


Examining the ontogeny of the Pennsylvanian cladid crinoid *Erisocrinus typus* Meek and Worthen, 1865

Noel J. Hernandez Gomez,^{1,2,^} Lisette E. Melendez,^{1,3,^} Whitney A. Lopic,¹ Sarah L. Sheffield,^{1*}  and Ronald D. Lewis⁴

¹School of Geosciences, University of South Florida, 4202 E. Fowler Ave., NES 107, Tampa, FL 33620, USA <ssheffield2@usf.edu>, <lopicwa@gmail.com>

²Department of Earth and Planetary Sciences, University of Tennessee, 1621 Cumberland Ave., 602 Strong Hall, Knoxville, TN 37996, USA <nherna13@vols.utk.edu>

³Department of Earth, Atmospheric, and Planetary Sciences, Purdue University, 610 Purdue Mall, West Lafayette, IN 47904, USA <melendl@purdue.edu>

⁴Department of Geosciences, Auburn University, Beard-Eaves Memorial Coliseum, 2050, Auburn, AL 36849, USA <lewisrd@auburn.edu>

Non-technical Summary.—Crinoids, the group known today as the sea lilies, were a major constituent of ocean environments from the late Carboniferous (323–299 million years ago). However, crinoid fossil-forming potential is poor, and they typically fell apart quickly after death. This limits our ability to study much about their life histories, including how they would have grown. Through the discovery of an area of exceptional fossil preservation in the Barnsdall Formation of Oklahoma, we have a rare chance to learn about the growth of one of these species of crinoids, *Erisocrinus typus*. Here we perform a growth analysis of a well-preserved series of fossils and discuss the patterns that it showed from its juvenile stage to adulthood.

Abstract.—Crinoids were major constituents of late Carboniferous (Pennsylvanian) marine ecosystems, but their rapid disarticulation rates after death result in few well-preserved specimens, limiting the study of their growth. This is amplified for cladids, who had among the highest disarticulation rates of all Paleozoic crinoids due to the relatively loose suturing of the calyx plates. However, *Erisocrinus typus* Meek and Worthen, 1865 has been found in unusually large numbers, most preserved as cups but some as nearly complete crowns, in the Barnsdall Formation in Oklahoma. The Barnsdall Formation, a Konzentrat Lagerstätte, is composed predominantly of fine- to medium-grained sandstone, overlain by mudstone and shale; severe compaction of the fossils in the mudstone and shale layer in this formation allowed for exceptional preservation of the plates. Herein, we summarize a growth study based on 10 crowns of *E. typus*, showcasing a well-defined growth series of this species from the Barnsdall Formation, including fossils from juvenile stages of development, which are rarely preserved. We used high-resolution photographs imported into ImageJ and recorded measurements of the cup and arms for all nondistorted or disarticulated plates. Results show that the plates of the cup grew anisometrically with both positive and negative allometry. The primibrachial plates of *E. typus* grew with positive allometry. The brachial plates started as uniserial (i.e., cuneiform) as juveniles but shifted to be biserial. *Erisocrinus typus* broadly shares similar growth trajectories with other cladids. These growth patterns provide insight into feeding strategies and can aid in understanding crinoid evolutionary paleoecological trends.

Introduction

Although crinoids were a major component of Paleozoic marine communities (Sepkoski, 1981; Simms, 1999), there are gaps in our knowledge of a number of species' systematics, morphology, and ontogeny due to a differential preservation potential among different crinoid clades, causing many taxa to have few complete, well-preserved specimens across multiple growth stages. Crinoid

skeletons are composed of numerous calcareous plates that are connected by soft tissues (i.e., muscles and ligaments); after death, the crinoid is prone to rapid disarticulation as the muscles and ligaments decay (Brett et al., 1997; Thomka et al., 2011). As a result, there is a distinct lack of articulated crinoid skeletons in the fossil record, which has hampered investigations regarding ontogeny (Meyer, 1971; Liddell, 1975; Thomka et al., 2011). However, not all crinoids have the same disarticulation potential due to differences in their construction. Camerate crinoids have tight suturing of the plates of the calyx, and the arms are incorporated into the cup by interrachial and interbrachial plates, which results in a relatively high percentage of crown preservation (Brower, 1974; Brower and Venous, 1978). Compared with the

[^]These authors contributed equally to this study and can both list themselves as first author in their CVs.

*Corresponding author



camerates, cladid crinoids have looser suturing of the plates of the calyx and a lack of interradiol and interbrachial plates, allowing the arms to fall away from the cup soon after death as the muscles and ligamentary tissues holding them together begin to decay (Liddell, 1975; Ubaghs, 1978; Ausich and Baumiller, 1993; Kammer and Ausich, 2007; Brower, 2010; Thomka et al., 2012). Cladid taxa are often represented by single specimens (e.g., Sheffield, 2015) and complete, preserved growth series are much scarcer compared with other subclasses of the class Crinoidea (Brower, 1974; Ausich and Wood, 2012).

The lack of well-preserved collections of cladids places limitations on what can be learned from them. However, the discovery of crinoid-bearing Lagerstätten, fossil deposits of exceptional preservation (Seilacher, 1970), can often provide a more complete picture of fossil crinoids than is usually seen. The Barnsdall Formation, exposed near Copan, Oklahoma, USA (Fig. 1), is a Konzentrat-Lagerstätte with a rich diversity of Late Pennsylvanian crinoids (Oakes, 1951; Lewis et al., 1998; Thomka, 2010; Thomka et al., 2011). The crinoids in the Barnsdall Formation were preserved largely via rapid burial from distal storm events in an area that essentially lacked background sedimentation. In such deposits, burial allows organisms to be shielded from natural processes that actively degrade them. Rapid burial by storm events heightens the chances of exceptional fossil preservation because the organism is protected from scavenging and destruction by macro- and microorganisms due to the depth and anaerobic conditions (McMahon et al., 2016; Muscente et al., 2017; Parry et al., 2018).

The Barnsdall Formation has yielded more than 1,000 cladid crinoid fossils across a number of species and genera, providing a

rare look into Pennsylvanian crinoid diversity. While many of these specimens are preserved as simple cups, there are a number of complete crowns from a full ontogenetic range. In this study, we examine one such ontogenetic range from *Erisocrinus typus* Meek and Worthen, 1865 (Fig. 2), a Pennsylvanian cladid crinoid with a dicyclic cup, mild basal concavity, smooth cup surface, and small, circular stem facet (Sheffield, 2013). As noted in the preceding (Ubaghs, 1978; Thomka et al., 2012), cladid crinoids are less likely to be fossilized due to their weak suturing, but *Erisocrinus* has a significantly higher preservation potential compared with other cladid crinoids. This is shown in studies performed at the genus level using bulk samples of the Wann and the Barnsdall formations (Lewis, 1986; Thomka, 2010). Higher preservation potential, combined with ideal preservation conditions, has yielded a series of 10 crowns belonging to *Erisocrinus* recovered from the Barnsdall Formation (Oklahoma, USA), which provides insight into the ontogeny of late Paleozoic crinoids that are rarely found in high enough numbers to study in such detail. It is notable that the series includes an ontogenetic sequence with multiple juvenile specimens, which are even less common than the typical cladid specimen, considering their small size, thin plates, and typically poorly sutured calyx plates (Strimple, 1977; Ausich and Göncüoğlu, 2020).

Background

Barnsdall Formation.—The Upper Pennsylvanian (Missourian) Barnsdall Formation is exposed in northeastern Oklahoma near the small town of Copan in Washington County (36°55′24.58″N, 95°54′56.51″W; Fig. 1). The Barnsdall

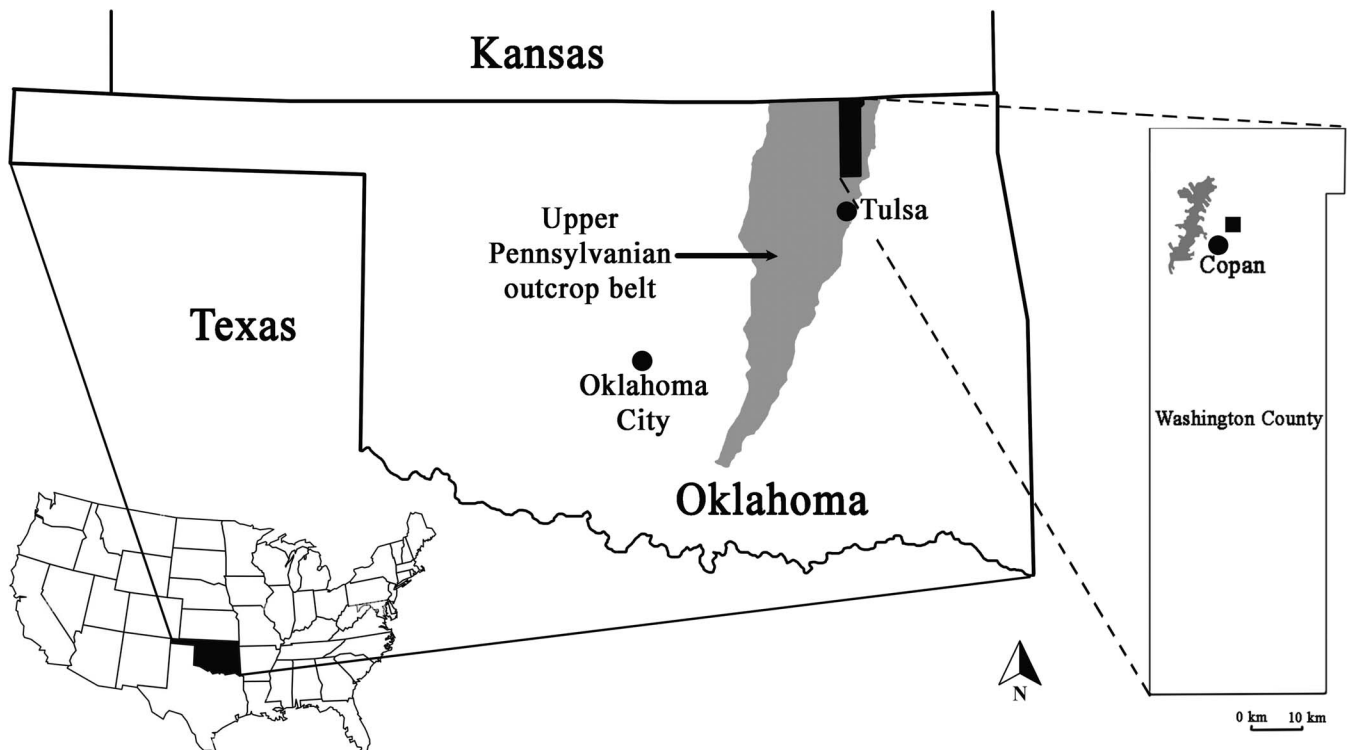


Figure 1. Map of the location of the Barnsdall Formation (black square), a crinoid-bearing Lagerstätte near Copan, Oklahoma, USA (modified from Thomka et al., 2011).

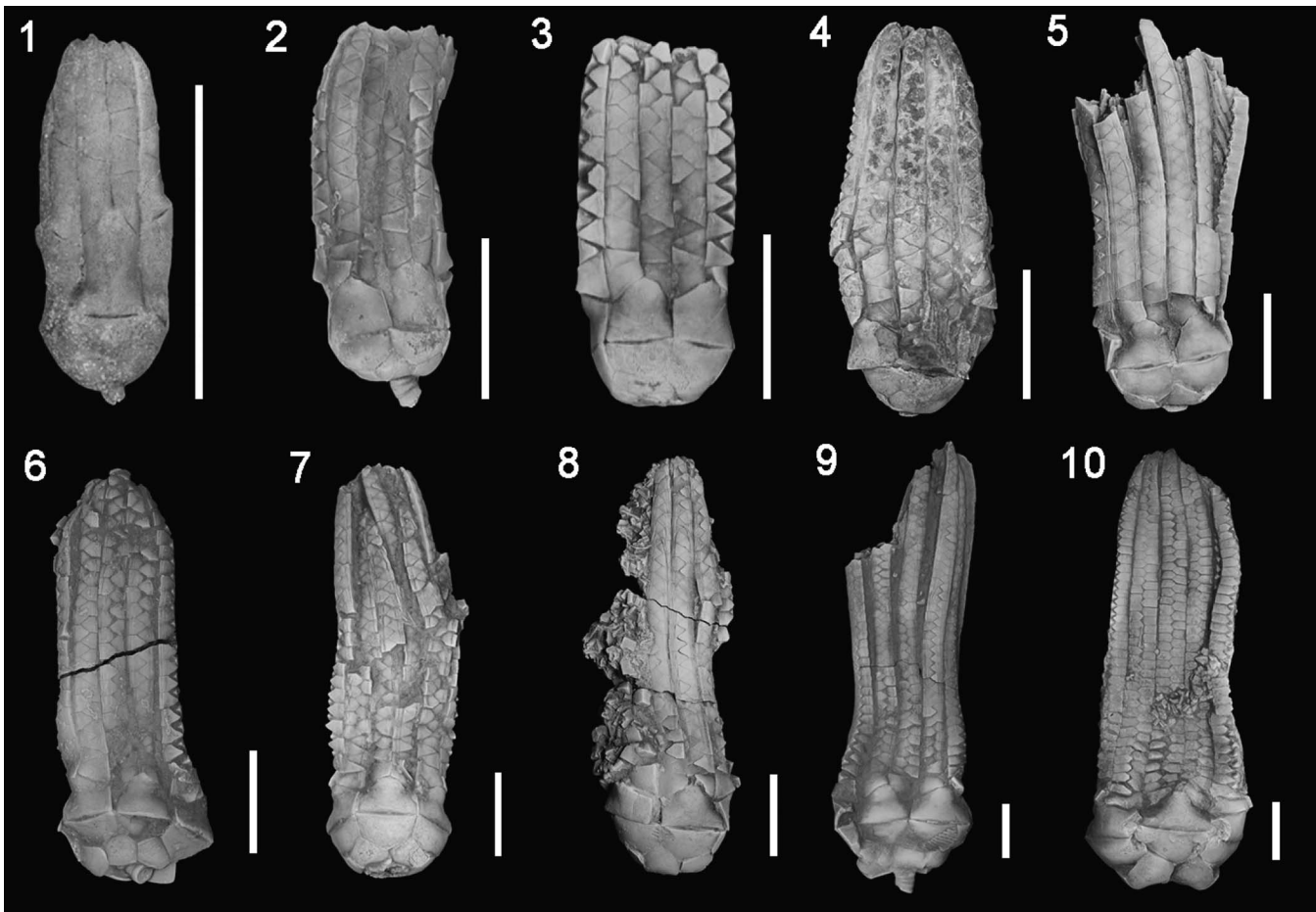


Figure 2. Growth series of *Erisocrinus typus*. The fossils are organized from most juvenile (1) to adult (10). In its juvenile stage, *E. typus* (1, 2) had uniserial brachial plates and a rounded cup; as the crinoid matured, the brachial plates became biserial and the infrabasal plates became invaginated, which are obscured from view in these specimens due to lateral compaction of the theca. Specimens whitened with ammonium chloride sublimated. (1) UNSM 36189. (2) UNSM 36190. (3) UNSM 36191. (4) UNSM 36192. (5) UNSM 36193. (6) UNSM 36194. (7) UNSM 36195. (8) UNSM 36196. (9) UNSM 36197. (10) UNSM 36198. Scale bars = 10 mm.

Formation, with its exceptional preservation of the delicate, multi-element crinoid skeletons, allows for unique insight into the variability of crinoids at low taxonomic levels. The 10 crinoid specimens studied in this paper were retrieved from a mudstone-dominated interval measuring approximately 50 cm in thickness (Thomka, 2010). This interval's paleoenvironment is characterized by muddy substrates, oxygenated bottom waters, and slow sedimentation rates (Holterhoff, 1997; Lewis et al., 1998; Thomka et al., 2011). After rapid burial from obrution events (Thomka et al., 2011), many crinoids within the unit were also preserved through post-depositional compaction, which encapsulated these crinoid communities into sequential layers.

Within the Barnsdall Formation, the majority (approximately 91%) of the preserved crinoids are cladids and within that area a number of cladid genera, dominated by *Erisocrinus*, *Apographiocrinus*, *Stellarocrinus*, *Stenopecrinus*, *Galateacrinus*, and *Exocrinus* (Thomka et al., 2011). Taphonomic processes can help explain both the distribution of each of these genera (i.e., how commonly each of them is preserved) and the likelihood of their complete preservation. While a full description of the genus-level taphonomic variation can be found in Thomka et al. (2011), the major controls can be

explained first by the flexibility the cup would have had during life and second by the type of compaction it experienced. Genera with more tightly sutured cups would likely have rotated slightly during compaction (oblique compaction). The rotation would have allowed the cup to have been preserved, commonly unaltered, but would have caused a separation of the cup from the arms and subsequent loss of the arm. In contrast to that, those genera with more flexible suturing between the thin cup plates, such as *Erisocrinus*, were more often found laterally compacted, parallel to the long axis of the crown, which resulted in a greater possibility of arm-plate retention (Thomka, 2010; Thomka et al., 2011). This lateral compaction allows the study of ontogenetic trends as the majority of plates and arms are well preserved and not distorted in two dimensions, although measurements involving cup width are unreliable due to cup distortion during compaction.

Previous studies concerning cladid ontogeny.—There are few studies concerning the ontogeny of cladid crinoids from the Middle or Late Pennsylvanian (Peters and Lane, 1990), and many of them are limited by a lack of specimens from the smallest sizes (Strimple, 1977). While studies on cladids have generally been more limited, some ontogenetic studies have

been published over the past 50 years (e.g., Strimple, 1977; Pabian and Strimple, 1979; Lewis and Strimple, 1990; Peters and Lane, 1990; Ausich and Wood, 2012). These studies provided a range of qualitative and quantitative growth studies. Strimple (1977) described rare juvenile specimens of Pennsylvanian crinoids in the genus *Stenopecrinus*, where even an extremely limited number of specimens showed clear differential rates of growth in plates of the cup. Pabian and Strimple (1979) found that *Cibolocrinus conicus* Strimple, 1951 showed clear anisometric change in the shape of the cup as it grew, with some changes in the number of plates in the circlets. Lewis and Strimple (1990) qualitatively described ontogenetic changes in the shape of the cup and in arm branching patterns in *Sciadiocrinus*. Peters and Lane (1990) performed an ontogenetic study of a series of five moderately well-preserved *Erisocrinus typus* specimens from the Millersville Limestone of eastern Illinois, USA (although the arms were incomplete). Through their analysis, Peters and Lane (1990) concluded that *E. typus* grew with virtually no change in the shape of either the plates of the cup or the cup itself (i.e., it grew isometrically), with the exception being the arms, which grew much taller first and then widened later. Peters and Lane (1990) also found that *Apographiocrinus* grew in a similar manner. Other work found that cladid species grew with a combination of allometry and isometry, with the isometry being limited to the plates of the cup and allometry in the feeding arm structures, such as in the Mississippian crinoid *Hypselocrinus hoveyi* (Ausich and Wood, 2012).

Materials and methods

Materials.—The specimens of *Erisocrinus typus* discussed here are part of a larger group of 1,200 specimens of cladid crinoids collected from the middle portion of the Barnsdall Formation (Pabian et al., 1995). The growth series comprises 10 well-preserved crowns and ranges from juvenile (1.0 cm in height) to adult (7.6 cm in height) (Fig. 2).

Methods.—Both sides of each *Erisocrinus typus* specimen were used in this study. Each side was whitened using ammonium chloride sublimated to highlight plate suture boundaries and then photographed with scale using a Nikon D850 camera. Images of each specimen were imported into ImageJ (Rasband, 2016); units were scaled to match the scale bar in the photograph before any measurements were taken to ensure consistency between measurements. The measurement parameters were determined on the basis of the maximum distance between the top and bottom, for height, and the maximum width possible for each plate of the cups and of the arms (Fig. 3). Only those plates that were complete and nondistorted were used in this study; due to lateral compaction, cup width was not a reliable measurement, and some radial and basal plates that sit on the sides of the cup could not be reliably measured. Due to the basal concavity in adult specimens of *Erisocrinus*, the infrabasals and the stem facet diameter were also not available for measurement as the lateral compaction caused distortion in the majority of the specimen's infrabasal plates. In addition, due to taphonomic

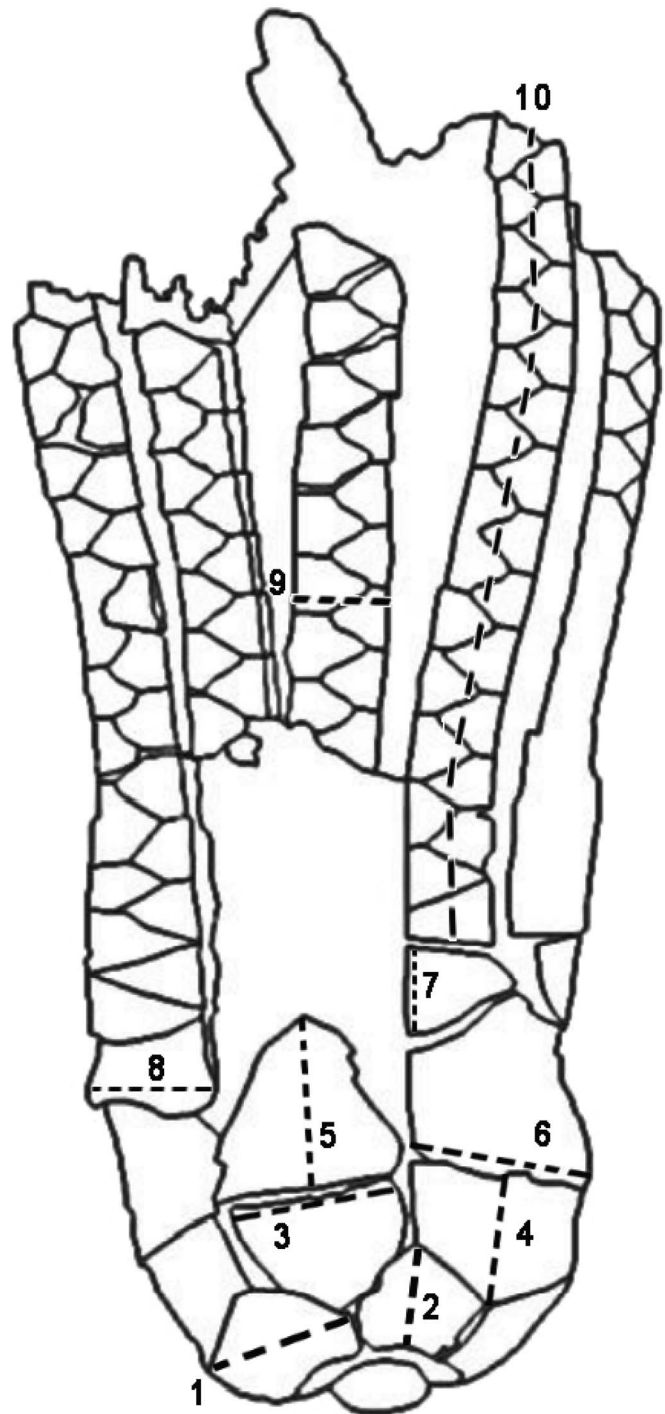


Figure 3. Measurement parameters for each plate as done in this study. Line drawing is based on UNSM 36193. (1) Basal plate width. (2) Basal plate height. (3) Radial plate width. (4) Radial plate height. (5) Primibrachial height. (6) Primibrachial width. (7) Secundibrachial height. (8) Secundibrachial width. (9) Arm width. (10) Arm length. Modified from Sheffield (2013).

features such as jumbling of the plates and loss of the distal tips of the arms (common taphonomic patterns documented by Thomka et al., 2011), some plates of the arms were also not measurable. The measurements taken include the following: the length and width of basal and radial plates; primibrachial length and width; brachial length, width, and area; and arm

width and length (see Supplemental Material for all measurements).

The averages of the radial, basal, primibrachial, and secundibrachial plates for each specimen were used to measure allometric growth. We used a Reduced Major Axis (RMA) model in the software PAST (Hammer et al., 2001, 2006), applied to the log-transformed data of the averaged measurements.

Repository and institutional abbreviation.—All specimens for this study are repositated at the University of Nebraska State Museum (UNSM).

Results

Here we report statistics related to the growth of the basal, radial, primibrachial, and secundibrachial plates to determine whether there are changes in the proportions of the morphological features of the specimens through ontogeny. Following Ausich and Wood (2012), we report the following statistics: the correlation coefficient r^2 ; the probability of no correlation ($p(\text{uncorr.})$), the probability of no correlation based on a

permutation test ($\text{permut } p$); and the probability that the slope of the line is one ($p(a) = 1$). We use these statistics to differentiate isometric (a slope of one) from allometric growth patterns and determine whether allometric growth is positive (a slope greater than one) or negative (a slope less than one).

Due to compaction and disarticulation, changes in the cup width and growth of the infrabasals could not be measured in this study. However, we can clearly see the cup outline change from a shape with a rounded bottom to a cup that is bowl shaped with basal concavity (Fig. 4). This is a common anisometric change within cladid crinoid growth (e.g., Mirantsev and Arendt, 2012).

We find that *E. typus* grew anisometrically in both the plates of the cup and in the arm structures, with a mixture of positive and negative allometric growth; the RMA analysis indicates that these results are significant and clearly distinguishable from isometric growth in nearly all of the measurements (Table 1). The basal plate width and height grew with positive allometry with respect to the height of the aboral cup. The basal plate width grew with slightly negative allometry with respect to basal plate height. The radial plate height and width

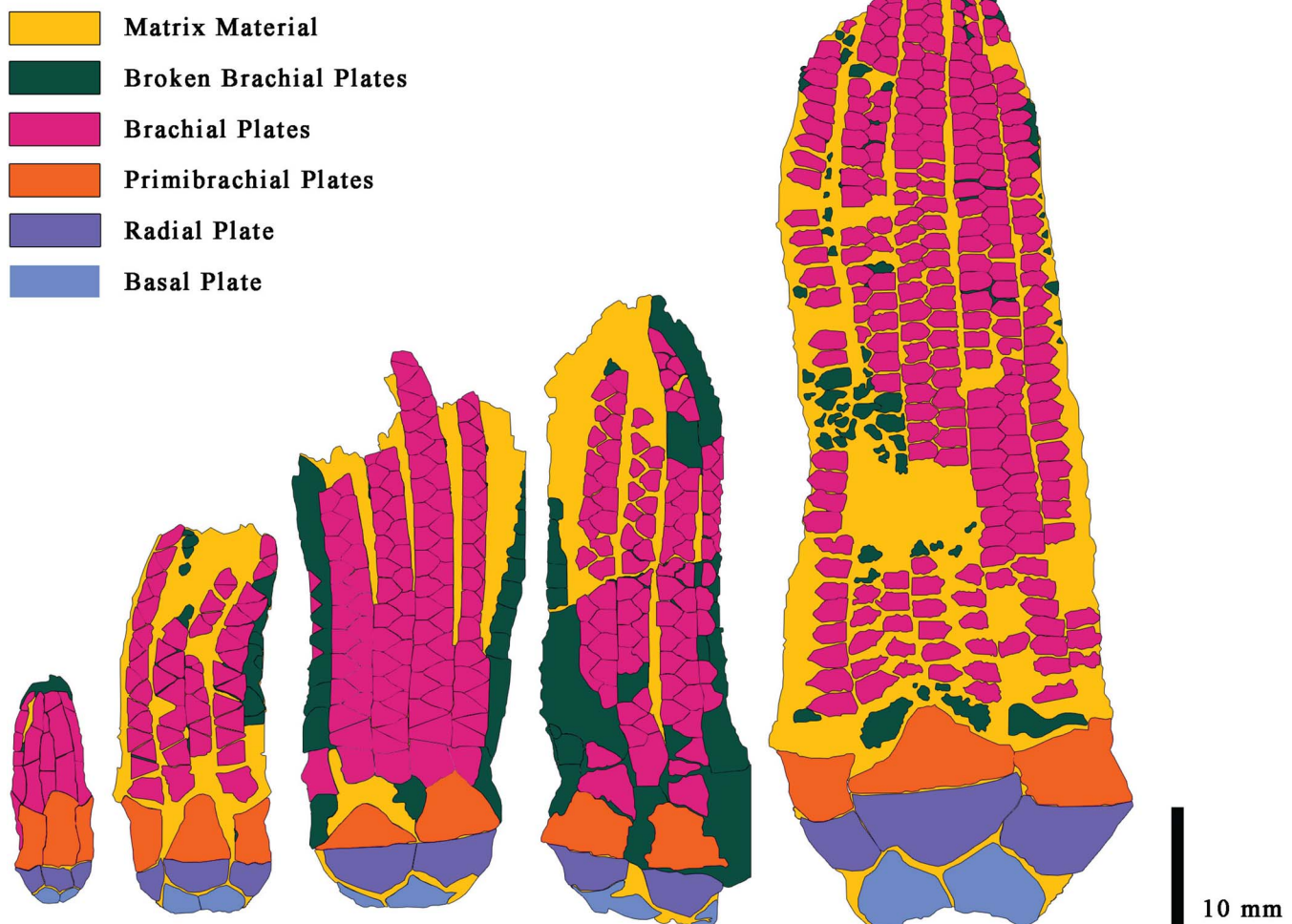


Figure 4. A simplified outline of five benchmark specimens (as imaged in Fig. 2.1, 2.2, 2.5, 2.8, 2.10) of the growth series of *E. typus*. Note the shape change of the primibrachial plates, which are taller than wide in juvenile stages and become wider than tall in the adult stages, likely to support the increased weight of the arm. The arms also transitioned from uniserial to biserial from juvenile to adult. Shape changes of the plates of the cup (i.e., the basal and radial plates) is subtle.

Table 1. Results from the RMA analysis in PAST. H = height; W = width; L = length; RP = radial plate; Cu = cup; BP = basal plate; PB = primibrachial plate; SB = secundibrachial plate; AR = arm.

Log Y axis	Log X axis	Slope	Y intercept	r ²	p (uncorr)	permut p	p (a = 1)
RP H	Cu H	1.003	-0.136	0.952	1.43 × 10 ⁻⁶	0.0002	1.18 × 10 ⁻⁶
RP W	Cu H	1.168	-0.006	0.934	5.44 × 10 ⁻⁶	0.0001	4.20 × 10 ⁻⁶
RP W	RP H	1.116	0.152	0.989	2.33 × 10 ⁻⁸	0.0001	2.17 × 10 ⁻⁸
BP H	Cu H	1.264	-0.332	0.921	1.12 × 10 ⁻⁵	0.0001	8.21 × 10 ⁻⁶
BP W	Cu H	1.24	-0.238	0.937	4.30 × 10 ⁻⁶	0.0001	3.37 × 10 ⁻⁶
BP W	BP H	0.981	0.088	0.99	2.67 × 10 ⁻⁹	0.0001	2.57 × 10 ⁻⁹
PB H	Cu H	0.505	0.318	0.912	1.68 × 10 ⁻⁵	0.0002	1.19 × 10 ⁻⁵
PB W	Cu H	1.214	-0.066	0.949	1.78 × 10 ⁻⁶	0.0001	1.46 × 10 ⁻⁶
PB W	PB H	2.406	-0.831	0.907	2.15 × 10 ⁻⁵	0.0001	1.50 × 10 ⁻⁵
SB H	Cu H	0.417	0.143	0.443	3.56 × 10 ⁻²	0.0343	5.31 × 10 ⁻³
SB W	Cu H	1.168	-0.373	0.801	4.03 × 10 ⁻⁵	0.0001	2.65 × 10 ⁻⁵
SB W	SB H	2.806	-0.772	0.329	8.26 × 10 ⁻²	0.0879	8.64 × 10 ⁻³
AR W	Cu H	0.993	-0.294	0.847	1.59 × 10 ⁻⁴	0.0001	8.90 × 10 ⁻⁵
AR L	Cu H	1.453	0.538	0.884	5.13 × 10 ⁻⁵	0.0001	3.292 × 10 ⁻⁵

grew with slight positive allometry with respect to cup height. The radial height grew with slight positive allometry with respect to radial width. The slight allometric growth means that the shape change of the overall plates is subtle (Fig. 4). All of these measurements are statistically significant, indicating that the growth is very unlikely to be isometric (Table 1).

In each of the specimens, one of the primibrachials is taller than the others in the cup. This taller primibrachial is interpreted as belonging to the A ray, which was added first in other related crinoids (Peters and Lane, 1990) and is therefore larger. Study of the specimens shows that the primibrachial plates grew in height faster than in width in young crinoids and then grew more wide than tall as the crinoid aged (Fig. 4). The growth of the primibrachial plate height and width as compared with the cup height is significantly anisometric; the primibrachial height grew with negative allometry with respect to the cup height, and the width grew with positive allometry. The growth of the primibrachial width with respect to primibrachial height indicates positive allometric growth, and this is statistically significant.

The secundibrachials began as uniserial in the most juvenile specimen and became biserial as the crinoid aged (Fig. 4). The first secundibrachial height grew with negative allometry with respect to cup height. The first secundibrachial width grew with positive allometry with respect to cup height. Both of these results are statistically significant. The first secundibrachial width with respect to the first secundibrachial height grew with positive allometry but is statistically insignificant and may not be distinguishable from isometric growth.

The total arm length also grew with positive allometry and changed from approximately four times to eight times the cup height. Arm width grew with negative allometric growth with respect to cup height.

Discussion

Previous studies of cladid crinoids, including *Erisocrinus typus*, have been limited due to the small number of well-preserved specimens (Lewis and Strimple, 1990), especially in juvenile samples; this means that many growth studies that have been performed have not been able to utilize a substantial ontogenetic sequence. Peters and Lane (1990) conducted a similar study to the one presented here on a smaller growth series of *E. typus* from five specimens of the Millersville Limestone of eastern

Illinois, USA. They concluded that the plates of the cup in *E. typus* grew isometrically, and the primibrachials of the arms grew anisometrically. However, with the broader range of ontogenetic stages in this study, the interpretation of *E. typus* growth changes. With the addition of more juvenile specimens, which were unavailable in the Peters and Lane (1990) study, the data show that the growth of the plates in both the cup and arms was anisometric. The plates of *E. typus* exhibited a mixture of positive allometric growth strategies, which is a similar growth strategy noted in other cladid crinoids and some disparid crinoids (Strimple, 1977; Peters and Lane, 1990; Ausich and Wood, 2012).

The primibrachial plates grew anisometrically, with the height and width increasing at different rates, indicating both negative and positive allometry, respectively. The primibrachials in the youngest specimens of *E. typus* are much higher than wide at first and then become much wider than tall through the ontogenetic sequence. This growth strategy is likely related to its paleoecology and possible evidence that the species described here could have employed limited mucus-net feeding (Ausich, 1980). Peters and Lane (1990) hypothesized that this pattern could be related to the establishment of the filtration fan mode; by having the height become established more quickly, this would allow for faster gains in the volume of water that the arms would have been able to filter. Later, the width increased, likely for higher strength of the arm. The fact that *E. typus* arms also shift from uniserial to biserial could be an indication of increasing surface area for greater feeding structures through growth. Growth patterns such as these have been documented in other late Paleozoic cladids as well (Peters and Lane, 1990; Ausich and Wood, 2012). This shift from uniserial to biserial arm elements has implications for understanding skeletal element origins and homologies, as well (Sumrall et al., 2023). Early crinoid arms are composed of axial floor plates and extraxial brachial elements (Guensburg et al., 2015); however, in more-derived crinoids, such as *Erisocrinus*, the axial plates are lost. When the extraxial arm elements become biserial, they mimic the ocular plate rule (where plates are added at the growing tip of a plate series, immediately proximal to a terminal ossicle or ocular plate; this type of terminal growth is typically recognized as evidence for presence of axial skeleton) and become nearly indistinguishable from axial skeleton (Kammer et al., 2013). This indicates that the definitions of axial and extraxial skeleton in echinoderms,

typically treated as separate entities, may be more complex (Sumrall et al., 2023).

The total arm length also exhibits positive allometry: the arm length increases from four times the cup height in the juvenile specimens to nearly eight times in the adult specimens. The increase in width occurs far less dramatically, and the width of the arm maintains relatively similar proportions from juvenile to adult. While the change in width is less dramatic, it does indicate, as Peters and Lane (1990) also stated, that individuals of *E. typus* may have fed on slightly differently sized food particles, and juveniles and adults were likely not in direct competition with one another.

Similar patterns of arm growth can be found in different cladid taxa across the early and later Paleozoic; in particular, one pattern that can be noted, shared between *Erisocrinus typus* and some Ordovician crinoids, is in the growth pattern of the first arm plate. Brower (2007) noted that in the Middle Ordovician cladid *Cupulocrinus plattevilensis* Kolata, 1975 that the width of the primibrachials exhibited positive allometric growth with respect to the height of the primibrachials, a pattern also seen in the growth of the primibrachials of *E. typus*, as discussed. Similar growth trajectories are also uncovered in the positive allometric growth observed in arm length throughout ontogeny (Brower, 1992), as seen in *E. typus* and in Ordovician cladids, such as *Cupulocrinus crossmani* Brower, 1992 and *Praecupulocrinus conjugans* (Billings, 1857). These growth patterns, shared between crinoids that had quite different morphologies (e.g., *C. crossmani* has branching arms, unlike *E. typus*), can likely provide further study into paleoecological trends in evolutionary history. Unfortunately, without complete stems of *E. typus* in the growth series presented in this study, full comparisons of how these crinoids across ontogenetic stages and geologic time may have subdivided niches in the water column cannot be fully explored at this time.

Quantifying the growth of crinoids can inform us of the feeding strategies that these organisms may have used. Research has shown that different arm morphologies can shed light on niche differentiation and community structures (e.g., Ausich, 1980; Kitazawa et al., 2007; Baumiller, 2008; Cole et al., 2019), which can certainly be used to better explore evolutionary paleoecological questions (Macurda, 1968; Lamsdell, 2021). In this study of the ontogeny of *E. typus*, we find that arms grew taller first and then wider, likely to increase its food gathering surface first and then wider to support the arm structure. The change in width of the arms also indicates that there was possibly some niche differentiation, and thereby reduced competition, in food resources, where juveniles and adults of *E. typus* may have preferentially accepted different sizes of food particles.

Conclusion

Lack of a detailed, well-preserved growth series of crinoids hampers our ability to fully quantify the growth trajectories used by extinct organisms. Juvenile specimens, which are less commonly preserved, add important information about these growth trajectories. A pristine growth series of Pennsylvanian-age *Erisocrinus typus* from the Barnsdall Formation (Oklahoma, USA) is an example of how adding new fossil data from a

broad ontogenetic range can change interpretations of their growth patterns. Earlier studies of *E. typus* found that the plates of the cup grew isometrically; by contrast, this study shows that the cup grew anisometrically with a combination of positive and negative allometry. The arms of *E. typus*, whose arm elements begin as uniserial and transition to biserial, increased in height at a rate far faster than the increase in width, which is an indication that the growth pattern would have allowed quicker establishment of a food-gathering surface and then a subsequent width increase to support the weight of the arm itself, a pattern seen in other crinoids. The change in width of the arms also indicates that there was possibly some niche differentiation, and thereby reduced competition, in food resources, where juveniles and adults of *E. typus* may have preferentially accepted different sizes of food particles. Many of these growth patterns are also seen in earlier Paleozoic cladid crinoids, as well. Ontogenetic data such as this can be added to the growing conversations of crinoid paleoecology and to studying overall phylogenetic ontogenetic and paleoecological trends in Paleozoic crinoids.

Acknowledgments

We thank R. Diffendal and G. Corner at the University of Nebraska State Museum for access to specimens. These specimens were originally collected by D. Mosher. Helpful comments on earlier drafts of this work were made by J. Bauer, B. Deline, L. Zachos, J. Bright, and D. King. We thank S. Zamora, J. Botting, V. Syverson, and an anonymous reviewer for their comments that improved this paper. This study was partially funded by a Geological Society of America student research grant awarded to S. Sheffield.

Declaration of competing interests

The authors declare none.

Data availability statement

All measurements of the specimens can be found in Supplementary Material 1. Alternative text of images can be found in Supplementary Material 2. Supplementary material available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.h18931zrx>.

References

- Ausich, W.I., 1980, A model for niche differentiation in Lower Mississippian crinoid communities: *Journal of Paleontology*, v. 54, p. 273–288.
- Ausich, W.I. and Baumiller, T.K., 1993, Taphonomic method for determining muscular articulations in fossil crinoids: *Palaios*, v. 8, p. 477–484.
- Ausich, W.I. and Göncüoğlu, M.C., 2020, Juvenile eucladid crinoid from the Middle Devonian of Turkey: *Geodiversitas*, v. 42, p. 215–221.
- 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.
- Baumiller, T., 2008, Crinoid ecological morphology: *Annual Review of Earth and Planetary Sciences*, v. 36, p. 221–249.
- Billings, E., 1857, New species of fossils from Silurian rocks of Canada: *Canada Geological Survey, Report of Progress 1853–1856, Report for the Year 1856*, p. 247–345.
- Brett, C., Moffat, H., and Taylor, W., 1997, Echinoderm taphonomy, taphofacies, and Lagerstätten, in Waters, J.A., and Maples, C.G., eds., *Geobiology of Echinoderms: Paleontological Society Papers*, v. 3, p. 147–190.

- Brower, J.C., 1974, Ontogeny of camerate crinoids: The University of Kansas Paleontological Contributions 72, 53 p.
- Brower, J.C., 1992, Cupulocrinid crinoids from the Middle Ordovician (Galena Group, Dunleith Formation) of northern Iowa and southern Minnesota: *Journal of Paleontology*, v. 66, p. 99–128.
- Brower, J.C., 2007, Upper Ordovician crinoids from the Platteville Limestone of Northeastern Iowa: *Journal of Paleontology*, v. 81, p. 103–115.
- Brower, J.C., 2010, Camerate and cladid crinoids from the Upper Ordovician (Katian, Shermanian) Walcott–Rust Quarry of New York: *Journal of Paleontology*, v. 84, p. 626–645.
- Brower, J.C., and Venous, J., 1978, Middle Ordovician crinoids from the Twin Cities area of Minnesota: *Bulletin of American Paleontology*, v. 74, p. 373–506.
- Cole, S.R., Wright, D.F., and Ausich, W.I., 2019, Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechtin Lagerstätte, Ordovician): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 521, p. 82–98.
- Guensburg, T.E., Blake, D.B., Sprinkle, J., and Mooi, R., 2015, Crinoid ancestry without blastozoans: *Acta Palaeontologica Polonica*, v. 61, p. 253–266.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, Past: paleontological statistics software package for education and data analysis: *Palaeontologia Electronica*, v. 4, no. 1, p. 1–9, http://palaeoelectronica.org/2001_1/past/issue1_01.htm.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2006, Past: paleontological statistics, version 1.32: University of Oslo, Norway.
- Holterhoff, P.F., 1997, Paleocommunity and evolutionary ecology of Paleozoic crinoids, in Waters, J.A., and Maples, C.G., eds., *Geobiology of Echinoderms: Paleontological Society Papers*, v. 3, p. 69–106.
- Kammer, T., and Ausich, W., 2007, Soft-tissue preservation of the hind gut in a new genus of cladid crinoid from the Mississippian (Visean, Asbian) at St Andrews, Scotland: *Palaeontology*, v. 50, p. 951–959.
- Kammer, T.W., Sumrall, C.D., Zamora, S., Ausich, W.I., and Deline, B., 2013, Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms: *PLoS ONE*, v. 8, p. e77989.
- Kitazawa, K., Oji T., and Sunamura, M., 2007, Food composition of crinoids (Crinoidea: Echinodermata) in relation to stalk length and fan density: their paleoecological implications: *Marine Biology*, v. 152, p. 959–968.
- Kolata, D.R., 1975, Middle Ordovician echinoderms from northern Illinois and southern Wisconsin: *Memoir 7, Paleontological Society Journal of Paleontology*, Pt. II of II, Supplement to v. 49, no. 3, 74 p.
- Lamsdell, J.C., 2021, The conquest of spaces: exploring drivers of morphological shifts through phylogenetic palaeoecology: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 583, p. 110672.
- Lewis, R.D., 1986, Relative rates of skeletal disarticulation in modern ophiuroids and Paleozoic crinoids: *Geological Society of America Abstracts with Programs*, v. 18, p. 672.
- Lewis, R.D., and Strimple, H.L., 1990, *Sciadiocrinus*, convergence on the family Pirasocrinidae (Crinoidea: Echinodermata): *Journal of Paleontology*, v. 64, p. 293–300.
- Lewis, R.D., Holterhoff, P.F., Mosher, D., and Pabian, R.K., 1998, Taphonomy of a crinoid Lagerstätte deposit, Barnsdall Formation (Upper Pennsylvanian), northeastern Oklahoma: *Geological Society of America Abstracts with Programs*, v. 30, p. 31.
- Liddell, W.D., 1975, Recent crinoid biostratigraphy: *Geological Society of America Abstracts with Programs*, v. 7, p. 1169.
- Macurda, D.B., 1968, Ontogeny of the crinoid *Eucalyptocrinites*: *Journal of Paleontology*, v. 42, p. 99–118.
- McMahon, S., Anderson, R.P., Saupe, E.E., and Briggs, D.E.G., 2016, Experimental evidence that clay inhibits bacterial decomposers: implications for preservation of organic fossils: *Geology*, v. 44, p. 867–870.
- Meek, F.B., and Worthen, A.H., 1865, Note in relation to a genus of crinoids [*Erisocrinus*] from the Coal Measures of Illinois and Nebraska: *American Journal of Science*, v. 39, p. 350.
- Meyer, D.L., 1971, Post-mortem disarticulation of recent crinoids and ophiuroids under natural conditions: *Geological Society of America Abstracts with Programs*, v. 3, p. 645.
- Mirantsev, G.V., and Arendt, Y.A., 2012, A new anobasicrinid (Crinoidea, Cladida) from the Upper Carboniferous of the Moscow Region: *Paleontological Journal*, v. 47, p. 470–479.
- Muscente, A.D., Schiffbauer, J.D., Broce, J., Laflamme, M., O'Donnell, K., et al., 2017, Exceptionally preserved fossil assemblages through geologic time and space: *Gondwana Research*, v. 48, p. 164–188.
- Oakes, M.C., 1951, The proposed Barnsdall and Tallant formations in Oklahoma: *Tulsa Geological Society Digest*, v. 19, p. 119–122.
- Pabian, R.K., and Strimple, H.L., 1979, Notes on biometrics, paleoecology and biostratigraphy of *Cibolocrinus conicus* Strimple from Oklahoma, Kansas and Nebraska: *Journal of Paleontology*, v. 53, 421–437.
- Pabian, R.K., Mosher, D., Lewis, R.D., and Holterhoff, P.F., 1995, Crinoid assemblage from the Barnsdall Formation, Late Pennsylvanian (Missourian), Washington County, Oklahoma: *Geological Society of America Abstracts with Programs*, v. 27, p. 78.
- Parry, L.A., Smithwick, F., Nordén, K.K., Saitta, E.T., Lozano-Fernandez, J., Tanner, A.R., Caron, J.-B., Edgecombe, G.D., Briggs, D.E.G., and Vinther, J., 2018, Soft-bodied fossils are not simply rotten carcasses—toward a holistic understanding of exceptional fossil preservation: *BioEssays*, v. 40, p. 1700167.
- Peters, J., and Lane, N.G., 1990, Ontogenetic adaptations in some Pennsylvanian crinoids: *Journal of Paleontology*, v. 64, p. 427–435.
- Rasband, W.S., 2016, Image J 1.50 i: Bethesda, Maryland, U.S. National Institutes of Health, <http://imagej.nih.gov/ij/>.
- Seilacher, A., 1970, Arbeitskonzept zur Konstruktions-morphologie: *Lethaia*, v. 3, p. 393–396.
- Sepkoski, J., 1981, A factor analytic description of the Phanerozoic marine fossil record: *Paleobiology*, v. 7, p. 36–53.
- Sheffield, S.L., 2013, The Pennsylvanian cladid crinoid *Erisocrinus*: ontogeny and systematics [M.S. thesis], Auburn, Alabama, Auburn University, 165 p.
- Sheffield, S.L., 2015, A brief history and revision of the systematics of the cladid crinoid *Sinocrinus*: *Palaeoworld*, v. 24, p. 460–469.
- Simms, 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*, Cambridge University Press, p. 31–40.
- Strimple, H.L., 1951, Some new species of Carboniferous crinoids: *Bulletins of American Paleontology*, v. 33, no. 137, 41 p.
- Strimple, H.L., 1977, A youthful specimen of *Stenopecrinus ornatus* (Crinoidea: Inadunata): *Journal of Paleontology*, v. 51, p. 423–424.
- Sumrall, C.D., Sheffield, S.L., Bauer, J.E., Thompson, J.R., and Waters, J.A., 2023, A review and evaluation of homology hypotheses in echinoderm paleobiology: *Elements of Paleontology*, 44 p.
- Thomka, J., 2010, Genesis and taphonomy of a crinoid Lagerstätte in the Upper Pennsylvanian Barnsdall Formation of northeastern Oklahoma [M.S. thesis]: Auburn, Alabama, Auburn University, 195 p.
- Thomka, J., Lewis R., Mosher D., Pabian R.K., and Holterhoff P., 2011, Genus-level taphonomic variation within cladid crinoids from the Upper Pennsylvanian Barnsdall formation, Northeastern Oklahoma: *Palaaios*, v. 26, p. 377–389.
- Thomka, J.R., Mosher, D., Lewis, R.D., and Pabian, R.K., 2012, The utility of isolated crinoid ossicles and fragmentary crinoid remains in taphonomic and paleoenvironmental analysis: an example from the Upper Pennsylvanian of Oklahoma, United States: *Palaaios*, v. 27, p. 465–480.
- Ubaghs, G., 1978, Skeletal morphology of fossil crinoids, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2: Lawrence, Kansas, and Boulder, Colorado, University of Kansas Press and Geological Society of America*, p. T58–T216.

Accepted: 23 May 2023