

# Contributions

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## **ATELESTOCRINUS BAUMILLERI, N. SP., A NEW EARLY MISSISSIPPIAN (VISÉAN) CRINOID, AND RELATED PSEUDOMONOCYCLIC FORMS**

BY

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*Abstract* — *Atelestocrinus* is a rare cladid crinoid that ranges from the Middle Devonian (Givetian) to Mississippian (Viséan) of Iran, Ireland, and North America. Unlike most crinoids, it has quadrangular symmetry, possessing only four arm-bearing rays; the anterior radial usually lacks an arm and associated facet. The type species of the genus is clarified as *Atelestocrinus robustus* Wachsmuth and Springer 1885, by monotypy. A lectotype is established for *A. robustus*. *Atractocrinus* and *Fiannacrinus* are synonyms of the genus. *Atelestocrinus indianensis* and *Atelestocrinus kentuckyensis* are likely monocyclic crinoids, but they are too poorly preserved to be reasonably diagnostic for any genus or species. They are considered *nomina dubia*. *Atelestocrinus baumilleri* is a new species from the Ramp Creek Formation of Montgomery, County, Indiana. Stratigraphically, it is the youngest known species of the genus. The only known specimen bears a regenerated ray that shows evidence of autotomy. Cooccurring with *A. robustus* and *A. baumilleri* are similar monocyclic forms, both of which violate the typical symmetry principles for crinoids. They are interpreted as pseudomonocyclic crinoids that have lost their basal circlets. *Belemnocrinus*, currently classified as a disparid, has likely been misdiagnosed for 160 years. Instead of possessing five arm-bearing radials, it has a radial circlet constructed of only four arm-bearing plates; the basals and anterior radial are entirely absent. It represents an extremely reduced developmental form of *Atelestocrinus* or its direct descendant. Patterns of symmetry suggest the cup base circlets of most monocyclic crinoids from the Paleozoic are better interpreted as infrabasals than basals.

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### INTRODUCTION

Wachsmuth and Springer pondered an unusual crinoid. They considered it abnormal until acquiring more specimens of the new genus, which they later named *Atelestocrinus* for the Greek ἀτελής, incomplete. Ironically, two of the three specimens they possessed were very complete for fossils, preserving fine details of the stem, dicyclic calyx, and arms. However, it is in this last trait *Atelestocrinus* is lacking. It has an anterior (or “A”) radial that fails to develop an arm, giving

the genus only four arm-bearing rays with eight arms total. Rather than having pentamerous symmetry typical of most crinoids, the crown of *Atelestocrinus* is quadrangular, though without perfect bilateral symmetry because of a posterior interray that includes three anal plates.

This armless radial not only puzzled Wachsmuth and Springer in the late 19<sup>th</sup> century, but it continues to generate confusion in the 21<sup>st</sup>. In a recent paper, focused on the anal plates of Paleozoic crinoids, Ausich et al. (2020: fig. 3) mistook the anterior side of the animal for its posterior,

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identifying the A radial as the radianal. As discussed near the end of this contribution, I made a similar mistake while considering a new population of crinoids from the Wassonville Formation of Iowa.

The first specimen in the possession of Wachsmuth and Springer was collected from the Early Mississippian (upper Tournaisian) Burlington Limestone of Iowa. They named it *Atelestocrinus delicatus* Wachsmuth and Springer, 1896. They assigned the other two specimens to a second species, *Atelestocrinus robustus* Wachsmuth and Springer, 1895 (Figs. 1A–F, I; 2A) with one specimen each from the Burlington Limestone of Iowa and the lower Viséan Fort Payne Formation of Tennessee. The latter specimen is figured here for the first time (Fig. 1B–F). McIntosh (1983: pl. 26, fig. 7) recognized a third specimen of *A. robustus* from the Burlington Limestone, but despite the thousands of crinoids amassed from this formation since the 19<sup>th</sup> century, no additional specimens of *A. delicatus* or *A. robustus* are known.

Two additional North American species were later described from rocks of similar age, *Atelestocrinus indianensis* Ausich and Lane, 1982 (Fig. 3) from the Edwardsville Formation (Viséan) and *Atelestocrinus kentuckyensis* Lee, Ausich, and Kammer, 2005 from the Nada Member of the Borden Formation (Tournaisian). These species are likewise known from few specimens (one and two, respectively) but only as incomplete calyxes, specifically little more than radial circlets. Despite naming the genus for its incompleteness, this is not the kind of imperfection Wachsmuth and Springer had in mind. Regardless, the scant morphology available for study in these specimens is more consistent with coeval monocyclic crinoids, but it is impossible to know if *A. indianensis* and *A. kentuckyensis* were monocyclic or dicyclic since no morphology is preserved below the radial plates.

A specimen recovered from Indiana that does preserve the lowermost plate circlets, and can be confidently assigned to the genus, is *Atelestocrinus baumilleri*, n. sp., from the Ramp Creek Formation (Viséan) of Indian Creek, Montgomery County (Fig. 4A–B, E–G). This is the stratigraphically youngest known species of the group. As usual for its congeners, *A. baumilleri* is known from a single dicyclic specimen. It is associated with another individual from the same locality that is nearly identical except for possessing only one plate circlet below the radials (Fig. 4I), meaning it is monocyclic rather than dicyclic as is the holotype of *A. baumilleri*. Curiously, there is also a monocyclic specimen labelled as *A. robustus* (USNM S2410; Figs. 1G–H, J–K; 2B) that is likewise similar to its dicyclic counterpart (Figs. 1A–F, I; 2A).

Such morphological equivalence, despite differing numbers of cup base circlets, is noteworthy given that higher-level (e.g., ordinal) crinoid classification is largely grounded in the number of plate circlets below the radials. An extreme example of this is Bather's (1900) proposal to divide all crinoids into two grand subclasses, the Dicyclica and Monocyclica, based on this difference alone. Generally, dicyclic crinoids bear two plate circlets below the radials:

infrabasals and basals; and monocyclic crinoids possess only one, variably interpreted as either infrabasals or basals (Guensburg and Sprinkle, 2003). However, some groups of crinoids are known to exhibit both dicyclic and monocyclic forms, even within the same species (e.g., *Uintacrinus socialis* Grinnell 1876; Springer, 1901).

Monocyclic crinoids that originated from within a dicyclic clade are termed pseudomonocyclic. As originally applied, pseudomonocyclic refers to the loss of the infrabasal circlet as is characteristic of extant crinoids (Ubaghs, 1978). The Triassic crinoid *Aszulcicrinus* provides a compelling example of this transition (Hagdorn, 2020). However, pseudomonocyclic crinoids may also emerge from dicyclic clades through the loss of basals (McIntosh, 1979) or radials (Lane, 1967).

With the above in mind, the monocyclic semblances of *A. robustus* and *A. baumilleri* prompt unresolved questions. Do they represent undescribed taxa that are morphologically convergent with species of *Atelestocrinus*, or are they simply aberrant forms of this same genus? If they are pseudomonocyclic, did they achieve this condition (developmentally or phylogenetically) through loss of the infrabasal, basal, or radial circlets? The purpose of this contribution is to consider these questions, in addition to describing a new species, *Atelestocrinus baumilleri*, within the context of Mississippian forms of the genus. Finally, I discuss the relationship between *Atelestocrinus* and *Belemnocrinus* (White, 1862), a genus currently assigned to the monocyclic Disparida (Moore and Laudon, 1943; Moore and Lane, 1978a), and potential implications for the homology of the primary cup circlets of Paleozoic crinoids.

## MATERIALS AND METHODS

The holotype and only known specimen of *Atelestocrinus baumilleri*, n. sp., was commercially collected from private land on Indian Creek, Montgomery County, Indiana. Scott Vergiels prepared the crinoid on behalf of Tom Witherspoon. Vergiels brought the specimen to my attention knowing I was interested in both *Atelestocrinus* and *Belemnocrinus*. I purchased the specimen from Witherspoon, and commissioned Vergiels to remove the crown from the matrix, so both the anterior and posterior sides could be studied and described. Vergiels also provided me with a cast and photograph of the monocyclic semblance of *A. baumilleri* (Fig. 4I). That specimen was likewise commercially collected from Indian Creek, but by Bob Howell in 1990. Unfortunately, the original has yet to be located despite querying numerous private collectors, universities, and museums. George McIntosh (pers. comm., 2021) saw the specimen in the possession of Gary Lane at an annual meeting of the Geological Society of America. Because of restrictions related to the SARS-CoV-2 pandemic, I was unable to visit Lane's collection at Indiana University. However, Claudia Johnson and David Polly searched for it on my behalf but were unable to locate it.

Restrictions imposed by the pandemic also made it

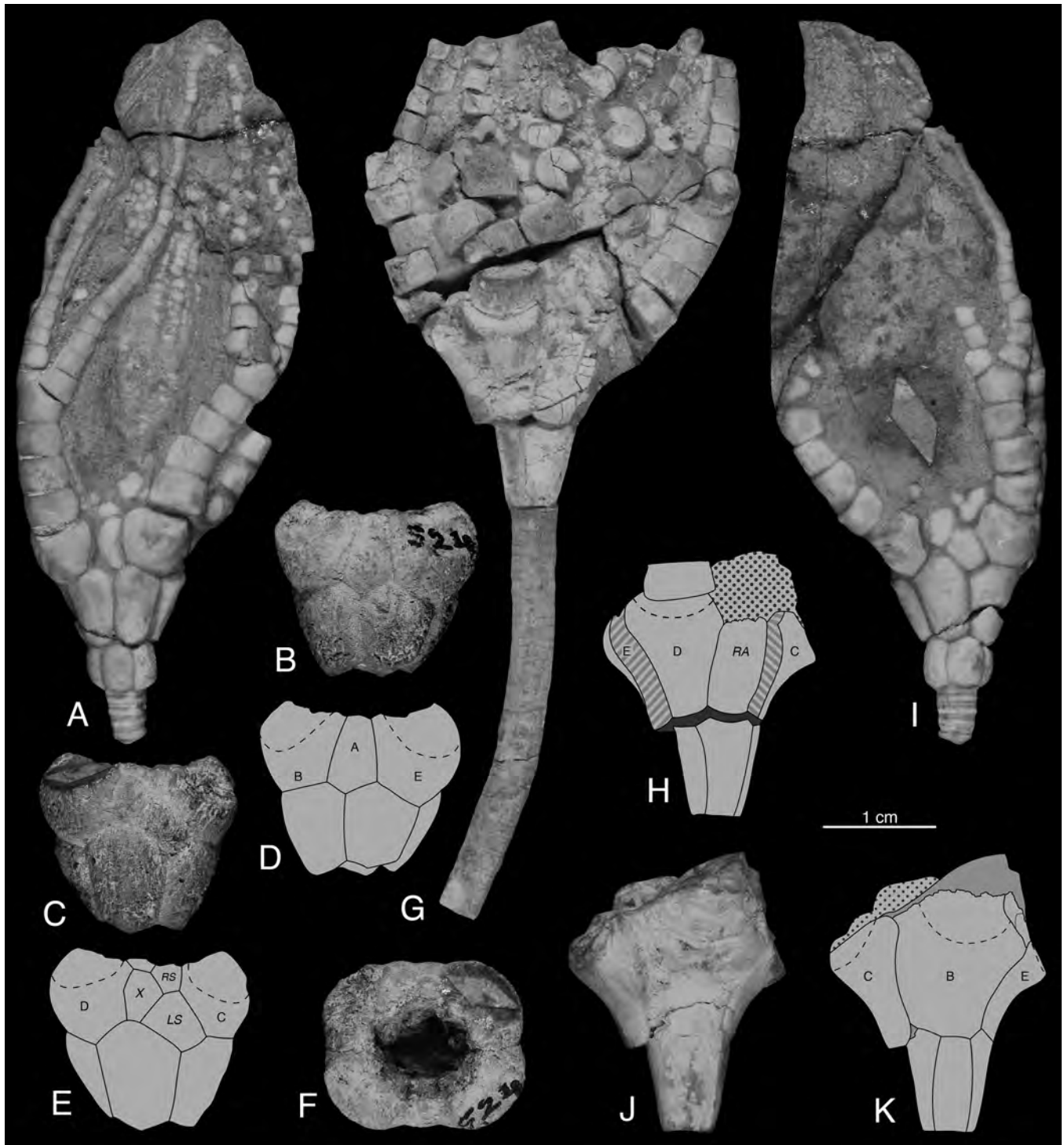


FIGURE 1 — Specimens of *Atelestocrinus robustus* and a related pseudomonocyclic form. **A, I**, anterior (A) and posterior (I) views of the lectotype of *A. robustus* (USNM S2409) from the Burlington Limestone, Iowa. **B–F**, anterior (B, D), posterior (C, E), and ventral (F) views of the paralectotype of *A. robustus* (USNM S2411) from the Fort Payne Formation, Tennessee. **G–H, J–K**, left posterior (G, H) and right anterior (J, K) views of the pseudomonocyclic specimen labeled and identified as *Atelestocrinus robustus* in the NMNH (USNM S2410); compare with Figure 2B. Scale bar is 1 cm for all specimens.

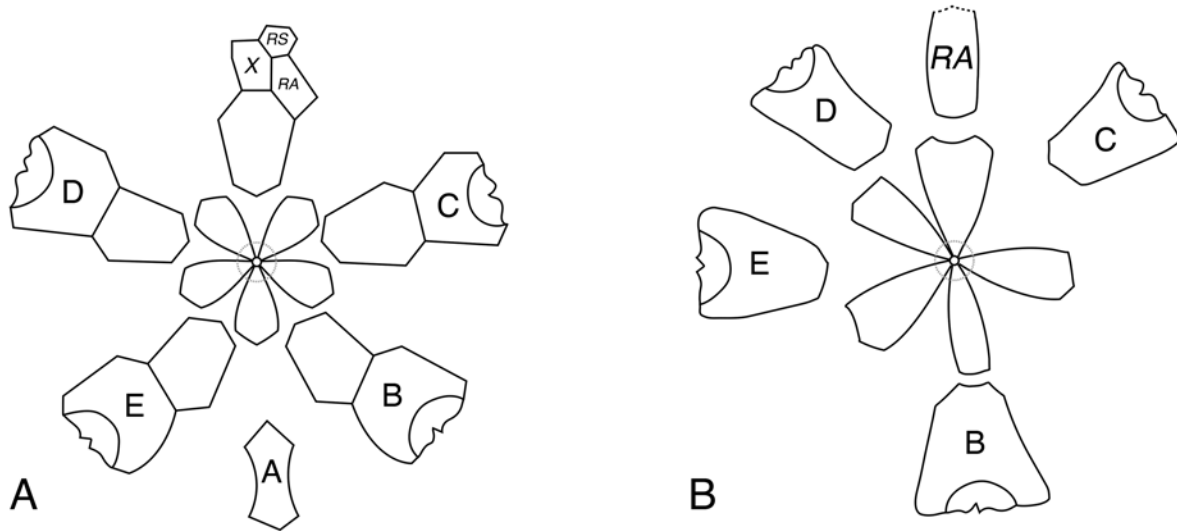


FIGURE 2 — Plate diagrams for *Atelestocrinus* and a related pseudomonocyclic form. **A**, *Atelestocrinus robustus*, modified from the original diagram of Wachsmuth and Springer, 1885: pl. 6, fig. 4. **B**, Diagram of a pseudomonocyclic specimen labeled and identified as *Atelestocrinus robustus* in the NMNH (USNM S2410). The basal circling and anterior radial are entirely missing forcing a radical change in calyx plate morphology and symmetry.

impossible to visit the National Museum of Natural History to more carefully examine specimens of *Atelestocrinus*, including the monocyclic form similar to *A. robustus* (Figs. 1G–H, J–K; 2B). Ideally more precise descriptions for these fossils would have been provided (as for *A. baumilleri*; see “Systematic Paleontology”), but given the circumstances, the best I could do was evaluate the specimens from photographs and notes I took fifteen years prior. Specimens from the Wassonville Formation and *A. baumilleri* were accessible in the research collections of Brigham Young University, Idaho, Department of Geology, where they currently reside. These were photographed with a Nikon D7100 connected to a MacBook Pro and using the most recent version of Helicon Remote [heliconsoft.com]. Stacked images, up to 40 for some specimens, were then combined using the default settings in Helicon Focus. Unless otherwise stated in the figure captions, all photos were taken without coating or immersion. Measurements of *A. baumilleri* were taken using digital calipers under a binocular microscope and are included with the species description. Species of *Atelestocrinus* not mentioned above were examined from McIntosh’s unpublished PhD dissertation (1983; University of Michigan) and the primary literature (Kirk, 1948; Ausich and Lane, 1982; Ausich and Sevastopulo, 2001; Webster et al., 2003; Lee et al., 2005). Classification, terminology, and abbreviations generally follow the *Treatise on Invertebrate Paleontology* (Ubaghs, 1978), but for the latest interpretation of crinoid classification see Wright et al. (2017). For clarity and convenience, a list of abbreviations used in the text and figures is provided below. Note that crinoid orientation is consistently given in capital letters, and specific plates that compose the crown are given in italics; thus, the position of the B radial is clearly differentiated from a basal plate, *B*.

#### INSTITUTIONAL ABBREVIATIONS

SUI	—	University of Iowa, Iowa City, Iowa, U.S.A.
UMMP	—	University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.
USNM	—	United States National Museum, National Museum of Natural History (NMNH), Washington D.C., U.S.A.

#### MORPHOLOGY AND MEASUREMENT ABBREVIATIONS

<i>IAx</i>	primaxil	DE	left posterior interray
<i>IBr</i>	primibrachial	E	E ray
<i>IIBr</i>	secundibrachial	EA	left anterior interray
A	A ray, anterior	<i>IB</i>	infrabasal plate
AB	right anterior interray	H	height
B	B ray, right anterior	<i>LS</i>	left sac plate
<i>B</i>	basal plate	<i>R</i>	radial
BC	right posterior interray	<i>RA</i>	radial
C	C ray, right posterior	<i>RS</i>	right sac plate
CD	posterior interray	W	width
D	D ray, left posterior	X	anal X plate

## SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA Miller, 1821

Subclass CLADIDA Moore and Laudon, 1943

Order DENDROCRINIDA Bather, 1899

Genus *Atelestocrinus* Wachsmuth and Springer, 1885

Fig. 2A

*Atelestocrinus* Wachsmuth and Springer, 1885, pl. 6, fig. 4; pl. 9, fig. 4.*Atractocrinus* Kirk, 1948, pp. 701–703.*Fiannacrinus* Ausich and Sevastopulo, 2001, p. 85.*Type species.*— *Atelestocrinus robustus* Wachsmuth and Springer, 1885: pl. 6, fig. 4; pl. 9, fig. 4, by monotypy.*Other species.*— *Atelestocrinus baumilleri* n. sp.; *Atelestocrinus campanulatus* (Kirk, 1948); *Atelestocrinus concinnus* (Kirk, 1948); *Atelestocrinus curtus* (Kirk, 1948); *Atelestocrinus delicatus* Wachsmuth and Springer, 1886; *Atelestocrinus hutkensis* Webster, Maples, Mawson, and Dastanpour, 2003; *Atelestocrinus meszarosi* Kammer and Roeser, 2012; *Atelestocrinus quinquangularis* (Austin & Austin, 1843), n. comb.; and *Atelestocrinus tenuis* (Kirk, 1948).*Distribution.*— Middle Devonian (Givetian) to Mississippian (Viséan) of Canada, Iran, Ireland, and the United States, specifically: Indiana, Iowa, Michigan, New York, Ohio, and Tennessee.*Discussion.*— *Atelestocrinus* has been most commonly assigned to the family Mastigocrinidae (Jaekel, 1918; Moore and Laudon, 1978b; Webster et al., 2003; Lee et al., 2005; Kammer and Roeser, 2005). Many of the genera previously included within the Mastigocrinidae, as defined by the *Treatise on Invertebrate Paleontology* (Ubahgs, 1978), have been formally reassigned to other families (e.g., McIntosh and Brett, 1988; McIntosh, 2001). *Atelestocrinus* should likewise be removed from the Mastigocrinidae based on differences in the construction of the posterior interradius and arms. However, since higher-level cladid taxonomy remains in significant need of revision (McIntosh, 1983; Wright et al., 2017), but is beyond the scope of the present study, I leave *Atelestocrinus* unassigned at the family level. Regardless, I address some relationships among *Atelestocrinus* and other crinoid genera in the subsequent section.The publication date for *Atelestocrinus* is typically given as “Wachsmuth and Springer, 1886” and the type species as *A. delicatus* by subsequent designation (Miller, 1889: 226; Jaekel, 1918; Moore and Laudon, 1943; Ausich and Lane, 1982; Kammer and Gahn, 2003; Webster et al., 2003; Lee et al., 2005; Kammer and Roeser, 2012). However, *Atelestocrinus robustus* was named and figured nearly a year earlier (Wachsmuth and Springer, 1885: pl. 6, fig. 4; pl. 9, fig. 4). The figures include a labeled plate diagram for the genus (Fig. 2A) and a drawing of the specimen of *A. robustus* (USNM S2409) from the Burlington Limestone. Thus, the genus name *Atelestocrinus* was established by Wachsmuth and Springerin 1885 rather than 1886 (following ICZN, 1999: Article 23.1). Likewise, *A. robustus* gained nominal priority in 1885 since it satisfies all nomenclatural requirements (ICZN, 1999: Articles 11, 12.1, 12.2.7).Although Wachsmuth and Springer (1885, 1886) did not explicitly define a type species for the genus, it is reasonable to assume *A. robustus* best captures their concept given it was the only species they figured; they never illustrated *A. delicatus*. Moreover, *A. delicatus* is ineligible as the type because it was published after the establishment of the genus (ICZN, 1999: Article 67.2). When only a single species is named under a new genus, that species must be considered the type species (ICZN, 1999: Article 68.3). Simply put, Miller (1889: 226) was incorrect in recognizing *A. delicatus* as the type — a mistake repeated by subsequent authors. The type species for *Atelestocrinus* is corrected herein as *Atelestocrinus robustus* Wachsmuth and Springer, 1885 by monotypy (ICZN 1999: Article 70.3).*Atelestocrinus delicatus* Wachsmuth and Springer 1886 was originally published under a misspelling of the genus, “*Attelesocrinus*”, likely a typesetting error, but it is the only spelling of the name in the entire *Revision of the Palaeocrinoidea*. Fortunately, they provided an erratum at the end of that work (Wachsmuth and Springer, 1986: 229–303), in which they corrected numerous “exceedingly annoying” errors, including that for *Atelestocrinus delicatus* (ICZN, 1999: Article 32.5.1.1).Webster et al. (2003) provided a revised diagnosis for the genus that is largely followed here. The only correction is that in addition to being pentagonal, the stem of *Atelestocrinus* may also be round or nearly so. The most pertinent revisions to the genus (Webster et al., 2003) relate to the radials and brachials. Although the most diagnostic feature of the genus is an atrophied anterior radial without an arm or facet, rarely an atavistic facet may develop as in the holotype of *A. concinnus* (USNM S4608). This arm facet may or may not be functional, occasionally bearing a few extremely reduced brachials; and rarer still, it may possess a functional arm. Within a population of 25 undescribed *Atelestocrinus* from the Early Mississippian (Tournaisian) Wassonville Formation of Iowa, two individuals bear atavistic facets in a reduced anterior ray that supports at least one atrophied brachial (Fig. 4C), and one specimen has an arm of normal thickness (Fig. 4D). Another relevant revision of Webster et al. (2003) is that *Atelestocrinus* may possess two to six primibrachials. This is a highly variable character for the genus, even among individuals of the same species and within different rays of the same specimen. On one end of this spectrum is *A. delicatus*, which has only two primibrachials in each ray, and on the other end are species such as *A. campanulatus*, *A. hutkensis*, and *A. quinquangularis*, in which the sixth primibrachial may be axillary.McIntosh (1983) proposed synonymizing *Atractocrinus* (Kirk, 1948) with *Atelestocrinus*, a move formalized by Webster et al. (2003). The two genera are indistinguishable given the current genus concept for *Atelestocrinus*. Webster (2014: 1141) also considered *Fiannacrinus* Ausich and

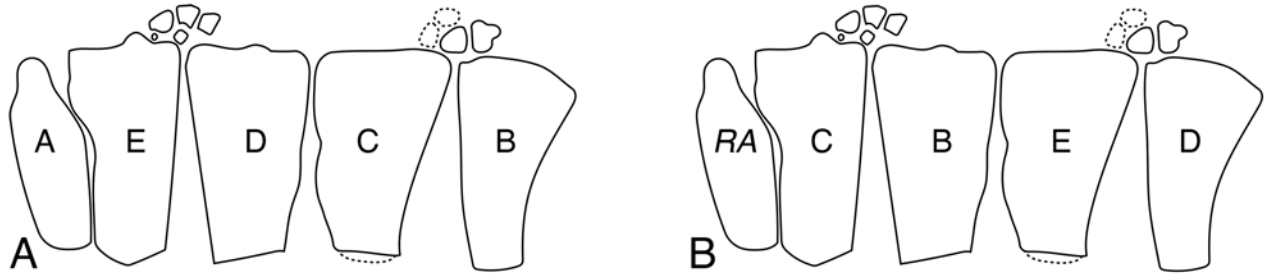


FIGURE 3 — Plate diagrams for *Atelestocrinus indianensis*, modified from Ausich and Lane, 1982: fig. 2. Note the paucity of preserved morphology above and below the radial cirlet, the series of plates labeled with capital letters. **A**, Plate interpretation of the original authors. **B**, Plate interpretation of this paper.

Sevastopulo (2001) a synonym of *Atelestocrinus*, a change formalized here. The diagnostic differences separating *Atelestocrinus* from *Fiannacrinus* were presented as the latter genus having “three anal plates in the cup, a radianal of typical size and shape, small C radial, and four or more primibrachials” (Ausich and Sevastopulo, 2001: 85). *Atelestocrinus* has 3 anal plates in the cup (not 2 as indicated by Ausich and Sevastopulo, 2001; see Fig. 2A), a pentagonal radianal that is in contact with the basals (not the infrabasals as indicated by Ausich and Sevastopulo, 2001), and a C radial that may be the smallest in the cup. As such, *Fiannacrinus* is synonymized with *Atelestocrinus* (following ICZN 1999: Article 23.3). When compared to *A. robustus*, *A. quinquangularis* has a more strongly pentagonal stem, less bulbous infrabasals, and in some specimens, depressed triple-plate junctions and an additional primibrachial, but these are species-level, not genus-level, differences. In fact, many of these traits are variable within individuals of the same species.

Known primarily from radial cirlets, *A. indianensis* (Ausich and Lane, 1982) and *A. kentuckyensis* (Lee et al., 2005) are here considered *nomina dubia*. They simply lack enough characters to be reasonably diagnostic for any species (see Fig. 3). Webster et al. (2003: 11), citing as evidence the uncharacteristically long radials, rejected *A. indianensis* from the genus and instead suggested it was a disparid. I disagree with this opinion and present evidence below for both species being cladids that are missing the basal cirlets. However, this cannot be unquestionably demonstrated given the dearth of characters preserved in the holotypes of these two species (Ausich and Lane, 1982; Lee et al., 2005).

*Atelestocrinus robustus*, Wachsmuth and Springer, 1885  
Figs. 1A–F, I; 2A

*Atelestocrinus robustus* Wachsmuth and Springer, 1885, pl. 6, fig. 4; pl. 9, fig. 4. Wachsmuth and Springer, 1886, p. 147. Miller, S. A., 1889, p. 226. Weller, S., 1898, p. 101. Moore and Lane in Moore and Teichert, 1978b, p. T621, fig. 404, no. 2. Ausich and Lane, 1982, p. 1350. Webster,

1986, p. 69. Webster, 1988, p. 40. Kammer and Ausich, 1996, p. 838. Kammer and Gahn, 2003, p. 122, figs. 1.1–1.2. Webster et al., 2003, p. 13. Lee et al., 2005, p. 349. Kammer and Roeser, 2012, pp. 475–476. Ausich et al., 2020, p. 528, fig. 3.

*Atelestocrinus robustus* (Wachsmuth and Springer, 1886).  
Bassler and Moodey, 1943, p. 314.

*Lectotype*.— USNM S2409 *Atelestocrinus robustus* Wachsmuth and Springer, 1885: pl. 9, fig. 4. from the uppermost Burlington Limestone, Cedar Fork Member, near Burlington, Iowa.

*Other material*.— Paralectotype USNM S2411 from the Fort Payne Formation, Whites Spring Creek, Davidson County, Tennessee. McIntosh (1983: pl. 26, fig. 7) figured a third specimen of *A. robustus* from the NMNH, but I have not had the opportunity to examine it except from the dissertation. Additionally, USNM 2410, a specimen from the collection of Wachsmuth and Springer labeled as *A. robustus* despite being monocyclic.

*Discussion*.— Wachsmuth and Springer (1885, 1886) established *A. robustus* with two specimens in hand, syntypes USNM S2409 and USNM S2411. The latter specimen from the Fort Payne Formation is based on a partial calyx, figured here for the first time (Fig. 1B–F). Despite a paucity of characters, including the absence of an infrabasal cirlet, it convincingly belongs to the genus given the armless anterior ray and the structure of the posterior interray. Regardless, because of the incomplete nature of this specimen, and considering it was never figured by Wachsmuth and Springer, USNM S2411 is established as a paralectotype, leaving USNM S2409 as the lectotype of *A. robustus*.

The stratigraphic provenance of the lectotype has been a point of confusion. Wachsmuth and Springer (1886: 147) described it as being from the “Burlington and Keokuk Transition bed near Burlington, Iowa.” Based on accompanying specimen labels, Kammer and Gahn (2003: 122) questionably reported it as being from “either the upper part of the Burlington Limestone or Montrose Chert Member

of the Keokuk Limestone.” The first author and I disagreed on this point, so both views were presented at the time. However, I am confident the lectotype is from the Cedar Fork Member of the Burlington Limestone. In southeast Iowa, the uppermost Burlington Limestone is characterized by thin bedded, orange dolomitic mudstones that alternate with medium bedded crinoidal packstones and some chert. In addition, there are several interspersed bone beds with a rich chondrichthyan fauna, often bearing abundant glauconite. Conodont research places the “transition beds” in the *Gnathodus bulbosus* Zone (Thompson, 1967; Brenckle, 2005) of the Cedar Fork Member. This zone accumulated during a lowstand period of reduced sedimentation on the Burlington Shelf immediately prior to the transgressive event associated with Keokuk deposition (Witzke and Bunker, 1996; Lane and Brenckle, 2005). The thin orange mudstones at the top of the Cedar Fork Member preserve some of the most spectacular crowns in the Burlington Limestone, consistent with the preservation and associated matrix of the lectotype (Fig. 1A, D). In contrast, fossils from the lowermost Keokuk Limestone are more heavily silicified, and the fossil preservation is different, mostly yielding crushed, solution-weathered calyxes; crowns of any quality are rare. Finally, the “Montrose Chert” has been abandoned as a formal division of the Keokuk Limestone (Witzke and Bunker, 2005) because of stratigraphic misplacement by Keyes (1895). The chert at Montrose, Iowa, is positioned near the top, not the base, of the Keokuk Limestone.

Although a precise description of *A. robustus* is not possible because of the current inaccessibility of the NMNH, much can be said of the types from available photographs (Fig. 1A–F, D). Among the most diagnostic characters of the species are the uniformly tumid plates and relatively large radial facets that support four to five heavy primibrachials. The radial facets and associated brachials of this species appear to be proportionally larger than those of any other *Atelestocrinus*. The lectotype (Fig. 1A, D) appears more gracile and with less tumid plates than the paralectotype (Fig. 1B–F), but the absence of infrabasals in the latter gives it a deceptively globose aspect. Other differences include faint granulose ornamentation on the paralectotype (especially visible on the A and E radials) and more equant basals, but this could represent intraspecific variation, if indeed the two fossils represent the same species. The specimen of *A. robustus* figured by McIntosh (1983: pl. 26, fig. 7) likewise has more equant basals than the lectotype. It also has less tumid plates and shorter infrabasals. Regrettably, the rarity of *A. robustus* limits our understanding of intraspecific variation in this species. Fortunately, large numbers of some *Atelestocrinus* species are available for study (McIntosh, 1983), including the undescribed population from the Wassonville Formation (see Fig. 4C–D). In short, some of the most variable characters seem to include plate ornamentation and tumidity, relative size of the basals, the number of primibrachials, and whether the ramules branch — which is variable even along single arms of some individuals.

The monocyclic specimen described as *A. robustus* (USNM S2410; Fig. 1G–H, J–K; 2B) exhibits many of the

same traits as the lectotype of the species. Most notably, it has a nearly round stem, large radial facets, and thick arms with four to five primibrachials. However, it also exhibits some exceptional differences, the most glaring being only a single plate circling below very elongate radials. When I first saw the specimen, I thought it might represent a new species of *Belemnocrinus*, or perhaps even a new genus. Yet another possibility is that it is an abnormal specimen of *A. robustus*. Upon further examination of the calyx, which is free from the matrix, it has a radial circling consisting of five plates, only four of which are arm-bearing. The two most reasonable interpretations of the armless plate are that it is either a typical anterior radial for *Atelestocrinus* or it represents the posterior interray, conceivably a hypertrophied radial or anal X. Given the former interpretation, it is inconsistent with *Atelestocrinus* because it would lack any posterior plates. Given the latter interpretation, it is inconsistent with *Belemnocrinus*, at least as historically defined, because that genus is described as having five arm-bearing rays with one radial-sized posterior plate in the cup, resulting in a radial circling composed of six plates (White, 1862; Wachsmuth and Springer, 1877; Moore and Lane, 1978a). Under any interpretation, the calyx is unusual (Fig. 2B). The plates of the lowermost circling are variable in shape, width, and some of the lateral sutures are bowed. This specimen appears to have lost entirely the basals and anterior radial. Moreover, the calyx deviates from the typical pattern of 36° offset of superadjacent plate circlets.

*Atelestocrinus baumilleri*, n. sp.  
Fig. 4A–B, E–G

*Holotype*.— UMMP 75465, which consists of a strongly compressed partial crown and stem; the crown was removed from the matrix for more thorough study. The holotype and only known specimen is from the Mississippian (Viséan) Ramp Creek Formation, Indian Creek, Montgomery County, Indiana, U.S.A.

*Diagnosis*.— The most distinctive feature of *A. baumilleri* is the fine, granulose texture that covers all plates of the dorsal cup. Proximally, these granules are weakly organized into radiating ridges that run across the basals and infrabasals. Such radiating granulose ornamentation has not been observed in any other species of *Atelestocrinus*. It is clearly distinguished from *A. robustus*, *A. delicatus*, and *A. meszarosi* by the absence of a bulbous infrabasal circling and the presence of a strongly pentagonal stem. In this regard it is most similar to *A. hutkensis* and *A. quinquangularis*; however, *A. baumilleri* differs from those taxa in possessing fewer primibrachials, nodose tegmen plates, and ornamented cup plates.

*Etymology*.— This species is named in honor of Tomasz K. Baumiller for his monumental contributions to crinoid paleontology, stellar mentorship, and invaluable friendship. Like the holotype specimen, long may he regenerate.

*Description*.— The crown of *A. baumilleri* is tall and gracile with eight ramulate arms that make up 75% of crown height. It has a high conical cup that is slightly higher than wide (H:W 1.1). The plates of the calyx are relatively thin.

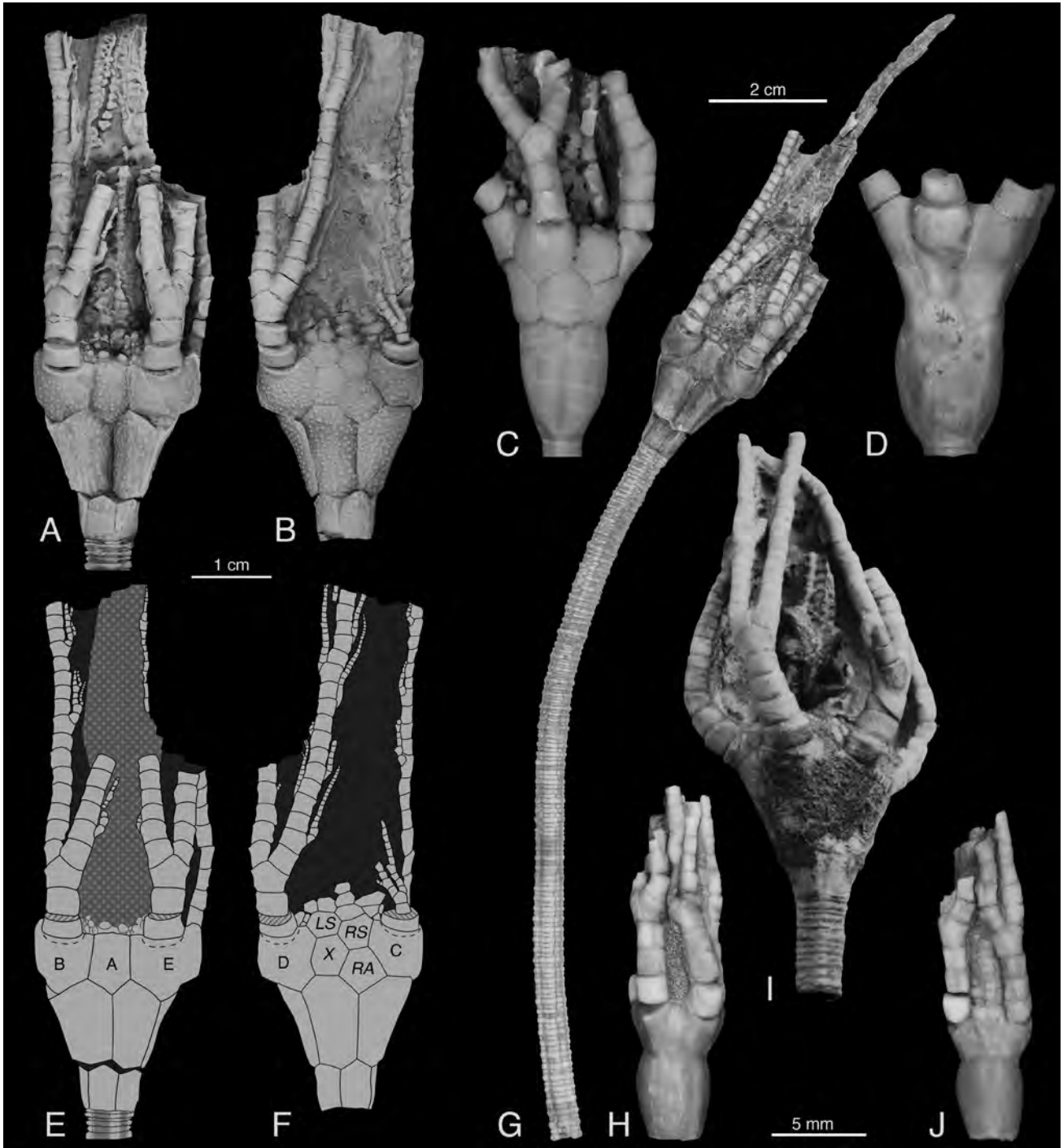


FIGURE 4 — Specimens of *Atelestocrinus*, *Belemnocrinus*, and another pseudomonocyclic individual. **A–B**, **E–F**, anterior (A, E) and posterior (B, F) views of the crown of *Atelestocrinus baumilleri*, n. sp. (UMMP 75465) from the Ramp Creek Formation, Indiana (left scale bar, 1 cm); specimen coated with ammonium chloride. **G**, anterior view of the same specimen (UMMP 75465) with stem (upper right scale bar, 2 cm). **C–D**, **H**, **J**, undescribed crinoids from the Wasonville Formation of Iowa, including: (C) An *Atelestocrinus* with an atavistic radial facet and primibrachial in the A ray (SUI 148482); (D) an abnormal specimen of the same species (SUI 98386); and anterior (H) and posterior (J) views of a *Belemnocrinus* specimen (SUI 148483) (all lower right scale bar, 5 mm). **I**, a pseudomonocyclic crinoid similar to *A. baumilleri* from the Ramp Creek Formation, Indiana, that has an ophiuroid attached to its anal sac (left scale bar, 1 cm).



The five infrabasal plates are higher than wide (H:W 1.5–1.6), uniformly pentagonal, entirely visible in side view, and make up about 24% of cup height. The five basal plates are higher than wide with the DE and EA basals being notably tall and thin (H:W 2.3 and 1.8, respectively) relative to the AB, BC, and CD basals (H:W 1.5–1.6). All the basals are hexagonal except for CD, which is septagonal. The AB, DE, and EA basals have peaked upper surfaces, whereas those of BC and CD are flat. The basal circlet makes up roughly 43% of cup height. The five radial plates are slightly higher than wide (H:W 1.1–1.3), except for the C radial, which is slightly wider than high (H:W 0.9). The A radial is the tallest and thinnest radial plate and lacks an arm or associated facet. The C radial is the smallest arm-bearing plate. All radials are roughly septagonal with the exception of the A radial, which is hexagonal. All of the radials have peaked lower surfaces except for the C radial, which articulates with the underlying CD basal along a flat surface, the two plates being perfectly aligned and lacking the 36° offset typical of superadjacent plate circlets. Because of the atrophied A radial and relatively wide posterior interray, the C radial is shifted into the BC interradial position. The radial circlet makes up about 33% of cup height. The radial facets are peneplenary, moderately declivate, and are broadly U-shaped with weakly developed marginal rims. They occupy approximately 23–33% of radial height, with the C radial being an outlier (43%), and 63–73% of radial plate width.

Three plates are fully incorporated into the posterior interray of the dorsal cup. These include a pentagonal radianal (H:W 0.9) equally supported by the BC and CD basals, a hexagonal anal X (H:W 0.8), and a hexagonal right sac plate (H:W 0.7). The left sac plate is also partially integrated into the dorsal cup, being supported by the upper right shoulder of the D radial. The anal sac is incomplete but extends to at least the height of longest preserved arm in the B ray. It appears to be relatively narrow and elongate, composed of eight uniserial rows of thin, hexagonal plates that are uniformly wider than high. Small circular pores are developed at the plate corners. The anal sac emerges from a tegmen composed of numerous tiny, nodose plates that are irregularly arranged. Embedded within this pebbly integument, along the outer margins of most interrays, are two to three larger elongate plates with their long axes directed radially toward the center of the calyx. Near the base of the sac is a large, elongated dome-shaped plate, possibly an oral, directed perpendicularly to the anterior-posterior axis though slightly displaced taphonomically. Ambulacra on the tegmen are not apparent, possibly due to partial disarticulation and severe compression of the holotype.

The longest preserved arm, right branch of the D ray, is approximately four times longer than the dorsal cup and consists of 42 secundibrachials. The arms branch once isotomously on the third primibrachial, resulting in eight arms total, and are of moderate thickness. Their lateral margins are sharply rounded and deep. Primibrachials are about twice as wide as high ( $IBr_1$  H:W 0.4–0.6), and proximal secundibrachials are more equant (H:W 0.8–0.9). All the brachials possess nearly parallel articular surfaces and form a relatively linear stack of uniserial plates. Each arm gives

rise to a ramule on alternating secundibrachials, beginning with  $IIBr_2$ . The ramules are heterotomous and complexly branched, emerging from robust, rimmed facets that occupy about half the height of their supporting brachials. Where visible, all secondary ramule branches arise first from the second ramular and subsequently from every third ramular; the smallest branches are directed away from the main arm branch. The ventral groove may be observed in two places in the holotype,  $IIBr_{8-10}$  and  $IIBr_{25-26}$  of the right branch of the D ray. The groove is deep and U-shaped, occupying nearly 40% of secundibrachial width proximally and 50% distally, where it also appears to become shallower. Two rows of paired cover plates adorn the ventral grooves of both the brachials and ramulars.

The stem is strongly pentagonal with the lobes oriented interradially. In the holotype, the stem appears to be pentameric (Fig. 4G), but this is not the case. What appears to be meres are irregular fractures generated by compaction. Proximally, the noditaxis pattern is N3231323, and it becomes N212 distally. Proximal nodals are nearly four times thicker than the thinnest internodals, and their points bear bulbous ornamentation. The columnals have well developed crenulae on their outer margins, which are clearly visible in side view; otherwise the articular surfaces are smooth. The lumen is tiny, its shape obscured by compaction. Evidence for cirri or cirral scars is lacking.

*Measurements.*— All in mm. Length of the full specimen, 225. Crown H, 90.8. Calyx H:W, 22.8:20.8. H:W for the following plates:  $IB A$ , 5.6:3.7;  $IB B$ , 5.8:3.6;  $IB C$ , 6.1:3.9;  $IB D$ , 6.3:7;  $IB E$ , 5.7:3.6;  $B AB$ , 10.9:7.2;  $B BC$ , 11.8:7.4;  $B CD$ , 11.9:7.8;  $B DE$ , 12.1:5.1;  $B EA$ , 11.4:6.4;  $R A$ , 7.8:5.8;  $R B$ , 9.5:7.9;  $R C$ , 6.9:7.8;  $R D$ , 8.7:7.8;  $R E$ , 9.6:8.9;  $RA$ , 5.8:6.1;  $X$ , 5.2:4.9;  $RS$ , 3.8:4.5;  $LS$ , 3.2:4.2.  $IBr_1 B$ , 2.5:4.9;  $IBr_1 C$ , 2.2:5;  $IBr_1 D$ , 2.4:4.8;  $IBr_1 E$ , 3:5.1;  $IAx_1 B$ , 3.5:4.9;  $IAx_1 C$ , 1.6:1.9;  $IAx_1 D$ , 3.8:5;  $IAx_1 E$ , 4.3:5.1. Radial facet height from the bottom of the facet to the top of the radial plate: the width of the radial facet:  $R B$ , 5.8:2.4;  $R C$ , 5.2:3;  $R D$ , 5.6:2.3;  $R E$ , 5.6:2.9. Height of the primibrachial series:  $B$ , 10.3;  $C$ , 5.1;  $D$ , 10.2;  $E$ , 10.6. Length of the longest preserved arm (including primibrachials), 90.1. Length of the longest preserved ramule, 12.1; Stem length, 134.2. Proximal stem width, 6.3. Proximal nodal thickness, 1.3. Proximal internodal thickness, 0.3.

*Discussion.*— For the most part, *Atelestocrinus* is exceedingly rare, even from localities world renowned for producing thousands of complete specimens in dense, multispecies associations such as Crawfordville. Despite searching major crinoid collections, public and private, having close ties to individuals in the commercial fossil community, and even posting queries to large social media groups, I was unable to discover a second specimen of *A. baumilleri*. As far as is known, this species is also the last surviving member of a lineage that first appears in the Middle Devonian (Givetian) of North America (McIntosh, 1983).

Fitting for its namesake, Tom Baumiller, and our collaborative research on predation, the holotype bears a regenerated arm in the C ray. The entire arm is regenerated above the first primibrachial. The absence of any mechanical

damage to this plate is consistent with autotomy of the arm whether the loss was triggered by an exploitive biotic interaction or otherwise. McIntosh (1983; pl. 26, fig. 9) figured a similarly regenerated arm in the D ray of an *A. campanulatus*, also originating from an unfractured first primibrachial. This suggests at least some brachials in *Atelestocrinus* may have had an autotomy function like the cryptosyzygies of some extinct and extant crinoids (Gahn and Baumiller, 2010).

Geographically and temporally, *A. baumilleri* shows some affinities with *A. indianensis* (Ausich and Lane, 1982: pl. 1, figs. 5, 9, 13). They have similar radial facet development, and although not mentioned in the original description, *A. indianensis* appears to have finely granulose ornamentation. However, the comparison must largely end there given the holotype of *A. indianensis* lacks a stem, infrabasals, basals (if it had them), tegmen, anal sac, and arms. Unlike *A. baumilleri*, *A. indianensis* has only five plates in the radial circlet. These were interpreted by Ausich and Lane (1982) as five radials with an armless A ray as in *Atelestocrinus* but without the posterior plates characteristic of the genus (Fig. 3A). The arrangement of the radial circlet in *A. indianensis* is like that of the monocyclic form of *A. robustus* (USNM S2410; Figs. 1G–H, J–K; 2B), and it is also reinterpreted as being composed of only four radials and a hypertrophied radialian (Fig. 3B).

*Atelestocrinus kentuckyensis* (Lee et al., 2005) is in most ways identical to *A. indianensis* in both preservation and morphology. It is known from little more than a radial circlet that is composed of only five plates, interpreted by the original authors as representing five radials without any anal plates. It also has similarly developed radial facets and granulose ornamentation. The plate they interpreted as the armless anterior radial has a peaked upper surface, forming two facets that each support large, equant “tegmens” plates (Lee et al., 2005: fig. 1.12). This is not an armless A radial with two tegmen plates but rather three posterior plates. A similar configuration is seen in some individuals of *Belemnocrinus*.

The radial circlets of *A. indianensis* and *A. kentuckyensis* bear resemblance to the unusual form of *A. robustus* (Figs. 1G–H, J–K; Fig. 2B; Fig. 3). They are also similar to the undescribed (and as of yet unlocated) monocyclic crinoid from Indian Creek (Fig. 4I). Based on the photograph and cast I have of this specimen, it has similarly elongated radials. There is no clear evidence of a fifth arm-bearing ray, but this is difficult to rule out since the specimen is embedded in matrix. However, the proportions of the visible plates are consistent with a radial circlet composed of four arm-bearing radials and a large posterior plate. Under magnification, there is some indication in the 1990-vintage photograph (Fig. 4I) of a possible fifth arm-bearing ray, mostly buried in the matrix; but it’s difficult to say without the specimen in hand.

The monocyclic specimen from Indian Creek (Fig. 4I) shares numerous similarities with *A. robustus*, and especially with *A. baumilleri*. Like *A. robustus*, it has four to five primibrachials in each ray. Like *A. baumilleri*, it has a strongly pentagonal stem with bulbous ornamentation at the lobes. It

also has finely granulose plate ornamentation on the dorsal cup, somewhat obscured by heavy pyritization. It has similarly developed radial facets and arms that are less “robust” than those of *A. robustus* and with complexly branched ramules. Finally, the monocyclic semblance of *A. baumilleri* has on the tegmen, radially oriented, elongate plates at the margins of the interradian areas like those of its dicyclic counterpart. See below for a discussion on possible explanations for this unusual crinoid from Indian Creek and other monocyclic crinoids that share similarities with *Atelestocrinus*.

#### EVOLUTIONARY AND DEVELOPMENTAL IMPLICATIONS OF *ATELESTOCRINUS*

The documentation of new species is foundational to paleontological science, but such efforts have their greatest value when framed in questions of organismal development, evolution, and ecology. The description of *Atelestocrinus baumilleri* is no exception. What may have driven the loss of an entire food gathering ray in *Atelestocrinus*? How do the morphologically similar but monocyclic crinoids relate to *Atelestocrinus*, and developmentally, how did they achieve this form? Some possible answers to these questions, among other considerations, are addressed in the following paragraphs.

McIntosh (1983) suggested *Atelestocrinus* is closely related to *Bactrocrinites*, both genera rife with abnormal individuals (McIntosh, 1979). *Bactrocrinites* is a dicyclic crinoid that includes teratological monocyclic forms, in addition to intermediates that retain basals in some interrays but not others. For example, McIntosh (1979) considered *Hypsocrinus*, *Perissocrinus*, and *Kalpidocrinus* to be aberrant forms of *Bactrocrinites fieldi* (Springer and Slocum, 1906). Abnormalities in these crinoids were associated with the midcup, generating a rarely demonstrated type of pseudomonocycly. Whereas pseudomonocycly is mostly associated with loss of the infrabasal circlet, these individuals lost some or all their basal plates. The reduction or elimination of the midcup in these taxa often disrupted typical patterns of calyx plate symmetry. *Belanskicrinus westoni* (Belanski, 1928), a species formerly aligned with *Bactrocrinites*, likewise shows midcup instability, but instead of reducing or eliminating the midcup, it added plates immediately below the radials (Strimple and Leverson, 1969). Both the addition and subtraction of plates can disrupt expected patterns of calyx plate symmetry.

Wachsmuth and Springer (1885) highlighted fundamental differences in patterns of symmetry between dicyclic and monocyclic crinoids with pentagonal stems and lumens, the so-called “Law of Wachsmuth and Springer” (LWS; Bather, 1898). Among such dicyclic crinoids, stem lobes are interradian and lumen lobes are radial. Monocyclic crinoids show the opposite: Stem lobes are radial and lumen lobes are interradian. These structural principles are valuable for determining whether monocycly was achieved through infrabasal loss. For example, among articulates with pentagonal stems, the stem lobes are interradian, providing evidence in favor of these

crinoids having originated from dicyclic ancestors via loss of the infrabasal circlet; a pattern consistent with ontogeny (Amemiya et al., 2016).

In crinoids that develop monocyclally through loss of the basals, McIntosh (1979) observed they lack the expected 36° offset of superadjacent plate circlets. This generates inconsistent patterns of symmetry, with radial stem lobes in some rays and interradial stem lobes in others. This pattern is here defined as “McIntosh’s rule” and may be used as evidence for identifying monocyclic crinoids that originated from dicyclic ancestors through loss of the midcup. For example, in *Hypsocrinus*, McIntosh (1979: 27) observed two interradial and three radial stem lobes. Moreover, some of the infrabasals in this specimen have sinuous lateral sutures; the plates are radially disposed proximally, and they are interradially disposed distally. This pattern of midcup instability is an indication of plate reorganization and compensatory growth due to loss of the basals, most likely before the calyx plates became fixed during the cystidean stage of development (Springer, 1920; Amemiya et al., 2016). This same pattern is observed in *Belemnocrinus*, a genus McIntosh (1979: 28) suggested might likewise be a pseudomonocyclic cladid.

*Belemnocrinus* (White, 1862) is an unusual monocyclic crinoid that has been formally described only from the Burlington Limestone. It is currently classified as a disparid, the namesake of an entire superfamily, the Belemnocrinacea (Miller, 1883; Moore and Lane, 1978a). *Belemnocrinus* continues to be included in phylogenetic analyses of the Disparida (Ausich, 2018) despite numerous suggestions that it is a pseudomonocyclic cladid (Ubaghs, 1953; McIntosh, 1979; Sevastopulo and Lane, 1988; Gahn, 2006). New observations herein provide further evidence for the interpretation that *Belemnocrinus* is an abnormal cladid that possibly arose from *Atelestocrinus*, either phylogenetically or developmentally.

Since 1994, I have been collecting an undescribed crinoid fauna from the Wassonville Formation of Iowa that includes a substantial population of *Belemnocrinus* (Gahn and Baumiller, 2004). Stratigraphically, the Wassonville Formation immediately underlies the Burlington Limestone. Although I have collected hundreds of articulated crinoids from the Wassonville Formation and coeval strata in a dozen quarries from central Iowa to northeastern Missouri, all the *Belemnocrinus* specimens come from a single quarry and horizon. Alongside nearly 25 specimens of *Belemnocrinus* (Fig. 4H, J) are an equal number of crinoids that are dicyclic but otherwise nearly indistinguishable (Fig. 4C–D). They occur exclusively in the same quarry and horizon as the monocyclic *Belemnocrinus*. I initially considered these crinoids to be monocyclic and dicyclic variants of the same species.

When I first began unearthing this population of crinoids, and despite their simplicity, I did not fully appreciate the morphology of either the dicyclic or the monocyclic forms. *Belemnocrinus* is consistently described as having five armed rays and a single anal plate (White, 1862; Wachsmuth and Springer, 1877; Moore and Lane, 1978a). Since the

Wassonville specimens were embedded in matrix, I could typically observe only half of any crown. When I first observed a single, armless plate in the radial circlet of a “dicyclic *Belemnocrinus*”, I assumed it was the single anal plate diagnostic for that genus. However, I soon wondered if these dicyclic crinoids could be *Atelestocrinus*. The only way to resolve this question was to remove a dicyclic variant from the matrix, and so I did. The first extricated specimen had only four arm-bearing rays with an armless anterior radial and three plates in the posterior interray, fitting the diagnosis for *Atelestocrinus*.

Still working under a model of these monocyclic and dicyclic forms being of the same species of cladid, I faced a quandary. How could a crinoid with three cup circlets and four armed rays develop into a variant with two cup circlets and five armed rays? First, I searched the population of Wassonville *Atelestocrinus* for specimens with fully developed arms in the anterior ray. Strikingly, I discovered one such specimen (Fig. 4D) and two additional specimens with atavistic arm facets and brachials in the anterior ray (Fig. 4C).

Next, I turned to specimens of the monocyclic *Belemnocrinus* and started removing them from the matrix. The first specimen extracted had only five plates in the radial circlet — four arm-bearing radials (not five as expected) and a single, radial-sized anal plate (Fig. 4H–J). This is the same configuration as in the monocyclic form of *A. robustus* discussed previously (Figs. 1G–H, J–K; 2B). Did I serendipitously find yet another new species of an undocumented genus, specifically the one that includes the monocyclic forms of *A. robustus* and *A. baumilleri*? No, *Belemnocrinus* has likely been misdiagnosed for 160 years. Upon removing additional monocyclic variants from the matrix, I was unable to discover a single specimen of *Belemnocrinus* with five radials. Perhaps more importantly, I was unable to confirm that a single specimen of *Belemnocrinus typus* White, 1862 has five radials, even after examining all known specimens of the type species. *Belemnocrinus*, like *Atelestocrinus*, has only four arm-bearing radials. However, it has taken the reduction of the anterior ray one step further by eliminating it entirely. The loss of the anterior arm in *Atelestocrinus* and absence of the associated radial in *Belemnocrinus* may be explained by neoteny; in some Paleozoic crinoids, the A radial is the last to develop ontogenetically (Lane, 1978; Sevastopulo and Lane, 1988). This same radial is likewise missing in *Hypsocrinus* (McIntosh, 1979).

The degree of variation observed in both the dicyclic and monocyclic individuals from the Wassonville population is unusual but will not be fully documented here. However, to contextualize the monocyclic semblances of *A. robustus* and *A. baumilleri* (Figs. 1G–H, J–K; 4I), one abnormal *Atelestocrinus* from the Wassonville Formation (Fig. 4D) is especially insightful. Despite being dicyclic, it has starkly malformed calyx plates and misaligned cup circlets. The infrabasal and basal circlets appear to have been partly resorbed at the expense of one another, and the radials, which show evidence of thickening in areas consistent with normally

developed plates of this type (Fig. 4C), have thinner tongues of stereom extending into regions of the calyx typically occupied by the basals. This abnormal growth likely occurred prior to the pentacrinoid stage of development. Once closure of the calyx was completed, the nearly isometric growth that is typical of most calyx plates would have conserved this aberrant form in the adult. Regardless, this specimen (Fig. 4D) may provide insight into the development of the monocyclic forms of *A. robustus* and *A. baumilleri*, specifically their relatively elongate radials. Complete resorption of the basals and compensatory growth of the radials in early (cystidean) stages of growth could explain this difference between the monocyclic and dicyclic forms of these taxa.

Such compensatory growth is also observed among individuals of Wassonville *Belemnocrinus*, but the larger sample size permits study of variability. Relative to the dicyclic variants (*Atelestocrinus*), some specimens exhibit normal infrabasals with greatly extended radials. Others exhibit normal radials with greatly extended infrabasals, occasionally with sinuous lateral sutures as in *Hypsocrinus*. Yet others seem to have lost the basals without any compensatory growth of either the infrabasals or the radials. However, consistent with McIntosh's rule, many individuals deviate from the expected 36° offset of superadjacent plate circlets.

Another critical observation relates to the underlying explanation for the LWS and homology of the cup base circllet among dicyclic and monocyclic crinoids. Like *A. baumilleri* and its monocyclic counterpart (Fig. 4A, I), some specimens from the Wassonville *Atelestocrinus-Belemnocrinus* population have pentalobate stems. In all of these, the stem lobes are offset with the radially disposed infrabasals. However, whereas the infrabasals are aligned with the radials in dicyclic forms (*Atelestocrinus*), they are generally misaligned with the radials in monocyclic forms (*Belemnocrinus*). In other words, the radial circllets of most monocyclic variants, as well as their corresponding arms and ambulacra, are interradially disposed. The stem-infrabasal junction is fixed in both the dicyclic and monocyclic forms, but with the loss of the basals, the radial circllet generally rotates clockwise (from a ventral perspective) into an interradial position. With emphasis, using the infrabasals as a fixed reference, the alimentary system may be oriented interradially in monocyclic crinoids.

This observation rejects a fundamental assumption of Carpenter's (1878) plate homology system, which interprets the lowermost cup circllet of most monocyclic crinoids (e.g., disparids and monobathrids) as basal plates. Miller (1821), author of the Crinoidea, universally referred to the cup base circllets of all crinoids as the "pelvis". Likewise, Müller (1843) suggested the cup plates immediately above the stem were homologous for both dicyclic and monocyclic crinoids (based on the translation and interpretation of Carpenter, 1878: 366). Using current terminology, Müller (1843) would have referred to the lowermost plate circllet of both forms as infrabasals. Carpenter (1878) objected to this interpretation because he firmly held that a plate circllet could not be radially disposed in some taxa and interradially disposed in

others. This assumption was championed by Wachsmuth and Springer (1897) and perpetuated in subsequent publications (e.g., Moore and Laudon, 1943; Ubahgs, 1978). The Carpenter system of plate homology and concomitant view that radial and interradial plate positions are fixed in crinoids generally persist to this day. This is true despite evidence to the contrary, including the work of Lane (1978) who demonstrated that primary plate circllets, notably the orals, shift from a radial to an interradial position during ontogeny of the microcrinoid *Cranocrinus*. Similarly, the population of Wassonville *Atelestocrinus-Belemnocrinus* decisively rejects Carpenter's assumption by demonstrating that the radial circllet can be radially or interradially disposed. Careful examination of McIntosh's (1979) work illustrates this for individuals of the same species. The infrabasals and radials are aligned in normal specimens of *Bactrocrinites fieldi*, but they are misaligned in the pseudomonocyclic *Kalpidocrinus eriensis* Goldring, 1954, its aberrant junior synonym.

Variation in the orientation of the radial plates can even occur within a single individual. Such irregularity is normal for many cladids, including *Atelestocrinus*. The C radial is typically displaced (counterclockwise) into the BC interradial position, directly over the right posterior basal plate, to accommodate a wide posterior interray. This plate shift is also conserved in the transition to *Belemnocrinus*. However, with the loss of the basals and the anterior radial in this taxon, in addition to hypertrophy of the radianal, the remaining radials shift up to 36° in the opposite (clockwise) direction such that the D radial shifts into the DE interray, the E radial shifts into the EA interray, and the B radial shifts into the AB interray; thereby regaining the expected offset of superadjacent cup plate circllets.

Interpreting the lowest plate circllet of most monocyclic crinoids as infrabasals instead of basals (Müller, 1843) better explains the origin of symmetry patterns elucidated by the LWS than does the Carpenter system (1878). Keeping the infrabasals fixed in a radial position while rotating the radial circllet conserves the offset of the stem lobes with the lowermost plate circllet. Moreover, this rotation explains the observed alignment of the stem lobes with the radials, though now the radials are interradially, not radially, disposed. On the contrary, when the infrabasals are lost without rotation of superadjacent cup plates, leaving basals as the lowermost circllet, the LWS is violated, permitting recognition of true pseudomonocyclic (*sensu stricto*) crinoids such as extant articulate.

Based on the LWS, Simms (1994) likewise argued for using the stem-cup base junction, not the radials, as the foundation for evaluating the homology of primary plate circllets. He also noted the consistent patterns of symmetry between the stem and calyx base among dicyclic and monocyclic crinoids (as observed for *Atelestocrinus* and *Belemnocrinus*). However, instead of arguing for the loss of the basals and rotation of the radial circllet, he suggested that in many monocyclic crinoids, specifically disparids and glyptocrine camerates, the radials are missing, and the arms developed on basal plates.

Simms (1994) and I agree that the arms can be interradially disposed, but we differ in our explanation for the probable origin of this condition. Evidence presented here also supports the interpretation that the cup base circlets of most disparids and monobathrids are infrabasals, likewise proposed by Guensburg and Sprinkle (2003; see also Moore, 1954: 144), and in opposition to the widely favored Carpenter system (Ubaghs, 1978).

Consistent with McIntosh's rule and this contribution, Guensburg and Sprinkle (2003) argued that the midcup instability they observed among monocyclic camerates from the Early Ordovician suggests retention of infrabasals and radials in these taxa. I generally agree and suspect other examples of variable plate circlet alignment have been overlooked. Even in the absence of a stem, and perhaps especially so, the relative orientations of lumen lobes and radials may be analyzed from the cup base. Recall that according to the LWS, lumen lobes should be consistently aligned with the radials in dicyclic crinoids (e.g., cladids and diplobathrids) and offset by 36° in monocyclic crinoids (e.g., disparids and monobathrids). Variability in the orientations of lumen lobes among monocyclic crinoids is predicted for taxa that achieved this form through loss of the basal circlet. Examination of eight calyxes (USNM S1137) of *Thinocrinus scitulus* (Meek and Worthen, 1860), a monobathrid (Actinocrinitidae) from the Burlington Limestone, reveals stark inconsistency in the orientation of the lumen lobes and radial plates — only about half are interradially disposed. I observed similar inconsistency within large populations of Batocrinidae and Coelocrinidae. Such variability could be the result of reorganization of the radial circlet with loss of the midcup, but it could be also generated by the addition of a sixth plate to the radial circlet, the primanal, as is characteristic of compsocrines. A less ambiguous test could be made among glyptocrines (and disparids), which typically possess only a five-plate radial circlet. However, consistency in the alignment of superadjacent plate circlets does not necessarily rule out loss of the midcup. As demonstrated by *Belemnocrinus*, crinoids that have lost their basal circlets often regain the symmetry patterns expected from the LWS for monocyclic crinoids.

Returning to *Atelestocrinus*, there are at least three competing hypotheses for the relationship among the dicyclic and monocyclic forms of the genus. First, despite their many similarities, *Atelestocrinus* and *Belemnocrinus* may represent distinct genera. The Wassonville population could simply be capturing the origin of a genus. As these lineages continued to evolve independently, they could have done so in parallel. Under this scenario, the monocyclic forms of *A. robustus* and *A. baumilleri* are new species of *Belemnocrinus*. Second, the monocyclic *A. robustus* could represent a new pseudomonocyclic genus (not *Belemnocrinus*) that originated independently from its dicyclic counterpart, which perhaps in turn gave rise to the monocyclic *A. baumilleri*, also potentially a member of this same new genus. Under this scenario, *Atelestocrinus* gave rise to more than one genus of pseudomonocyclic crinoid. Third, *Belemnocrinus* could be

a phenotypic variant of *Atelestocrinus* that recurs iteratively throughout the range of the genus — a persistent abnormality. Under this scenario, the two genera are synonymous.

There is observational evidence for and against each of these hypotheses, but I withhold much further discussion until thoroughly documenting the Wassonville population, which will include extensive morphological and phylogenetic analysis of the associated clade. Presently, the weight of evidence seems to favor the Wassonville population of *Atelestocrinus-Belemnocrinus* being members of the same species that exhibit extreme phenotypic variation. Likewise, the monocyclic semblances of *A. robustus* and *A. baumilleri* may be best considered aberrant forms of their respective species, not unique taxa. Springer (1901) documented similarly dramatic polymorphism in large populations of *Uintacrinus socialis* (Grinnell, 1876), notably in the number of calyx plate circlets. In a population of specimens from the same lens, 44% of 435 individuals were dicyclic and the rest were monocyclic. It is inconceivable to regard these specimens of *Uintacrinus* as being from distinct species, and much less distinct genera or higher taxa, because of this difference alone.

Suffice it to say, *Belemnocrinus* is a pseudomonocyclic derivative of *Atelestocrinus*, whether developmentally or phylogenetically. But if the two are synonymized, *Belemnocrinus* has priority by over two decades (White, 1862; Wachsmuth and Springer, 1885). Perhaps *Atelestocrinus baumilleri* is *Belemnocrinus baumilleri*. Regardless of the verdict, both are remarkable forms that provide new evidence for a compelling developmental and evolutionary narrative.

Finally, the Belemnocrinacea (Miller, 1883; Moore and Lane, 1978a) is nonmonophyletic. McIntosh (1979) removed *Hypsocrinus* and *Perissocrinus* from the group, and ironically, the namesake genus must now be rejected as well. Through the application of McIntosh's rule, additional dicyclic crinoids that have lost their basal circlets will undoubtedly be recognized. However, loss of the midcup may represent the rule, not the exception, for the origin of monocyclic crinoids in the Paleozoic.

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