus* has also been restricted almost exclusively to the Pennsylvanian. A large number of the species erected that were found in the Permian have been reassigned out of the genus. The study shows that only two species of *Erisocrinus* existed during the Early Permian.

Principal component analysis, cluster analysis, and a k-means cluster analysis showed that some synonymies were necessary. It is proposed that *E. knoxvillensis* be synonymized with *E. terminalis,* and *E. wapunucka* and *E. erectus* should be synonymized with *E. typus*. As a result, there are eight valid species within the genus: *E. typus* Meek and Worthen 1865, *E. propinquus* Weller 1909, *E. elevatus* Moore and Plummer 1940, *E. obovatus* Moore and Plummer 1940, *E. terminalis* Strimple 1962, *E. longwelli* Lane and Webster 1966, *E. mediator* Strimple and Watkins 1962, and *E. healdae* Pabian and Strimple 1974.

References

AUSICH, W.I., and WOOD, T.E., 2012, Ontogeny of *Hypselocrinus hoveyi*, Mississippian Cladid Crinoid from Indiana: Journal of Paleontology, v. 86, p. 1017–1020.

BATHER, F.A., 1889, The natural history of the Crinoidea, *in* Proceedings of the London Amateur Scientific Society: Oxford, p. 32–33.

BEEDE, J.W., 1899, New fossils from the Kansas coal measures: Kansas University Quarterly, v. 8, p. 123–130.

BOOS, M., 1929, Stratigraphy and fauna of the Luta Limestone (Permian) of Oklahoma and Kansas: Journal of Paleontology, v. 3, p. 241–253.

BOWSHER, A.L., and STRIMPLE, H.L., 1986, *Platycrinites* and associated crinoids from Pennsylvanian rocks of the Sacremento Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources, Circular 1, p. 1–37.

BROWER, J.C., 2006, Ontogeny of the food-gathering system in Ordovician crinoids: Journal of Paleontology, v. 80, p. 430-446.

DONOVAN, S.K., 1991, The taphonomy of echinoderms: calcareous multi-element skeletons in the marine environment, *in* Donovan, S.K., ed., The Processes of Fossilization: Columbia University Press, New York, p. 241–269.

GEINITZ, 1866, Carbonformation und Dyas in Nebraska, *in* Leopold-Carolin, K., ed., Verhandlungen Des Deutschen Akademi Naturforschenden: Dresden, p. 1-130.

HAMMER, Ø., HARPER, D.A.T., and RYAN, P.D., 2001, Paleontological statistics software package for education and data analysis: palaeontologia electronica, v. 4, p. 1–9.

HAMMER, Ø., and HARPER, D.A.T., 2006, Paleontological Statistics Software Package for Education and Data Analysis: Paleontological Data Analysis, Oxford, 351p.

KAMMER, T.W., 2008, Paedomorphosis as an adaptive response in pinnulate cladid crinoids from the Burlington Limestone (Mississippian Osagean) of the Mississippi Valley, *in* Ausich, W.I. and Webster, G.D., eds., Echinoderm Paleobiology: Indiana University Press, Bloomington, Indiana, p. 177–196.

KATZER, F., 1903, Grundzüge der Geologie des unteren Amazonasgebietes (des Staates Para in Brasilien): Leipzig, Max Weg, 248p.

LANE, N.G., and SEVASTOPULO, G.D., 1982, Growth and systematic revision of *Kallimorphocrinus astrus*, a Pennsylvanian microcrinoid: Journal of Paleontology, v. 56, p. 244–259.

LANE, N.G., WEBSTER, G.D., 1966, New Permian crinoid fauna from southern Nevada: University of California Publications in Geological Sciences, Los Angeles, San Diego, p. 1-60.

LEWIS, R.D., 1980, Taphonomy, *in* Echinoderms: Notes for a Short Course: Paleontological Society, p. 27–39.

MEEK, F.B., and WORTHEN, A.H., 1865a, Descriptions of new species of crinoidea , & c ., from the Palæozoic rocks of Illinois and Some of the adjoining states: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 17, p. 143–155.

MEEK, F.B., and WORTHEN, A.H., 1865b, Remarks on the Carboniferous and Cretaceous rocks of eastern Kansas and Nebraska: American Journal of Science, v. 39, p. 157–174.

MEEK, F.B., and WORTHEN, A.H., 1868, Remarks on some types of Carboniferous crinoidea, with descriptions of new genera and species of the same, and of one echinoid: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 20, p. 335–359.

MEEK, F.B., and WORTHEN, A.H., 1869, Descriptions of new Crinoidea and Echinoidea from the Carboniferous rocks of the western states, with a note on the genus Onychaster: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 21, p. 67–83.

MEYER, D.L., 1971, Post morten disarticulation of recent crinoids and ophiuroids under natural conditions: Geological Society of America Abstracts with Programs, v. 3, p. 645.

MEYER, D.L., and AUSICH, W.I., 1997, Morphologic variation within and among populations of the camerate crinoid *Agaricocrinus* (Lower Mississippian, Kentucky and Tennessee): breaking the spell of the mushroom: Journal of Paleontology, v. 71, p. 896–917.

MILLER, J.S., 1821, A natural history of the Crinoidea, or lily-shaped animals; with observations on the genera, Asteria, Euryale, Comatula and Marsupites: Bryan & Co, Bristol, England, 150p.

MILLER, S.A., and GURLEY, F.E., 1890, Description of some new genera and species of echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri, and Iowa, *in* Indiana Department of Geologic and Natural History Annual Report: Indiana University, p. 327–373.

MOORE, R.C., and LAUDON, L.R., 1943, Evolution and classification of Paleozoic crinoids: Geological Society of America, Special Paper, v. 46, p. 1–151.

MOORE, R.C., and PLUMMER, F.B., 1940, Crinoids from the Upper Carboniferous and Permian Strata in Texas: University of Texas Publication 3945, p. 468.

MOORE, R.C., and TEICHERT, C., 1978, Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea (R. C. Moore & C. Teichert, Eds.): Geological Society of America and University of Kansas Press, Boulder, CO and Lawrence, KS.

PABIAN, R.K., and RUSHLAU, W.J., 2002, Taphonomic Analysis and Systematic Descriptions of Some Late Pennsylvanian and Early Permian Crinoids from Southeastern Nebraska , Eastern Kansas and Southwestern Iowa University of Nebraska-Lincoln: Geological Survey, Paper 20, p. 1–45.

PABIAN, R.K., and STRIMPLE, H.L., 1974, Crinoid Studies Part I. Some Pennsylvanian crinoids from Nebraska. Part II. Some Permian crinoids from Nebraska, Kansas, and Oklahoma: Bulletins of American Paleontology, v. 64, p. 247–337.

PABIAN, R.K., and STRIMPLE, H.L., 1980, Some Crinoids from the Argentine Limestone (Late Pennsylvania-Missourian) of southeastern Nebraska and southwestern Iowa: Transactions of the Nebraska Academy of Sciences and Affiliated Societies: Nebraska Academy of Sciences, v. 8, p. 155–186.

PETERS, J., and LANE, N.G., 1990, Ontogenetic adaptations in some Pennsylvanian crinoids: Journal of Paleontology, v. 64, p. 427–435.

SEPKOSKI, J.J., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

SIMS, M.J., 1999, Systematics, phylogeny, and evolutionary history, *in* Hess, H., Ausich, W.I., Brett, C.E., and Simms, M.J., eds., Fossil Crinoids: Cambridge, p. 31–40.

STOLL, N.R., DOLLFUS, R., FOREST, J., RILEY, N.D., SABROSKY, C.W., WRIGHT, C.W., and MELVILLE, R.V., 1964, International Code of Zoological Nomenclature: International Trust for Zoological Nomenclature, London.

STRIMPLE, H.L., 1951, New species of crinoids from the Pennsylvanian of Kansas: Journal of Paleontology, v. 25, p. 372–376.

STRIMPLE, H.L., 1961, New species of *Bronaughocrinus* and *Stuartwellercrinus* from the Carboniferous of Oklahoma: Oklahoma Geology Notes, v. 21, p. 186–189.

STRIMPLE, H.L., 1962, Crinoids from the Oologah Formation: Oklahoma Geological Survey, Circ. 60, p. 1–75.

STRIMPLE, H.L., 1975, A rare inadunate crinoid from the Barnsdall Formation (Upper Pennsylvanian) of Oklahoma: Oklahoma Geology Notes, v. 35, p. 23–26.

STRIMPLE, H.L., and WATKINS, W.T., 1969, Carboniferous crinoids of of Texas with stratigraphic implications: Palaeontographica Americana, v. 6, p. 136–275.

THOMKA, J.R., 2010, Genesis and Taphonomy of a Crinoid Lagerstätte in the Upper Pennsylvanian Barnsdall Formation of Northeastern Oklahoma:Auburn University, Unpublished Masters Thesis, 210p.

TIEN, C.C., 1926, Crinoids from the Taiyuan series of north China, *in* Survey, G., ed., Paleontology of Sinica: China, p. 1–47.

TRAUTSCHOLD, H., 1867, Einige crinoideen und andere Thierreste des Jungeren Bergkalks im Gouvernment Moskau: Bulletin de la Societe imperiale des naturalistes de Moscou., v. 15, p. 1–49.

UBAGHS, G., 1978, Skeletal morphology of fossil crinoids, *in* Moore, R.C. and Teichert, K., eds., Treatise on Invertebrate Paleontology, Echinodermata, Pt. T (2): Geological Society of America and University of Kansas Press, Boulder and Lawrence, p. T58–T216.

WACHSMUTH, C., and SPRINGER, F., 1886, Revision of the Palaeocrinoidea: discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions., *in* Academy of Natural Sciences of Philadelphia, Proceedings: p. 140–302.

WANNER, J., 1916, Die Permischen echinoderm von Timor, I. Tiel: Palaontologie von Timor, v. 11, p. 1–329.

WANNER, J., 1921, Die Permischen Krinoiden von Timor: Verhand. Mijnw. Ned., Oost-Indie, 51p.

WELLER, S., 1909, Description of a Permian crinoid fauna from Texas: Journal of Geology, v. 17, p. 623–635.

WHITE, C.A., 1870, Descriptions of the new species of Carboniferous invertebrate fossils, *in* Proceedings of United States National Museum, V. 2: Washington Government Printing Office, Washington D.C., p. 499.

WRIGHT, J., 1939, The Scottish Carboniferous Crinoidea: Transactions of the Royal Society of Edinburgh, v. 60, p. 1–78.

WRIGHT, J., 1942, New British Carboniferous crinoids: Geological Magazine: Geological Magazine, v. 79, p. 269–283.

WRIGHT, J., 1945, *Tyriocrinus* (gen. nov) and *Scotiacrinus* (gen. nov) and seven new species of inadunate crinoids from the Carboniferous limestones of Scotland and Yorkhire: Geological Magazine, v. 82, p. 114–125.

YAKOVLEV, N.N., 1933, , Dve verkhpepermskhe morskie lilii iz zakavkaziya [Two Upper Permian crinoides from the transcaucasian]: Izvestiya Akademii Nauk SSSR, Leningrad, v. 7, p. 975-978.

YAKOVLEV, N.N., 1934, Crinoidi permiani di Sicilia: Palaeontographia Italica, v. 34, p. 269-283.

YAKOVLEV, N., and FAAS, A., 1938, Nuovi Echinodermi permiani di Sicilia: Palaeontograph. Ital, v. 38, p. 115–125.

YAKOVLEV, N.N., and IVANON, A.P., 1956, Crinoids and blastoids of the Carboniferous and Permian deposits of Russia: Vsesoyuznogo Nauchno-Issledovatelskii Geologicheskogo Institut Trudy, v. 11, p. 1–142.

ZACHOS, L.G., 2012, Morphometric analysis of fossils using heads-up digitization and geographic information system (GIS) software: Geological Society of America Abstracts with Programs, v. 44, p. 18:

Appendix I

Erisocrinus typus Morphometric Data

Radial Area Measurements for Growth Series

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width[6]	PBr Area (mm^2)
1.35	2.55	2.6	0.98	1.20	0.86	3.28	2.61	5.6
1.28	2.56	2.6	1.00	1.31	0.74	3.96	-	-
1.40	-	-	1.18	1.32	0.11	3.38	-	-
-	-	-	-	-	0.11	-	-	-
-	-	-	-	-	-	-	-	-

GS#1

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
2.50	4.09	7.9	1.85	2.68	3.2	4.01	3.79	11.5
2.40	4.08	7.2	1.69	-	3.6	-	-	-
2.51	-	-	-	-	2.5	-	-	-
2.42	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#2

---

[6] Width often deformed; generally only able to obtain one PBr plate where both height and width were undeformed (PBr area was taken using this plate for accuracy).

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
2.79	4.25	12.6	1.69	2.84	2.1	4.83	5.71	17.1
2.73	-	-	1.70	2.80	3.1	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#3

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
3.27	4.58	14.0	2.97	3.55	6.2	4.80	5.84	18.4
3.52	4.68	14.0	3.04	-	7.3	4.28	5.15	-
-	5.28	14.2	2.72	-	-	-	-	-
-	-	14.2	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#4

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
-	-	25.8	-	-	7.5	4.76	5.59	19.4
-	-	-	-	-	6.8	-	-	-
-	-	-	-	-	7.0	-	-	-
-	-	-	-	-		-	-	-
-	-	-	-	-		-	-	-

GS#5

Radial Height	Radial Width	Radial Area (mm^2)	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
4.49	7.80	26.0	3.47	5.17	10.7	5.26	7.97	29.5
4.24	7.76	-	3.23	5.21	-	-	-	-
4.20	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#6

Radial Height	Radial Width	Radial Area	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
6.91	12.2	62.5	4.93	8.02	35.0	5.45	8.26	29.8
6.49	11.1	53.4	4.70	-	26.9	-	-	-
-	-	44.4	-	-	25.7	-	-	-
-	-	57.6	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#7

Radial Height	Radial Width	Radial Area	Basal Height	Basal Width	Basal Area (mm^2)	PBr Height	PBr Width	PBr Area (mm^2)
7.02	1.28	78.1	6.22	7.22	43.0	6.99	14.1	64.5
6.73	1.30	81.1	6.25	8.58	32.2	-	-	-
-	-	69.8	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-

GS#8

TABLE 8-Morphometric data for radial and basal plates (all measurements in mm, unless specified).

Arm plate Area Data for Growth Series

GS1	GS2	GS3	GS4	GS5	GS6	GS7	GS8
0.26	1.45	12.37	2.54	2.14	2.85	6.53	4.63
0.56	1.49	12.45	2.58	2.16	2.87	6.56	4.63
0.58	1.58	12.48	2.58	2.19	2.89	6.60	4.68
0.67	1.60	12.66	2.59	2.19	2.91	6.66	4.73
0.70	1.61	12.80	2.63	2.20	2.93	6.76	4.74
0.70	1.64	13.05	2.83	2.22	2.93	6.98	4.75
0.70	1.71	13.34	2.84	2.24	2.95	7.35	4.81
0.76	1.73	13.43	2.90	2.25	2.98	7.45	4.81
0.90	1.74	13.49	2.94	2.25	3.06	7.68	4.83
1.15	1.82	14.01	3.05	2.25	3.10	7.96	4.84
1.17	1.88	14.24	3.12	2.33	3.11	7.97	4.84
1.27	1.94	14.25	3.14	2.34	3.15	8.40	4.88
1.35	2.05	14.34	3.27	2.43	3.17	10.47	5.02
1.53	2.16	14.63	3.77	2.58	3.21	13.65	5.14
2.07	2.55	14.70	4.12	2.63	3.33	14.78	5.19
2.09	2.95	15.45	5.13	3.49	3.35	15.47	5.23
2.64	3.18	15.93	6.75	5.57	3.42	20.09	5.25
2.83	3.26	16.47	9.38	6.89	3.64	21.05	5.31
3.19	7.78	17.11	16.98	13.70	3.87	30.04	5.34
5.59	8.18	18.31	19.21	17.71	5.84	45.44	5.36
	1.44	12.28	2.49	2.13	2.84	6.50	4.57

	1.39	11.97	2.47	2.11	2.82	6.22	4.57
	1.39	11.79	2.39	2.11	2.80	6.09	4.53
	1.32	11.74	2.37	2.11	2.79	5.82	4.48
	1.32	11.48	2.37	2.09	2.76	5.78	4.42
	1.31	11.31	2.34	2.03	2.75	5.41	4.40
	1.31	11.24	2.23	1.99	2.73	5.26	4.40
	1.23	10.83	2.22	1.89	2.71	5.13	4.38
	1.19	10.46	2.20	1.89	2.70	5.08	4.37
	1.18	10.25	2.20	1.83	2.69	4.80	4.36
	1.17	10.08	2.19	1.81	2.68	4.76	4.35
	1.17	9.77	2.18	1.80	2.68	4.75	4.34
	1.12	9.69	2.14	1.78	2.68	4.70	4.32
	1.02	7.55	2.13	1.77	2.67	4.68	4.32
	1.01	7.12	2.12	1.64	2.65	4.66	4.32
	1.00	6.47	2.09	1.60	2.65	4.61	4.31
	0.99	3.21	2.09	1.48	2.64	4.60	4.23
	0.97	2.87	2.07	1.45	2.61	4.54	4.22
	0.90	2.86	2.06	1.45	2.58	4.53	4.18
	0.87	2.77	2.06	1.39	2.58	4.51	4.14
	0.74	2.75	2.06	1.35	2.56	4.44	4.12
	0.67	2.73	2.01	1.27	2.56	4.40	4.06
	0.66	2.72	2.01	1.18	2.53	4.39	4.03
	0.61	2.56	2.00	1.16	2.53	4.21	4.03
	0.57	2.50	1.98	1.00	2.53	4.15	4.01

	0.26	2.45	1.97	0.84	2.52	4.07	3.99
		2.45	1.96		2.51	3.85	3.98
		2.42	1.95		2.50	3.77	3.97
		2.35	1.95		2.50	3.62	3.96
		2.30	1.94		2.50	3.54	3.92
		2.24	1.94		2.50	3.53	3.91
		2.15	1.94		2.49	3.01	3.91
		2.13	1.93		2.49	2.68	3.90
		2.13	1.93		2.48	2.57	3.87
		2.12	1.92		2.43	2.55	3.85
		2.10	1.91		2.35	2.54	3.81
		2.07	1.91		2.33	2.52	3.79
		2.05	1.89		2.32	2.50	3.78
		2.01	1.89		2.31	2.27	3.77
		2.01	1.86		2.28	1.99	3.77
		2.00	1.86		2.28		3.72
		2.00	1.84		2.24		3.71
		1.99	1.82		2.24		3.70
		1.99	1.80		2.24		3.69
		1.98	1.79		2.19		3.68
		1.98	1.78		2.19		3.65
		1.97	1.78		2.17		3.65
		1.96	1.75		2.16		3.64
		1.96	1.74		2.15		3.62

		1.94	1.73		2.13		3.61
		1.93	1.73		2.12		3.60
		1.92	1.72		2.12		3.59
		1.89	1.72		2.03		3.59
		1.88	1.72		2.01		3.58
		1.87	1.68		1.98		3.58
		1.86	1.66		1.97		3.55
		1.85	1.66		1.93		3.55
		1.84	1.65		1.92		3.54
		1.82	1.63		1.92		3.53
		1.80	1.58		1.90		3.53
		1.79	1.57		1.86		3.53
		1.77	1.55		1.80		3.52
		1.77	1.46		1.73		3.48
		1.73	1.45		1.65		3.46
		1.72	1.37		1.60		3.46
		1.71	1.35		1.50		3.42
		1.70	1.28		1.50		3.39
		1.68	1.25		1.47		3.39
		1.66	0.93		1.44		3.37
		1.63	0.89		1.40		3.37
		1.63	0.62		1.34		3.36
		1.63	0.58		1.33		3.35
		1.61			1.28		3.32

		1.59			1.25		3.32
		1.44					3.30
		1.42					3.29
		1.39					3.29
		1.35					3.29
		1.31					3.28
		1.27					3.28
		1.26					3.28
		1.17					3.28
		1.16					3.27
		1.12					3.23
		1.01					3.22
		0.99					3.21
		0.98					3.20
		0.97					3.20
		0.94					3.18
		0.86					3.18
		0.70					3.14
		0.60					3.12
		0.38					3.09
							3.08
							3.06
							3.06
							3.04

							3.03
							3.00
							2.97
							2.93
							2.91
							2.87
							2.84
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							2.83
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							2.44
							2.36
							2.34
							2.28
							2.26
							2.24
							2.23
							2.18
							2.15
							2.10
							2.08
							2.07
							1.98
							1.90
							1.87
							1.86

							1.82
							1.74
							1.73
							1.71
							1.71
							1.61
							1.53
							1.41
							1.25

TABLE 9-Arm Plate Area Data for *Erisocrinus typus* growth series (all measurements in cm^2).

Appendix II

Museum Collections of *Erisocrinus*

Museum	**Specimens Available**
Auburn University	*E. typus* (8), Barnsdall Fm
Cincinnati Museum Center (Cincinnati, OH)	*E. typus* (1), Iola Limestone *E. sp.* (4),Stanton Fm; (4) Ochelata Gp
Field Museum (Chicago, IL)	*E. propinquus* (1), Cibolo Limestone; *Spaniocrinus trinodos* (1), Cibolo Limestone
Indiana State University-Bloomington (Bloomington, Indiana)	*E. typus* (24), LaSalle Fm
Museum für Naturkunde-Invertebraten Paläontologie	*E. cernuus* (1), Myachkowo Quarry, Moscow
Sam Noble Museum of Natural History (Norman, OK)	*E. terminalis* (3), Oklahoma *E. mediator* (2), Oklahoma *E. wapunucka* (1), Oklahoma
Texas Memorial Museum	*E. obovatus* (1), Graford Fm *E. erectus* (1), Palo Pinto Limestone *E. elevatus* (1), Palo Pinto Limestone *E. conoideus* (1), Springfield, Illinois
U.S. National Museum (D.C.)	*E. erectus* (2), Gobbler Fm *E. longwelli*, (1),Birdspring Fm; 1 *E. planus,* (1); *E. lustrum* (1) *E. typus* (4),Kanwaka Fm; Gobbler Fm (7); Unknown (7) *E. sp* (1), Gobbler Fm
University of Nebraska (Lincoln, NE)	*E. typus* (60), Barnsdall Fm
Universita` di Pisa Museo di Storia Naturale	*E. stefaninii* (1), Valle del F. Sosio
Yale Peabody Musuem (New Haven, CT)	*E. typus* (6), Unknown *E. obliquus* (1), Timor, Indonesia

TABLE 10-Museum collections used for study in study of *Erisocrinus* systematics.

Appendix III

Previous Synonymies of *Erisocrinus*

Species	Date of Synonomy	Current Placement	Reason for Synonymy
Erisocrinus nebrascensis	Pabian and Strimple, 1993	*Erisocrinus typus*	Proportionally same size plates as *E. typus.*
Erisocrinus pelvis	Pabian and Rushlau, 2003	*Erisocrinus typus*	Proportionally same size plates as *E. typus.*
Erisocrinus inflexus	Pabian and Rushlau, 2003	*Delocrinus inflexus*	Rounded cup shape; thick radial plates; deep basal concavity (Fig. 51)
Erisocrinus tuberculatus	Moore and Plummer, 1940	*Ethelocrinus tuberculatus*	Distinctive plate ornamentation, bowl shaped cup, rounded cup outline. (Fig. 52)
Erisocrinus cognatus	Moore and Plummer, 1940	*Delocrinus planus*	Deep basal concavity, rounded cup shape, thick radial facets. (Fig. 53)
Erisocrinus antiquus	Kirk, 1947	*Natocrinus antiquus*	Mississippian age, uniserial arms; (Fig. 54)
Erisocrinus whitei	Kammer, 2008	*Graphiocrinus? whitei*	Mississippian age, uniserial arms. (Fig. 55)
Erisocrinus (Ceriocrinus) planus	Moore and Plummer, 1940	*Delocrinus planus*	See *Erisocrinus cognatus*
Erisocrinus megalobrachius	Moore and Plummer, 1940	*Delocrinus megalobrachius*	Rounded cup shape; spinose primibrachs; deep basal concavity. (Fig. 56)
Erisocrinus trinodus	Moore and Plummer, 1940	*Spaniocrinus? trinodus*	Upflared infrabasals; uniserial arms. (Fig. 57)

Erisocrinus malaianus[7]	Wanner, 1916	*Delocrinus malainus*	Rounded cup shape, thick radial plates; (Fig. 58)
Erisocrinus lutana	Moore and Plummer, 1940	*Pachylocrinus lutanus*	Uniserial arms; upflared infrabasals, hexagonal basals. (Fig. 59)
Erisocrinus carlopensis	Kammer and Ausich, 2008	*Exaetocrinus carlopsensis*	Upflared infrabasals. (Fig. 60)
Erisocrinus scoticus	Wright, 1945	*Apographiocrinus? scoticus*[8]	Rounded bowl shaped cup, uniserial arms. (Fig. 61)
Erisocrinus lustrum	Strimple and Watkins, 1969	*Exaetocrinus lustrum*	Upflared infrabasals. (Fig. 62)

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[7] I do not agree with the synonymy of *E. malainus* to *D. malainus;* the basal concavity and tumidity of the plates do not appear to align with the genus' description. However, no reassignment will be made. *E. malainus* does not belong to the genus *Erisocrinus* either.

[8] This specimen is referred to *Apographiocrinus?* due to the fact that no anal plate has ever been found with this species, whereas the genus *Apographiocrinus* is defined as having one. It otherwise fits the description of the genus.

FIGURE 52-*Delocrinus [Erisocrinus] inflexus* Geinitz 1866; rounded cup shape from oral view, thick radial plates and radial facets. Deep basal concavity not easily seen from views provided. (From Geinitz, 1866).

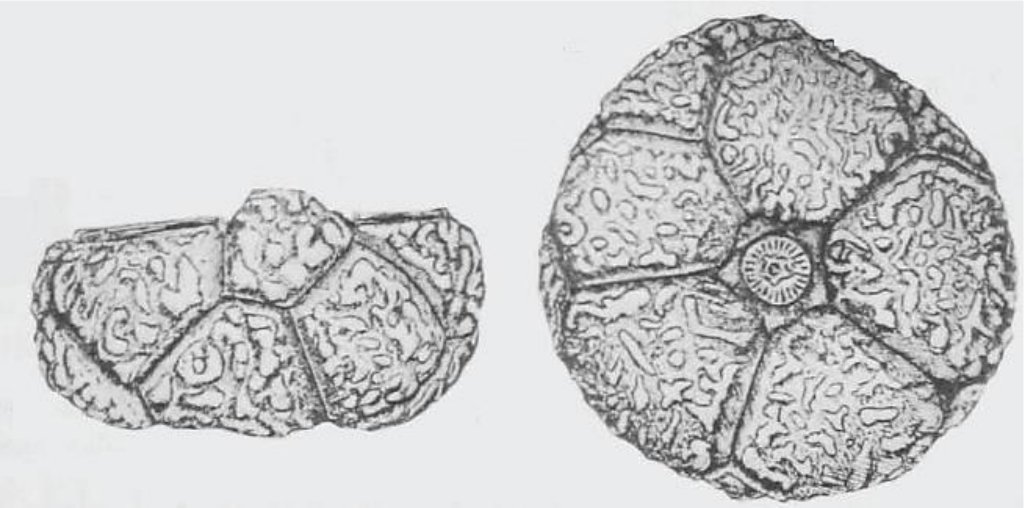

FIGURE 53-*Ethelocrinus*; rounded cup shape and distinctive plate ornamentation distinguish *Ethelocrinus* from *Erisocrinus*. (From Moore et al., 1978).

FIGURE 54-*Delocrinus planus;* A. note rounded cup shape, thick radial plates and facets. B. Note deep basal concavity. (From Moore et al., 1978).

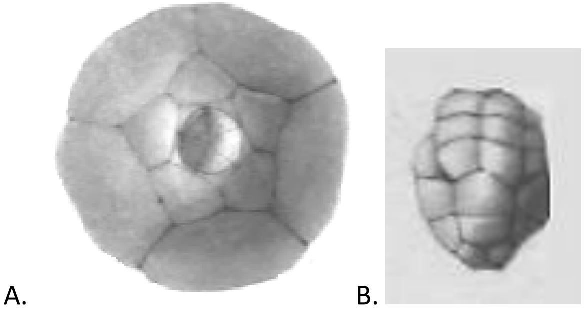

FIGURE 55-Natocrinus [*Erisocrinus] antiquus* Meek and Worthen; note uniserial arms in B. (From Meek and Worthen, 1868).

FIGURE 56-*Graphiocrinus [Erisocrinus] whitei* White 1869; note the uniserial arms. (Photo credit: Harvard University Zoological Museum 2013).

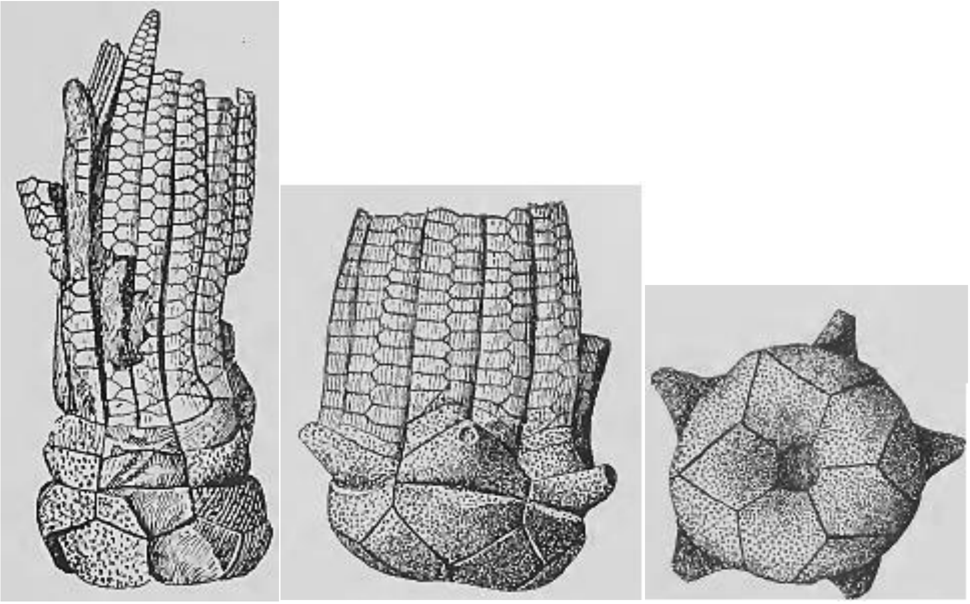

FIGURE 57-*Delocrinus [Erisocrinus] megalobrachiatus* Beede 1899; rounded cup outline, spinose primibrachial plates, deep basal concavity. (Modified from Beede, 1899).

FIGURE 58-*Spaniocrinus? trinodus* holotype (UC 13368); note upflared infrabasals. Crown (not pictured) exhibits uniserial arms. (Photo credit: Paul Mayer).

FIGURE 59-*Erisocrinus malainus* holotype; A. rounded cup shape and thick radial plates; B and C. High tumidity of basal and radial plates; note the more shallow basal concavity than expected for Delocrinus. (From Wanner, 1916).

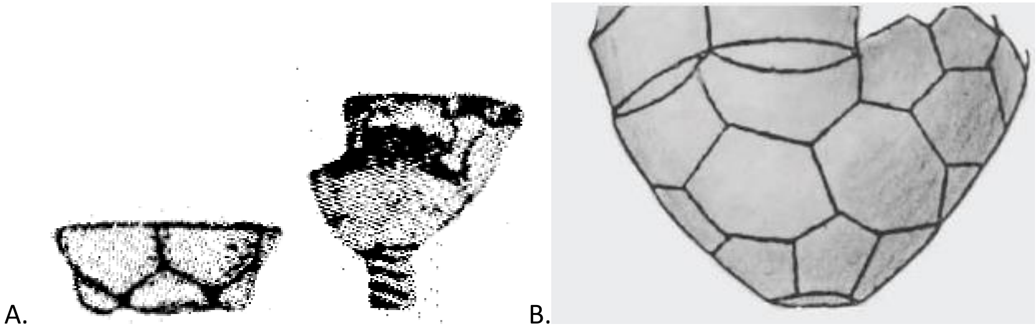

FIGURE 60-A. *Erisocrinus lutana* (From Boos, 1929); B. *Fifeocrinus wright*; note the hexagonal basal plates and upflared infrabasals in B. (From Moore et al., 1978).

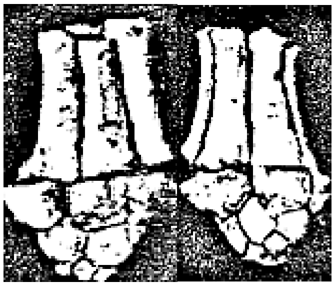

FIGURE 61-Juvenile specimen of *Exaetocrinus carlopsensis*; note the upflared infrabasals. (From Wright, 1939).

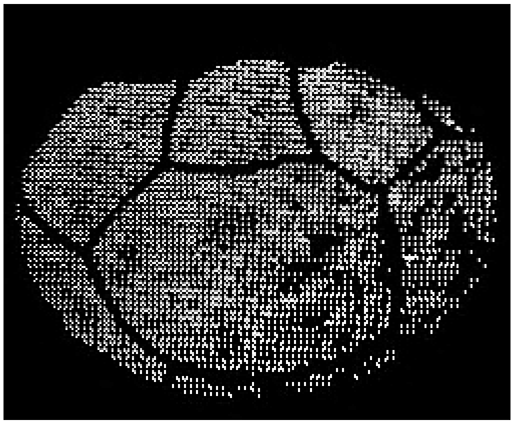

FIGURE 62-*Apographiocrinus? scoticus*; note closed low bowl cup shape. (From Wright, 1945).

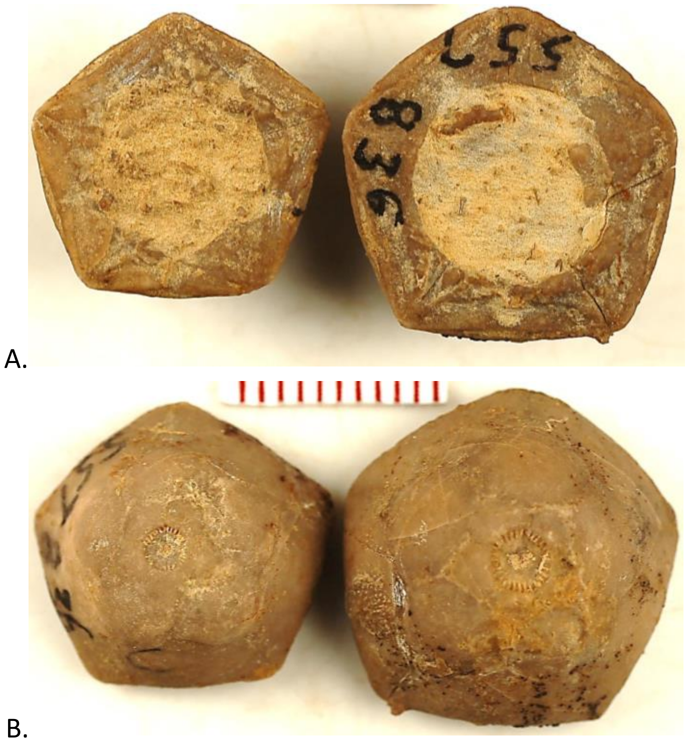

FIGURE 63-*Exaetocrinus lustrum* Strimple and Watkins 1969 (UNSM 557836) A. Note thick radial plates and radial plate facets. B. Note tumidity of basal plates.

Appendix III

Measurements of Museum Collections (Organized by Museum)

SAMPLE #	557849	557845	557844A	557844B	557844C	557841B	557841A
TAXON	*E. sp*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E.*	*E.*
CUP H	1.44	0.428	0.584	0.662	0.762	0.548	0.742
CUP W	2.16	0.936	1.80	1.67	1.39	1.69	2.04
STEM DIAMETER	N/A	0.188	0.344	0.320	0.280	0.220	0.316
BH1	0.782	0.296	0.4605	N/A	0.346	N/A	N/A
BH2	N/A	N/A	0.474	N/A	0.34	N/A	N/A
BH3	N/A	N/A	0.468	N/A	0.34	N/A	N/A
BH4	N/A	0.296	0.458	N/A	0.342	N/A	N/A
BH5	N/A	0.286	0.452	N/A	0.33	N/A	N/A
BW1	0.932	0.354	0.688	N/A	0.437	N/A	N/A
BW2	N/A	N/A	0.642	N/A	0.444	N/A	N/A
BW3	N/A	N/A	0.654	N/A	0.445	N/A	N/A
BW4	N/A	0.358	0.676	N/A	0.444	N/A	N/A
BW5	N/A	0.358	0.686	N/A	0.440	N/A	N/A
IBH1	N/A	N/A	0.180	N/A	0.156	N/A	N/A
IBH2	N/A	N/A	0.172	N/A	N/A	N/A	N/A
IBH3	N/A	N/A	0.181	N/A	N/A	N/A	N/A
IBH4	N/A	N/A	0.185	N/A	N/A	N/A	N/A
IBH5	N/A	N/A	0.180	N/A	N/A	N/A	N/A
IBW1	N/A	N/A	N/A	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A	N/A	N/A

IBW3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	N/A	N/A	N/A	N/A	N/A	N/A
IBW5	N/A	N/A	N/A	N/A	N/A	N/A	N/A
RH1	0.782	0.310	0.592	N/A	N/A	N/A	N/A
RH2	N/A	0.313	0.594	N/A	N/A	N/A	N/A
RH3	N/A	N/A	0.580	N/A	N/A	N/A	N/A
RH4	N/A	0.322	0.578	N/A	N/A	N/A	N/A
RH5	1.29	0.315	0.590	N/A	N/A	N/A	N/A
RW1	N/A	0.568	N/A	N/A	N/A	N/A	N/A
RW2	N/A	0.574	1.12	N/A	N/A	N/A	N/A
RW3	N/A	0.568	1.16	N/A	N/A	N/A	N/A
RW4	N/A	0.576	1.16	N/A	N/A	N/A	N/A
RW5	N/A	0.574	N/A	N/A	N/A	N/A	N/A

TABLE 11--UNSM specimen measurements used during study. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	118455	247910	247907	8037	5925	4289
TAXON	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*
CUP H	0.586	1.11	0.844	1.28	0.830	0.982
CUP W	1.29	1.96	1.83	2.94	1.764	2.12
STEM DIAMETER	0.254	0.486	0.292	N/A	0.301	0.351
BH1	N/A	N/A	N/A	0.786	N/A	0.696
BH2	0.340	N/A	0.568	0.71	N/A	N/A
BH3	0.348	N/A	0.550	N/A	N/A	0.664
BH4	0.389	N/A	0.528	N/A	0.664	0.684
BH5	0.366	N/A	0.507	N/A	N/A	0.724
BW1	N/A	N/A	N/A	0.968	N/A	N/A
BW2	0.402	N/A	0.696	1.00	N/A	N/A
BW3	0.450	N/A	0.660	N/A	N/A	0.740
BW4	0.472	N/A	0.674	N/A	N/A	0.756
BW5	0.48	N/A	0.674	N/A	N/A	N/A
IBH1	N/A	0.278	N/A	N/A	N/A	0.240
IBH2	N/A	0.244	N/A	N/A	N/A	0.224
IBH3	N/A	N/A	N/A	N/A	N/A	0.224
IBH4	N/A	0.280	N/A	N/A	N/A	0.222
IBH5	N/A	0.234	N/A	N/A	N/A	0.225
IBW1	N/A	0.428	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A	N/A
IBW3	N/A	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	0.354	N/A	N/A	N/A	N/A
IBW5	N/A	0.432	N/A	N/A	N/A	N/A

RH1	0.490	0.534	0.622	0.788	0.570	0.682
RH2	0.432	N/A	N/A	0.73	0.590	0.654
RH3	0.490	N/A	N/A	0.84	N/A	0.704
RH4	0.490	N/A	0.606	0.846	0.476	0.668
RH5	0.476	N/A	0.644	0.786	0.552	N/A
RW1	0.768	N/A	1.17	N/A	1.22	1.34
RW2	0.716	N/A	1.03	1.38	0.940	1.40
RW3	0.702	N/A	1.07	1.48	1.06	1.38
RW4	0.736	N/A	1.07	1.41	1.06	1.32
RW5	0.762	N/A	1.15	1.34	1.106	1.26

TABLE 12--UNSM specimen measurements used during study. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	S. 3935	S2289 A	S2289 B	S2289 C	2888	ACC271025
TAXON	*E. sp*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. sp*
CUP H	0.782	0.888	0.972	1.60	1.116	0.532
CUP W	1.59	1.84	2.32	2.33	0.358	0.691
STEM DIAMETER	0.253	0.376	0.558	0.414	N/A	0.212
BH1	0.443	N/A	N/A	0.801	N/A	N/A
BH2	0.427	N/A	N/A	0.813	N/A	N/A
BH3	0.448	N/A	N/A	0.838	N/A	N/A
BH4	0.478	N/A	N/A	0.792	N/A	N/A
BH5	0.448	N/A	N/A	0.801	N/A	N/A
BW1	0.529	N/A	N/A	1.01	N/A	N/A
BW2	0.568	N/A	N/A	N/A	N/A	N/A
BW3	0.553	N/A	N/A	N/A	N/A	N/A
BW4	0.572	N/A	N/A	1.02	N/A	N/A
BW5	0.594	N/A	N/A	0.976	N/A	N/A
IBH1	0.196	N/A	N/A	N/A	N/A	N/A
IBH2	0.192	N/A	N/A	N/A	N/A	N/A
IBH3	0.190	N/A	N/A	N/A	N/A	N/A
IBH4	0.174	N/A	N/A	N/A	N/A	N/A
IBH5	0.198	N/A	N/A	N/A	N/A	N/A
IBW1	0.256	N/A	N/A	N/A	N/A	N/A
IBW2	0.264	N/A	N/A	N/A	N/A	N/A
IBW3	0.268	N/A	N/A	N/A	N/A	N/A
IBW4	0.238	N/A	N/A	N/A	N/A	N/A
IBW5	0.248	N/A	N/A	N/A	N/A	N/A

RH1	0.486	0.614	0.728	0.654	N/A	N/A
RH2	0.47	N/A	0.748	0.662	N/A	N/A
RH3	0.538	N/A	0.710	N/A	N/A	N/A
RH4	0.494	N/A	0.742	0.622	N/A	N/A
RH5	0.500	N/A	0.77	0.68	N/A	N/A
RW1	0.948	1.258	1.37	1.356	N/A	N/A
RW2	0.949	N/A	1.35	1.358	N/A	N/A
RW3	0.980	N/A	1.35	N/A	N/A	N/A
RW4	1.01	N/A	1.40	1.37	N/A	N/A
RW5	0.392	N/A	1.396	1.41	N/A	N/A

TABLE 13--UNSM specimen measurements used during study. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	SPRGR 1	SPRGR2	SPRGR3	9450	557838A	557838B
TAXON	*E. sp*	*E. sp*	*E. sp*	*E. typus*	*E.?*	*E.?*
CUP H	0.778	0.725	0.934	0.782	0.585	0.529
CUP W	1.64	0.925	1.51	1.8	1.30	1.32
STEM DIAMETER	0.248	0.146	0.332	0.254	0.237	0.279
BH1	0.488	0.52	0.602	N/A	0.380	0.452
BH2	N/A	0.52	N/A	0.427	0.398	0.468
BH3	N/A	0.5	N/A	0.432	0.386	0.472
BH4	0.532	0.49	N/A	0.434	0.3822	0.4682
BH5	0.540	0.47	N/A	N/A	0.396	0.465
BW1	0.624	0.598	0.6	0.498	0.468	0.468
BW2	N/A	0.5925	N/A	0.4965	0.4565	0.474
BW3	0.62	0.522	N/A	0.491	0.464	0.464
BW4	N/A	0.588	N/A	0.492	0.465	0.470
BW5	0.652	0.568	N/A	0.426	0.462	0.476
IBH1	N/A	0.202	N/A	N/A	0.167	N/A
IBH2	N/A	0.222	N/A	N/A	0.120	N/A
IBH3	N/A	0.208	N/A	N/A	0.134	N/A
IBH4	N/A	0.206	N/A	N/A	0.120	N/A
IBH5	N/A	0.212	N/A	N/A	0.150	N/A
IBW1	N/A	0.284	N/A	N/A	0.278	N/A
IBW2	N/A	0.274	N/A	N/A	0.210	N/A
IBW3	N/A	0.258	N/A	N/A	0.182	N/A
IBW4	N/A	0.286	N/A	N/A	0.212	N/A
IBW5	N/A	0.232	N/A	N/A	0.239	N/A

RH1	0.506	0.422	0.543	0.732	0.486	0.442
RH2	0.522	0.45	0.529	0.736	0.479	0.446
RH3	0.541	0.436	N/A	0.717	0.466	0.44
RH4	0.545	0.432	0.532	0.692	0.462	0.443
RH5	0.524	0.44	0.570	0.712	0.484	0.449
RW1	1.02	0.652	0.940	1.06	0.72	0.763
RW2	0.992	0.6965	0.952	1.13	0.64	0.928
RW3	0.961	0.662	N/A	1.10	N/A	N/A
RW4	0.960	0.638	0.916	1.12	N/A	N/A
RW5	0.932	0.722	0.952	1.13	0.758	N/A

TABLE 14--UNSM specimen measurements used during study. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	557840	557835	557846	557833	529117a	529117b	529117c
TAXON	*E.?*	*Delocrinus*[9]	*Delocrinus*	*E.?*	*E. longwelli*	*E. longwelli*	*E. longwelli*
CUP H	0.882	N/A	0.5282	0.5628	1.27	1.83	1.14
CUP W	1.31	N/A	1.28	1.36	2.75	2.66	2.05
STEM DIAMETER	N/A	N/A	N/A	0.161	0.885	0.735	0.4
BH1	0.670	N/A	**N/A**	N/A	1.06	1.44	1.03
BH2	0.678	N/A	N/A	0.432	1.06	1.36	0.974
BH3	0.676	N/A	N/A	0.424	1.114	1.384	0.1002
BH4	0.678	N/A	N/A	N/A	1.04	1.37	1.09
BH5	0.680	N/A	N/A	N/A	1.05	1.40	N/A
BW1	0.856	N/A	N/A	N/A	1.31	1.68	1.20
BW2	0.826	N/A	N/A	0.538	1.28	1.74	1.14
BW3	0.810	N/A	N/A	0.534	1.46	1.59	1.07
BW4	0.838	N/A	N/A	N/A	1.38	1.58	1.22
BW5	0.894	N/A	N/A	N/A	1.36	1.68	1.15
IBH1	N/A	N/A	N/A	N/A	N/A	N/A	0.216
IBH2	N/A	N/A	N/A	0.122	N/A	N/A	0.200
IBH3	N/A	N/A	N/A	0.146	N/A	N/A	N/A
IBH4	N/A	N/A	N/A	0.152	N/A	N/A	N/A
IBH5	N/A	N/A	N/A	0.200	N/A	N/A	0.213
IBW1	N/A	N/A	N/A	0.200	N/A	N/A	0.387
IBW2	N/A	N/A	N/A	N/A	N/A	N/A	0.386

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[9] Renamed as *Delocrinus* during this study; UNSM designation currently reads *Erisocrinus planus*

IBW3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	N/A	N/A	N/A	N/A	N/A	N/A
IBW5	N/A	N/A	N/A	0.334	N/A	N/A	0.372
RH1	0.772	N/A	N/A	N/A	N/A	1.158	N/A
RH2	0.762	N/A	N/A	N/A	0.920	1.10	0.781
RH3	0.758	N/A	N/A	0.452	0.950	0.958	0.78
RH4	0.775	N/A	N/A	0.451	0.962	1.01	0.824
RH5	0.784	N/A	N/A	0.450	N/A	1.12	0.878
RW1	1.36	N/A	N/A	0.790	1.53	2.06	N/A
RW2	1.39	N/A	N/A	0.785	1.42	1.9185	1.40
RW3	1.37	N/A	N/A	0.79	1.57	N/A	1.43
RW4	1.42	N/A	N/A	0.764	1.57	2.01	1.47
RW5	1.39	N/A	N/A	0.776	1.56	2.07	N/A

TABLE 15--UNSM specimen measurements used during study. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	34239	519738	519376	16887	85431	85434
TAXON	*E. obliquus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*
CUP H	1.11	N/A	0.772	N/A	0.687	0.628
CUP W	2.80	1.25	1.99	N/A	1.52	1.28
STEM DIAMETER	N/A	0.44	0.268*(Estimated)	N/A	0.312	0.428* (estimated)
BH1	0.646	N/A	0.594	N/A	0.416	N/A
BH2	0.690	N/A	N/A	N/A	0.44	N/A
BH3	0.690	N/A	0.590	N/A	0.442	N/A
BH4	0.690	N/A	N/A	N/A	0.452	N/A
BH5	N/A	N/A	0.592	N/A	0.462	N/A
BW1	0.878	N/A	0.718	N/A	0.530	N/A
BW2	0.894	N/A	N/A	N/A	0.518	N/A
BW3	0.898	N/A	0.720	N/A	0.542	N/A
BW4	0.876	N/A	0.720	N/A	0.556	N/A
BW5	0.864	N/A	0.740	N/A	0.560	N/A
IBH1	N/A	N/A	N/A	N/A	0.132	N/A
IBH2	N/A	N/A	N/A	N/A	0.130	N/A
IBH3	N/A	N/A	N/A	N/A	0.130	N/A
IBH4	N/A	N/A	N/A	N/A	0.128	N/A
IBH5	N/A	N/A	N/A	N/A	0.132	N/A
IBW1	N/A	N/A	N/A	N/A	0.270	N/A
IBW2	N/A	N/A	N/A	N/A	0.280	N/A
IBW3	N/A	N/A	N/A	N/A	0.264	N/A
IBW4	N/A	N/A	N/A	N/A	0.260	N/A
IBW5	N/A	N/A	N/A	N/A	0.262	N/A

RH1	N/A	N/A	0.619	N/A	N/A	N/A
RH2	0.860	N/A	0.614	N/A	0.463	N/A
RH3	0.850	N/A	0.615	N/A	0.466	N/A
RH4	0.850	N/A	0.610	N/A	0.458	N/A
RH5	0.856	N/A	0.620	N/A	N/A	N/A
RW1	N/A	N/A	1.19	N/A	N/A	N/A
RW2	1.65	N/A	1.17	N/A	0.932	N/A
RW3	1.67	N/A	1.20	N/A	0.970	N/A
RW4	1.69	N/A	1.18	N/A	0.902	N/A
RW5	1.69	N/A	1.18	N/A	N/A	N/A

TABLE 16-Yale Peabody Museum Specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	85433	85432	16883
TAXON	*E. typus*	*E. typus*	*Delocrinus*[10]
CUP H	0.654	0.483	0.735
CUP W	1.43	0.970	2.09
STEM DIAMETER	0.290	0.150	0.502
BH1	N/A	0.258	N/A
BH2	0.346	0.264	N/A
BH3	N/A	N/A	N/A
BH4	N/A	N/A	N/A
BH5	N/A	0.262	N/A
BW1	N/A	0.356	N/A
BW2	0.456	0.336	N/A
BW3	N/A	N/A	N/A
BW4	N/A	N/A	N/A
BW5	N/A	0.342	N/A
IBH1	N/A	N/A	N/A
IBH2	N/A	N/A	N/A
IBH3	N/A	N/A	N/A
IBH4	N/A	N/A	N/A
IBH5	N/A	N/A	N/A
IBW1	N/A	N/A	N/A
IBW2	N/A	N/A	N/A

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[10] Specimen renamed to *Delocrinus* during this study; Yale Peabody Museum label reads *Erisocrinus typus.*

IBW3	N/A	N/A	N/A
IBW4	N/A	N/A	N/A
IBW5	N/A	N/A	N/A
RH1	N/A	0.228	N/A
RH2	N/A	N/A	N/A
RH3	0.446	N/A	N/A
RH4	0.440	N/A	N/A
RH5	0.450	N/A	N/A
RW1	N/A	0.503	N/A
RW2	N/A	N/A	N/A
RW3	0.858	N/A	N/A
RW4	0.860	N/A	N/A
RW5	0.862	N/A	N/A

TABLE 17-Yale Peabody Museum Specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	37177	53874A	53873B	53873C	53873D
TAXON	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*
CUP H	0.538	0.422	0.878	0.728	1.01
CUP W	1.47	0.794	2.42	2.08	2.60*(estimated)
STEM DIAMETER	0.250	0.127	N/A	0.414	0.425
BH1	N/A	N/A	N/A	N/A	0.656
BH2	N/A	N/A	N/A	N/A	N/A
BH3	N/A	N/A	N/A	N/A	N/A
BH4	N/A	N/A	0.663	N/A	N/A
BH5	N/A	N/A	N/A	N/A	N/A
BW1	N/A	N/A	N/A	N/A	0.884
BW2	N/A	N/A	N/A	N/A	N/A
BW3	N/A	N/A	N/A	N/A	N/A
BW4	N/A	N/A	0.930	N/A	N/A
BW5	N/A	N/A	N/A	N/A	N/A
IBH1	N/A	N/A	N/A	N/A	N/A
IBH2	N/A	N/A	N/A	N/A	N/A
IBH3	N/A	N/A	N/A	N/A	N/A
IBH4	N/A	N/A	N/A	N/A	N/A
IBH5	N/A	N/A	N/A	N/A	N/A
IBW1	N/A	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A
IBW3	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	N/A	N/A	N/A	N/A
IBW5	N/A	N/A	N/A	N/A	N/A

RH1	N/A	.250*(Estimated)	N/A	0.618	0.714
RH2	0.44	0.238	N/A	N/A	N/A
RH3	0.44	0.246	N/A	N/A	N/A
RH4	0.441	0.248	0.772	N/A	N/A
RH5	N/A	0.25	0.767	N/A	N/A
RW1	N/A	N/A	N/A	1.17	1.24
RW2	0.924	N/A	N/A	N/A	N/A
RW3	N/A	0.478	N/A	N/A	N/A
RW4	0.984	0.476	1.43	N/A	N/A
RW5	N/A	0.270	1.44	N/A	N/A
PBrH1	N/A	N/A	N/A	N/A	0.624
PBrH2	N/A	N/A	N/A	N/A	0.746
PBrW1	N/A	N/A	N/A	N/A	1.24
PBrW2	N/A	N/A	N/A	N/A	1.19

TABLE 18-Cincinnatti Museum Center specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal, PBr-primibrach. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	334	330	335	327	336	329
TAXON	E.*TYPUS*	E.*TYPUS*	E.*TYPUS*	E.*TYPUS*	E.*TYPUS*	E.*TYPUS*
CUP H	1.64* (estimated)	0.558	0.851	0.694	0.828	0.828
CUP W	0.884	0.782	1.46	1.13	1.18	1.27
STEM DIAMETER	N/A	0.144	0.288	0.228	0.260	0.278
BH1	0.584	0.302	0.528	0.468	0.5185	0.506
BH2	0.57	0.322	0.554	0.496	0.52	0.508
BH3	0.532	0.308	0.534	N/A	0.506	0.520
BH4	0.514	0.317	536	0.468	0.524	0.472*(estimated
BH5	0.562	0.292	0.510	0.492	0.572	0.490
BW1	0.668	0.348	0.638	0.500	0.540	0.626
BW2	0.676	0.342	0.600	0.520	0.582	0.668
BW3	0.690	0.324	0.612	N/A	0.675	0.663
BW4	0.652	0.349	0.648	0.542	0.707	.612*(estimated)
BW5	0.666	0.346	0.648	0.518	0.614	0.622
IBH1	0.240	N/A	N/A	N/A	N/A	N/A
IBH2	N/A	N/A	N/A	N/A	N/A	N/A
IBH3	N/A	N/A	N/A	N/A	N/A	N/A
IBH4	N/A	N/A	N/A	N/A	N/A	N/A
IBH5	N/A	N/A	N/A	N/A	N/A	N/A
IBW1	0.324	N/A	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A	N/A
IBW3	N/A	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	N/A	N/A	N/A	N/A	N/A

IBW5	N/A	N/A	N/A	N/A	N/A	N/A
RH1	0.570	0.314	0.583	0.440	0.502	0.498
RH2	0.546	0.318	0.596	0.438	0.458	0.564
RH3	0.518	0.328	0.572	0.460	0.594	0.496
RH4	0.516	0.298	0.517	0.458	0.576	0.582
RH5	0.577	0.280	0.552	0.443	0.514	0.510
RW1	1.02	0.5365	0.996	0.76	1.08	0.930
RW2	0.982	0.548	1.06	0.76	0.862	0.935
RW3	0.970	0.540	1.16	0.746	1.03	0.930
RW4	1.10	0.522	0.998	0.660	0.926	0.921
RW5	0.960	0.550	1.42	0.674	0.938	0.930
PBrH1	N/A	N/A	N/A	N/A	N/A	0.622
PBrH2	N/A	N/A	N/A	N/A	N/A	0.555
PBrH3	N/A	N/A	N/A	N/A	N/A	N/A
PBrH4	N/A	N/A	N/A	N/A	N/A	N/A
PBrH5	N/A	N/A	N/A	N/A	N/A	N/A
PBrW1	N/A	N/A	N/A	N/A	N/A	0.994
PBrW2	N/A	N/A	N/A	N/A	N/A	0.982
PBrW3	N/A	N/A	N/A	N/A	N/A	N/A
PBrW4	N/A	N/A	N/A	N/A	N/A	N/A
PBrW5	N/A	N/A	N/A	N/A	N/A	N/A

TABLE 19-Indiana University at Bloomington specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal, PBr-primibrach. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	316	325	331	313	324	321
TAXON	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*
CUP H	0.554	0.512	0.57	0.376	0.548	0.458
CUP W	0.914	0.804	0.84	0.714	1.16	0.804
STEM DIAMETER	N/A	0.200	0.206	0.136	0.182	0.18
BH1	0.362	N/A	0.385	0.245	0.392	0.26
BH2	0.402	N/A	0.376	0.258	0.372	0.259
BH3	0.351	N/A	0.332	0.256	0.386	0.266
BH4	0.360	N/A	0.388	0.248	0.362	0.270
BH5	0.348	N/A	0.384	0.246	0.394	0.266
BW1	0.452	N/A	0.406	0.288	0.434	0.310
BW2	0.430	N/A	0.420	0.294	0.450	0.324
BW3	0.464	N/A	0.454	0.306	0.484	0.310
BW4	0.440	N/A	0.452	0.308	0.498	0.322
BW5	0.448	N/A	0.420	0.320	0.498	0.301
IBH1	N/A	N/A	N/A	N/A	N/A	N/A
IBH2	N/A	N/A	N/A	N/A	N/A	N/A
IBH3	N/A	N/A	N/A	N/A	N/A	N/A
IBH4	N/A	N/A	N/A	N/A	N/A	N/A
IBH5	N/A	N/A	N/A	N/A	N/A	N/A
IBW1	N/A	N/A	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A	N/A
IBW3	N/A	N/A	N/A	N/A	N/A	N/A
IBW4	N/A	N/A	N/A	N/A	N/A	N/A
IBW5	N/A	N/A	N/A	N/A	N/A	N/A

RH1	0.354	N/A	0.358	0.242	0.410	N/A
RH2	0.378	N/A	0.338	0.254	0.430	0.280
RH3	0.376	N/A	0.358	0.248	0.415	0.278
RH4	0.386	N/A	0.334	0.238	0.388	0.276
RH5	0.388	N/A	0.332	0.208	0.400	0.280
RW1	0.618	N/A	0.630	0.446	0.734	N/A
RW2	0.620	N/A	0.682	0.435	0.724	0.510
RW3	0.626	N/A	0.692	0.430	0.704	0.514
RW4	0.625	N/A	0.680	0.428	0.684	0.498
RW5	0.600	N/A	0.656	0.428	0.738	0.476
PBrH1	N/A	N/A	N/A	N/A	N/A	0.364
PBrH2	N/A	N/A	N/A	N/A	N/A	0.394
PBrH3	N/A	0.532	N/A	N/A	N/A	0.392
PBrH4	N/A	0.554	N/A	N/A	N/A	0.378
PBrH5	N/A	N/A	N/A	N/A	N/A	0.372
PBrW1	N/A	N/A	N/A	N/A	N/A	0.488
PBrW2	N/A	N/A	N/A	N/A	N/A	0.510
PBrW3	N/A	0.396	N/A	N/A	N/A	0.514
PBrW4	N/A	0.584	N/A	N/A	N/A	0.498
PBrW5	N/A	N/A	N/A	N/A	N/A	0.476

TABLE 20-Indiana University at Bloomington specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal, PBr-primibrach. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	319	317	320	311	315	323
TAXON	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*	*E. typus*
CUP H	0.626	0.276	0.266	0.328	0.285	0.299
CUP W	1.10	0.491	0.546	N/A	0.446	0.486
STEM DIAMETER	0.22	0.101	0.100	N/A	0.074	N/A
BH1	0.406	N/A	0.168	N/A	N/A	N/A
BH2	0.400	N/A	N/A	N/A	N/A	N/A
BH3	0.402	N/A	N/A	N/A	N/A	N/A
BH4	0.406	N/A	N/A	N/A	N/A	N/A
BH5	0.402	N/A	N/A	N/A	N/A	N/A
BW1	0.502	N/A	0.212	N/A	N/A	N/A
BW2	0.490	N/A	N/A	N/A	N/A	N/A
BW3	N/A	N/A	N/A	N/A	N/A	N/A
BW4	N/A	N/A	N/A	N/A	N/A	N/A
BW5	0.482	N/A	N/A	N/A	N/A	N/A
IBH1	N/A	N/A	N/A	N/A	N/A	N/A
IBH2	N/A	N/A	N/A	N/A	N/A	N/A
IBH3	N/A	N/A	N/A	N/A	N/A	N/A
IBH4	N/A	N/A	N/A	N/A	N/A	N/A
IBH5	N/A	N/A	N/A	N/A	N/A	N/A
IBW1	N/A	N/A	N/A	N/A	N/A	N/A
IBW2	N/A	N/A	N/A	N/A	N/A	N/A
IBW3	N/A	N/A	N/A	N/A	N/A	N/A

IBW4	N/A	N/A	N/A	N/A	N/A	N/A
IBW5	N/A	N/A	N/A	N/A	N/A	N/A
RH1	0.408	N/A	0.172	N/A	N/A	N/A
RH2	0.402	N/A	0.168	N/A	N/A	N/A
RH3	0.400	0.168	0.172	N/A	N/A	N/A
RH4	NA	N/A	0.172	N/A	N/A	N/A
RH5	0.358	N/A	N/A	N/A	N/A	N/A
RW1	0.702	N/A	0.280	N/A	N/A	N/A
RW2	0.704	N/A	0.282	N/A	N/A	N/A
RW3	0.714	0.288	0.289	N/A	N/A	N/A
RW4	NA	N/A	0.312	N/A	N/A	N/A
RW5	0.722	N/A	N/A	N/A	N/A	N/A
PBrH1	0.506	0.284	N/A	0.306	0.312	0.386
PBrH2	0.454	0.308	N/A	N/A	0.364	0.344
PBrH3	0.455	0.312	N/A	N/A	0.332	N/A
PBrH4	0.468	0.308	N/A	N/A	0.264	0.368
PBrH5	0.702	0.328	N/A	N/A	0.286	0.332
PBrW1	0.702	0.314	N/A	0.332	0.298	0.350
PBrW2	0.718	0.348	N/A	N/A	0.286	0.324
PBrW3	N/A	N/A	N/A	N/A	N/A	0.350
PBrW4	N/A	0.330	N/A	N/A	0.310	0.348
PBrW5	0.722	0.330	N/A	N/A	0.286	0.350

TABLE 21-Indiana University at Bloomington specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal, PBr-primibrach. Numbers 1-5 self-designated, due to lack of information about A-E rays.

SAMPLE #	4566	4552	4565	3995	3994
TAXON	*E. mediator* Holotype	*E. mediator* paratype	*E. terminalis*	*E. terminalis* paratype	*E. terminalis* holotype
CUP H	0.694	0.542	0.45	0.465	0.572
CUP W	1.59	1.33	1.38	1.51	1.78
STEM DIAMETER	0.308	0.25	0.206	0.218	0.2865
BH1	0.416	N/A	0.324	N/A	0.390
BH2	0.432	N/A	0.285	N/A	0.370
BH3	0.454	N/A	0.310	N/A	0.382
BH4	0.430	0.376	0.306	N/A	0.322
BH5	N/A	N/A	0.310	N/A	0.344
BW1	0.494	N/A	0.378	N/A	0.484
BW2	0.518	N/A	0.408	N/A	0.530
BW3	0.520	N/A	0.432	N/A	0.528
BW4	0.510	0.416	0.367	N/A	0.480
BW5	N/A	N/A	0.420	N/A	0.372
IBH1	0.212	0.138	0.142	N/A	0.1815
IBH2	0.202	0.158	0.150	N/A	0.206
IBH3	0.192	0.1515	0.1425	N/A	0.182
IBH4	0.208	0.150	0.142	N/A	0.170
IBH5	0.238	0.165	0.140	N/A	0.167
IBW1	0.288	0.2165	0.190	N/A	0.258
IBW2	0.256	0.215	0.186	N/A	0.284
IBW3	0.256	0.228	0.1865	N/A	0.2565

IBW4	0.230	0.24	0.190	N/A	0.256
IBW5	0.298	0.220	0.194	N/A	0.258
RH1	0.592	0.474	0.446	0.53	0.550
RH2	0.564	0.470	0.454	N/A	0.468
RH3	0.574	N/A	0.416	N/A	0.501
RH4	0.578	0.48	0.420	N/A	0.560
RH5	0.588	N/A	0.420	N/A	0.550
RW1	0.850	0.788	0.834	0.892	1.088
RW2	0.906	0.798	0.802	N/A	1.08
RW3	0.908	N/A	0.816	N/A	1.11
RW4	0.902	0.808	0.860	N/A	1.06
RW5	0.900	N/A	0.830	N/A	1.08
PBrH1	N/A	N/A	N/A	N/A	N/A
PBrH2	N/A	N/A	N/A	N/A	N/A
PBrH3	N/A	N/A	N/A	N/A	N/A
PBrH4	N/A	N/A	N/A	N/A	N/A
PBrH5	N/A	N/A	N/A	N/A	N/A
PBrW1	N/A	N/A	N/A	N/A	N/A
PBrW2	N/A	N/A	N/A	N/A	N/A
PBrW3	N/A	N/A	N/A	N/A	N/A
PBrW4	N/A	N/A	N/A	N/A	N/A
PBrW5	N/A	N/A	N/A	N/A	N/A

TABLE 22-Sam Noble Museum specimens. H-height, W-width, R-radial, B-basal, IB-Infrabasal, PBr-primibrach. Numbers 1-5 self-designated, due to lack of information about A-E rays[11].

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[11] *E. wapunucka* was included; plate sutures were so faint, however, published measurements of the holotype were used in this study for accuracy (Strimple, 1961)

Appendix IV

Ratios of Cup Height to Other Measurements of *Erisocrinus* Species

(Arranged by Species)

Species	RH: CH	RW:CH	BH: CH	BW: CH	SD: CH
E. longwelli	0.699	1.234	0.758	1.022	0.494
E. knoxvillensis	0.800	1.517	0.783	0.833	0.483
E. terminalis	0.902	1.873	0.657	0.888	0.479
E. typus	0.715	1.249	0.633	0.769	0.444
E. georgeae	1.232	1.892	0.800	0.815	0.450
E. erectus	0.733	1.349	0.639	0.837	0.430
E. elevatus	0.685	1.185	1.435	0.924	0.402
E. obovatus	0.921	1.658	1.039	0.987	0.368
E. wapunucka	0.922	1.372	0.686	0.686	0.451
E. healdae	0.702	1.128	0.915	0.638	0.809

TABLE 23-Average ratios for all species of *Erisocrinus* used in principal component analysis