

# A Silurian (Homerian) pelmatozoan echinoderm fauna from west-central Ohio, USA

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**Non-technical Summary.**—Blastoid, ‘cystoid,’ and crinoid fossils (phylum Echinodermata) are described for Silurian strata of west-central Ohio. These fossils are from the Cedarville Member of the Laurel Limestone, which is a dolostone rock. All that is preserved in the dolostone are molds and casts of these echinoderms. In the Midcontinent, these rocks were formed in a series of reef and reef-related environments, but the poor preservation of the fossils has hampered their understanding. Crinoids were an important faunal element in these Silurian strata, so this paper is an important step in developing an understanding of these ancient seas. Eleven taxa are described in this fauna, with two new crinoid species.

**Abstract.**—A diverse echinoderm fauna lived in reef and non-reef Silurian facies of the upper Midwestern USA. However, these faunas are dominantly preserved in dolostones with moldic preservation, and fossils from dolostone facies have not been documented to the extent of Silurian crinoids in nondolostone strata. Herein, an echinoderm fauna is described from the dolostones of the Cedarville Member of the Laurel Limestone (Wenlock, Homerian) from the Pepcon Cement Quarry in west-central Ohio. The described fauna contains blastoids, hemicosmitoids, and crinoids, including *Troosticrinus subcylindricus* (Hall and Whitfield, 1875); *Caryocrinites* sp. indet.; an unidentifiable diplobathrid camerate; *Periechocrinus tennesseensis* (Hall and Whitfield, 1875); *Periechocrinus egani?* (Miller, 1881); *Stiptocrinus farringtoni* (Slocum, 1908); *Calliocrinus primibrachialis* Busch, 1943; *Calliocrinus poeppelmani* new species; *Calliocrinus hadros* new species; and *Lecanocrinus* sp. indet. Generic concepts for the Eucalyptocrinitidae are clarified; and, surprisingly, *Eucalyptocrinites* Goldfuss, 1831 is absent from this fauna. Additionally, lectotypes and paralectotypes are designated for *Periechocrinus tennesseensis* and *Calliocrinus primibrachialis*.

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## Introduction

Much of the Silurian in the upper Midwestern United States is represented by dolomitic strata. These dolostones preserve a variety of reef, reef-associated, and basin facies (e.g., Shaver, et al., 1978) that are commonly quite fossiliferous. Fossils in these strata are typically preserved as molds but also a few casts are present, which commonly makes identifications difficult. Consequently, understanding the systematic composition of these strata is commonly poorly constrained. Early workers who studied crinoids and ‘cystoids’ from these Silurian strata in North America include, among others, Hall (1864, 1865), Miller (1882), Weller (1900), Foerste (1920), and Springer (1926). The last comprehensive treatment of crinoid faunas was by Weller (1900). Busch (1943) described dolostone echinoderms from western Ohio, and Witzke and Strimple (1981) described Llandovery crinoid faunas from the Hopkinton Dolomite in eastern Iowa.

Hall and Whitfield (1875) first described *Troosticrinus subcylindricus*, based on a partial internal cast collected from the Cedarville Member in an outcrop located in southwestern Ohio. Foerste (1920) redescribed *Troosticrinus subcylindricus* based on more complete internal casts, which were also collected from the Cedarville dolostones exposed in southwestern Ohio. Most fossil invertebrates within the Silurian dolostones are preserved as internal casts, with occasional external casts present. In the case of *Troosticrinus subcylindricus*, the original and redescribed material were based on the internal casts alone, which provided very little diagnostic morphology.

Recently, an association of blastoids and crinoids were recovered from the Cedarville Dolomite Member of the Laurel Formation exposed within the Pepcon Cement Quarry, located south of Bradford, Ohio. The blastoid *Troosticrinus subcylindricus* was collected from a single discrete sedimentary layer, with a large fenestrate bryozoan colony forming the base of the association. More than 50 specimens of *Troosticrinus subcylindricus* were recovered, which consisted of both internal casts and external molds. The *Troosticrinus subcylindricus* specimens were also

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associated with several ‘cystoids’ and crinoids. The high-fidelity silicone casts of *Troosticrinus subcylindrius* provide an accurate means to properly redescribe the second oldest known blastoid species. A hemicosmitoid rhombiferan and crinoids are also described, including two new species of *Calliocrinus* d’Orbigny, 1850.

Several crinoids are also in this fauna, including an indeterminate diplobathrid; *Periechocrinus tennesseensis* (Hall and Whitfield, 1875); *Periechocrinus egani*? (Miller, 1881), *Stiptocrinus farringtoni* (Slocum, 1908); *Calliocrinus primibrachialis* Busch, 1943; *Calliocrinus poeppelmani* new species; *Calliocrinus hadros* new species.; *Calliocrinus* sp. indet.; and *Lecanocrinus* sp. indet.

### Echinoderm faunas of the Laurel Formation of Ohio

As noted above, the Cedarville Member of the Laurel Formation in west-central Ohio contains blastoids, rhombiferans, diploporans, and crinoids. Blastoids, rhombiferans, and crinoids are discussed in the systematic section below. *Holocystites greenvillensis* Foreste, 1917 was reported from west-central Ohio (Busch, 1943; see also Paul, 1971; Sheffield and Sumrall, 2017), but relatively few specimens of *Holocystites* Hall, 1861 are known from Pepcon Cement Quarry, and they were insufficiently preserved to be identified to species.

Dolomite faunas from the Silurian of Ohio are understudied, so it is not possible to draw any definitive conclusions about the distribution of Cedarville echinoderms. However, it should be noted that Foerste (1920) reported an echinoderm fauna from the Cedarville Member at Cedarville, Ohio with approximately the same biodiversity as that of the Pepcon Cement Quarry. At Cedarville, Ohio, the echinoderms were not from reef and reef-related facies, and these echinoderms were dominated by blastozoans rather than crinoids.

Frest et al. (1999) provided faunal lists for numerous localities in central and eastern North America. A dominant element in many of these faunas is *Eucalyptocrinites* Goldfuss, 1831, which is absent from the new fauna reported herein. Re-examination of other dolomite faunas is needed to determine whether the Pepcon fauna, which lacks *Eucalyptocrinites*, is an anomaly, or if *Eucalyptocrinites* is misidentified in some other faunas. Much new work is required to understand the temporal and paleoenvironmental distribution of echinoderms through the dolomite facies of the midcontinental USA.

### Geologic setting

Rocks of Llandoveryan through Ludlovian age (in North American regional stratigraphic nomenclature collectively referred to as the Niagaran Stage) are exposed along the northern flank of the Cincinnati Arch in southwestern and west-central Ohio. Although many nomenclatural systems have been proposed to describe the Silurian strata of the Cincinnati Arch, in this study, we follow the nomenclature of Brett et al. (2012), Sullivan et al. (2016), and Oborny et al. (2020). The lithological sequence in this portion of the Arch consists of the Brassfield (both ‘white’ and ‘red’ lithology), Dayton, Osgood, Lewisburg, and Massie formations, as well as the Laurel Formation, which includes

the Euphemia, Springfield, and Cedarville members (Fig. 1). These rocks are exposed in a variety of settings, both natural and man-made. Within the numerous active quarries in this region that mine limestones, dolomitic limestones, and dolostones, portions of or complete sequences of the Niagaran Series are present. A particularly clean exposure is present in the C. F. Poeppelman (Pepcon) Cement Quarry, 40°06’30”N, 84°25’30”W, located in Bradford, Ohio, a town that borders the east-central Darke County line and northwestern Miami County line (Fig. 2).

The lowest lithological units that occur at the Pepcon Cement Quarry include the Brassfield (the ‘red’ lithology), Dayton, Osgood, and Lewisburg formations (Fig. 3). These units are exposed in the deepest pits of the quarry, particularly around drainage areas. Throughout the main platform of the quarry, the Massie Formation and Laurel Formation (which includes the Euphemia Dolomite, Springfield Dolomite, and Cedarville Dolomite members) are actively mined. The uppermost bed, the Cedarville Dolomite, consists of light-blue gray to orange-gray, mottled, coarsely crystalline dolomitic limestone that is abundantly biomoldic and exhibits a vuggy porosity. At the Bradford locality, the thickness of the Cedarville Member is ~15 m, which is fairly consistent throughout the quarry.

Although pentamerid brachiopods are scattered throughout the Cedarville Dolomite, there is a discontinuous zone of pentamerid brachiopods concentrated in life position near the contact of the Springfield and Cedarville members. The pentamerid layer consists almost exclusively of the very large, moldic preserved brachiopod *Pentamerus oblongus* (Sowerby in Murchison, 1839). Above this concentrated layer, the Cedarville is quite vuggy and bioturbated. Higher up in the section, the vuggy, bioturbated dolomitic limestone grades into a more massive lithology. Throughout the Cedarville, a diverse fauna of crinoids, cystoids, and brachiopods are abundant. Corals, bryozoans, cephalopods, gastropods, and trilobites are also commonly scattered throughout the unit. Due to the extensive diagenesis of the unit, the preservation of the fossil fauna is moldic, yielding both internal casts and external molds (Fig. 4). Molds and casts of bryozoans, stromatoporoids, and corals tend to preserve poor surface details, but those of gastropods, brachiopods, and particularly echinoderms can be taxonomically diagnostic.

Within the quarry, the uppermost portion of the Cedarville Dolomite exposes a discontinuous band of biohermal masses. These small bioherms range from ridge-like to domal in shape and span a few centimeters to nearly a meter in overall length. Preservation within the bioherms is mostly moldic, with fenestrate bryozoans, stromatoporoids, gastropods, and brachiopod valves. The biohermal masses exposed within the Bradford locality are similar to those in both shape and size as those within the late Llandoveryan dolostones of eastern Wisconsin, particularly the Cordell Dolomite Member of the Manistique Formation and the Racine Formation, as well as the late Llandoveryan Hopkinton Dolomite of eastern Iowa (summarized by Witzke and Strimple, 1981). As is the case at these and other Niagaran dolostone localities, no one organism is solely responsible for construction of the calcareous bioherms (Schrock, 1939).

Crinoids within the Pepcon Cement Quarry include *Periechocrinus tennesseensis*; *Periechocrinus egani*?; *Stiptocrinus*

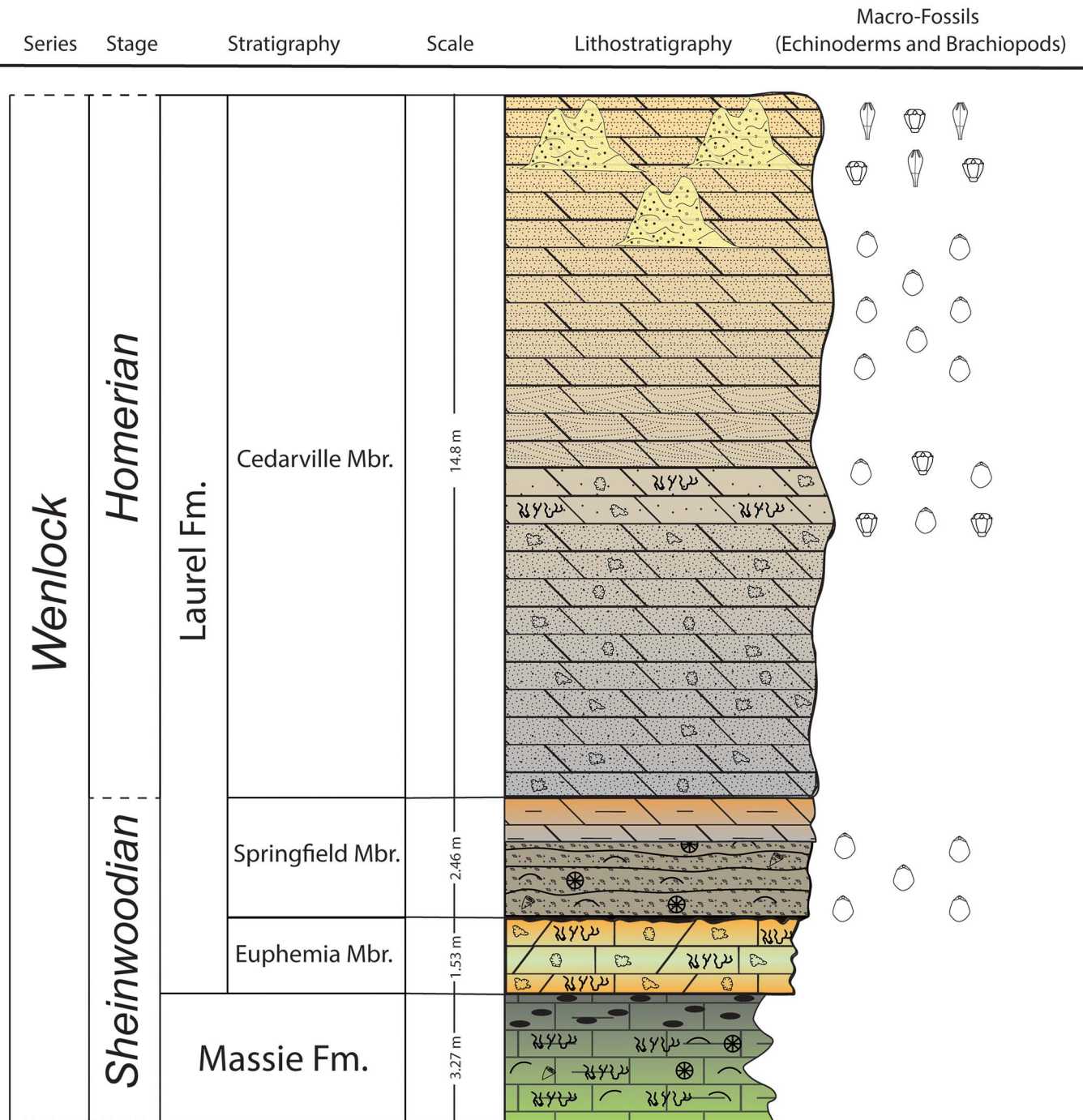


Figure 1. Stratigraphic section of the Pepon Cement Quarry, near Bradford, Ohio, indicating relative position of common fossils.

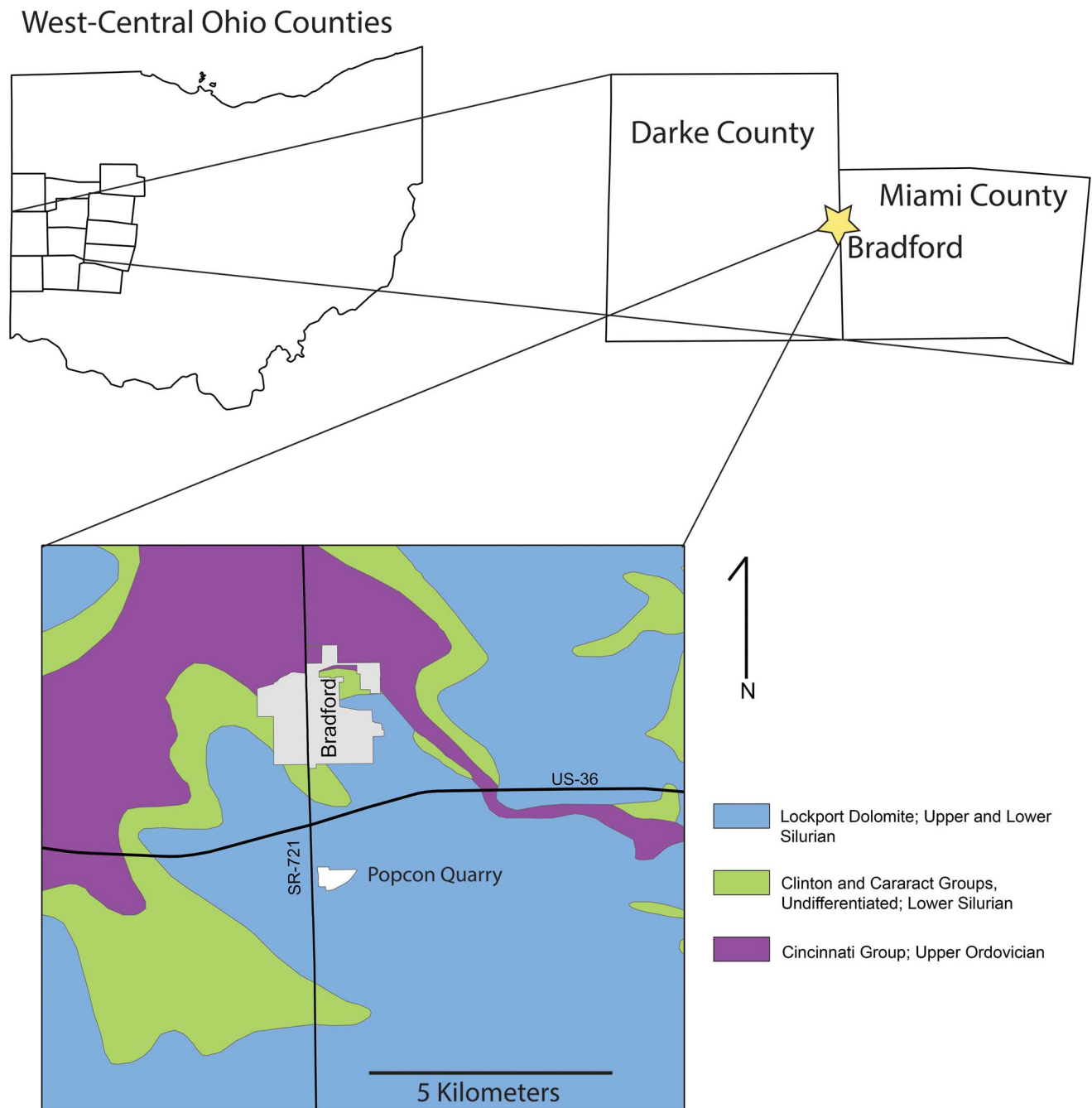
*farringtoni*; *Callioocrinus primibrachialis*; *Callioocrinus poepplemanni* n. sp.; *Callioocrinus hadros* n. sp.; *Callioocrinus* sp. indet., *Lecanocrinus* sp. indet.; and an indeterminate diplobathrid camerate. The rhombiferan, *Caryocrinites* sp. indet., and a diploporan, *Holocystites* Hall, 1861, are also present at this locality. Crinoids and ‘cystoids’ are scattered throughout the Cedarville Dolomite exposed at the quarry, but specimens tend to be most prevalent within the bioherms near the top of the unit. The specimens of *Troosticrinus subcylindricus*, both external molds and internal casts, were found in association with crinoids and cystoids within these biohermal units.

**Materials, methods, and preservation**

*Methods.*—As noted above, available specimens for this study include external and internal molds preserved in dolomitic rocks. Casts were made of external molds, both from collected specimens and in the field from large blocks and the quarry walls of the Pepon Cement Quarry. For the latter, a corresponding external mold is not deposited in the Orton Geological Museum. Casts were made with latex and/or silicone platinum-cure.

As noted in figure captions, some figures of external casts were retouched to eliminate air bubbles in the cast.





**Figure 2.** Locality map illustrating the position of the Popcon Cement Quarry in west-central Ohio.

As noted above, identification of fossils from dolomitic facies can be a challenge. Because of the crystallinity of the dolostone, the rock commonly breaks randomly rather than along bedding surfaces. In these strata, echinoderms are primarily preserved as external and internal (steinkern) molds. Casts can be made of external molds. However, plate boundaries are not always well defined, and the surface texture of external molds typically reflects the crystallinity of the dolostone rather than the fine details of plate sculpturing.

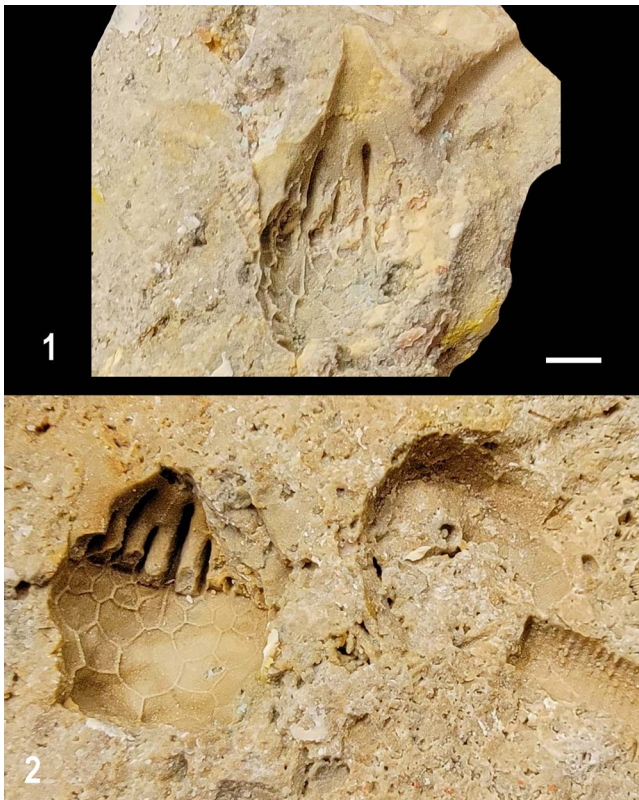
Because the majority of specimens are preserved as internal molds, it can be challenging to compare internal molds with intact specimens from nondolostone faunas, such as the Waldron

Shale of Indiana and Tennessee, the Rochester Shale of New York, and the Brownsport Formation of Tennessee. Generic assignments in dolomitic faunas can be challenging, and species assignments are commonly difficult or impossible, which can necessitate leaving a taxon in open nomenclature.

*Classification and terminology.*—Class and ordinal levels of blastoids and hemicosmitoids follow Waters and Horowitz (1993) and Sumrall and Waters (2012), and Sheffield et al. (2022), respectively. Ordinal and superordinal classification of crinoids follows Cole (2017, 2018), Wright (2017a, b), and Wright et al. (2017). Family-level classification of crinoids



**Figure 3.** Exposed strata in highwall in the Pepcon Cement Quarry (see Fig. 1 for thicknesses).



**Figure 4.** External molds of *Callioocrinus* from the Pepcon Cement Quarry: (1) *Callioocrinus poepplemanni* n. sp. (OSU 558856), note conical tegmen and impression of elongate spines (compare with Fig. 11.5, 11.6); (2) *Callioocrinus hadros* n. sp. (OSU 558858), note robust, short tegmen partition plates and urn-shaped calyx (compare with Fig. 12.1). Scale bar = 5 mm (1, 2).

follows Moore and Teichert (1978). Morphological terminology for hemicosmitoids and blastoids follow Kesling (1967) and Fay (1967), respectively. Morphologic terminology for crinoids is from Webster (1974), Ubaghs (1978b), Kammer et al. (2013), Webster and Maples (2008), Ausich et al. (2020), and Ausich and Donovan (2023). Interray plating is indicated by the number of plates in each range from the proximalmost plate to the last range before the tegmen (e.g., 1-2-2-1). In the posterior interray, the primanal is designated by ‘P,’ and in regular interrays the proximal most plate is designated by ‘1.’ A, B, C, D, and E represent echinoderm rays following the Carpenter Ray system (Ubaghs, 1978b, p. T63). Heteromorphic column patterns are indicated using the Webster (1974) system.

In specimen measurements, abbreviations are as follows: BH, basal plate height; BW, basal plate width; CaH, calyx height; CaW, calyx width; ColW, column width; IH, infrabasal height; Pbr1H, first primibrachial height; Pbr1W, first primibrachial width; RFW, radial facet width; RH, radial plate height; RW, radial plate width; TH, theca height; TW, theca maximum width; and TeH, tegmen height. All measurements in mm; \* after a measurement indicates that the specimen is crushed or that the feature is incomplete.

The lists of species within crinoid genera were taken uncritically from Webster (2014).

**Repositories and institutional abbreviations.**—New specimens reported in this study are in the Orton Geological Museum, The Ohio State University, Columbus, Ohio (OSU). Other museum designations are: FMNH P, Field Museum of Natural History, Chicago, Illinois; and USNM PAL, U.S. National Museum of Natural History, Washington, D.C.



## Systematic paleontology

Class Blastoidea Say, 1825  
 Family Troosticrinidae Bather, 1899  
 Genus *Troosticrinus* Shumard, 1866

*Type species.*—*Pentremites reinwardti* Troost, 1835.

*Troosticrinus subcylindricus* (Hall and Whitfield, 1875)  
 Figures 5–7

1875 *Pentremites subcylindrica* Hall and Whitfield, p. 129, pl. 6, fig. 13.

1920 *Troosticrinus subcylindricus*; Foerste, p. 65, pl. 3, fig. 3a–c.

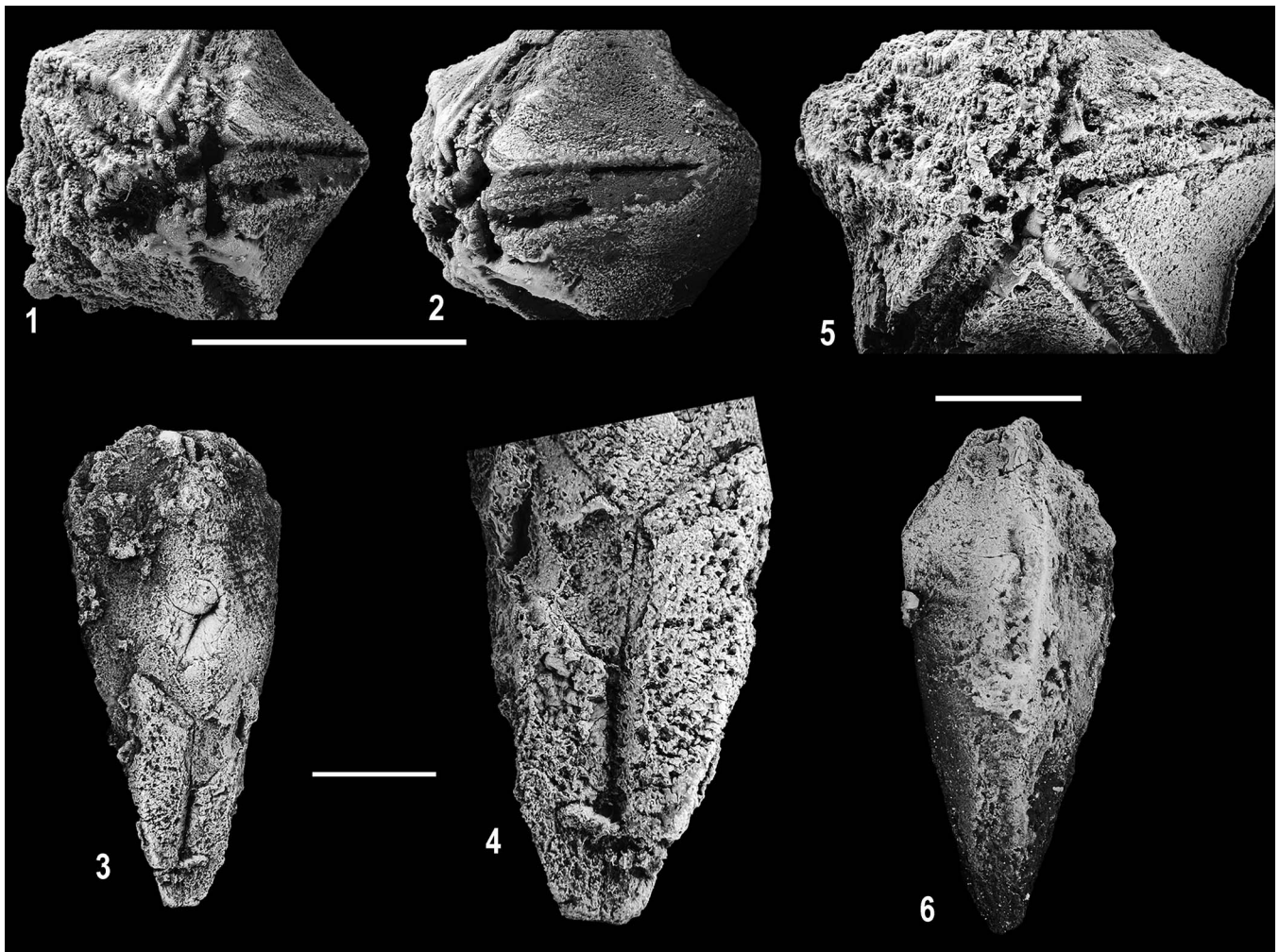
*Holotype.*—USNM PAL 558803.

*Diagnosis.*—Theca elongate and conical, upper portion pentagonal in cross section, below the ambulacra tapering slightly convexly toward the base; ambulacra linear, short and narrow, comprising < 10% of the length of the theca; deltoids

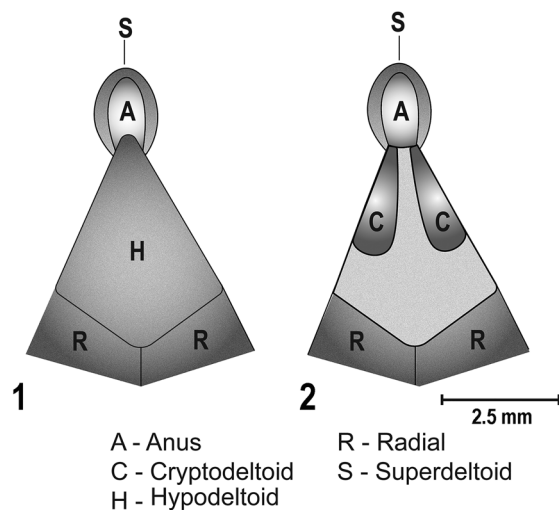
small and extending slightly above the summit. Five paired spiracles, including four spiracles and a paired anispiracle. Lancet not exposed and covered by side plates. One pore between each set of side plates.

*Occurrence.*—Cedarville Dolomite Member, Laurel Formation, Pepcon Cement Quarry, near Bradford, Ohio, USA.

*Description.*—Theca elongate and conical, below the ambulacra tapering convexly toward the base (Fig. 5.5). Ambulacra short, narrow, and linear, comprising < 10% of the height of the theca (Fig. 5.1, 5.2, 5.5). Five paired spiracles, including four paired spiracles and a paired anispiracle. Lancet concealed under side plates. Three hydrospire folds on each side of ambulacra. One pore between each set of side plates. Four deltoids, small, and only extending slightly above the summit (Fig. 5.6), with an additional hypodeltoid and superdeltoid (Fig. 6). Cryptodeltoids not visible but might have been preserved in the molds. Deltoids not visible in lateral view. Five radials forming a pentagonal outline. Radial plate sutures slightly depressed (Fig. 5.4). Theca with very fine growth lines. Three basals, two zygous and one azygous,



**Figure 5.** *Troosticrinus subcylindricus* (Hall and Whitfield, 1875): (1, 2) Oral and oblique oral views of OSU 558801: (1) CD interray at 2 o'clock; (2) D-ray ambulacrum. (3, 4) Lateral views of OSU 558802: (3) lateral view of entire theca; (4) lateral view of lower half of theca. (5, 6) OSU 558803: (5) oral view of ambulacra, posterior interray at base; (6) lateral view of entire theca. Scale bars = 10.0 mm; latex casts coated with ammonium oxide sublimate for photography.



**Figure 6.** Diagrammatic anal region of *Troosticrinus subcylindricus* (Hall and Whitfield, 1875): (1) anal plates; (2) anal plates with hypodeltoid removed, cryptodeltoids fully visible.

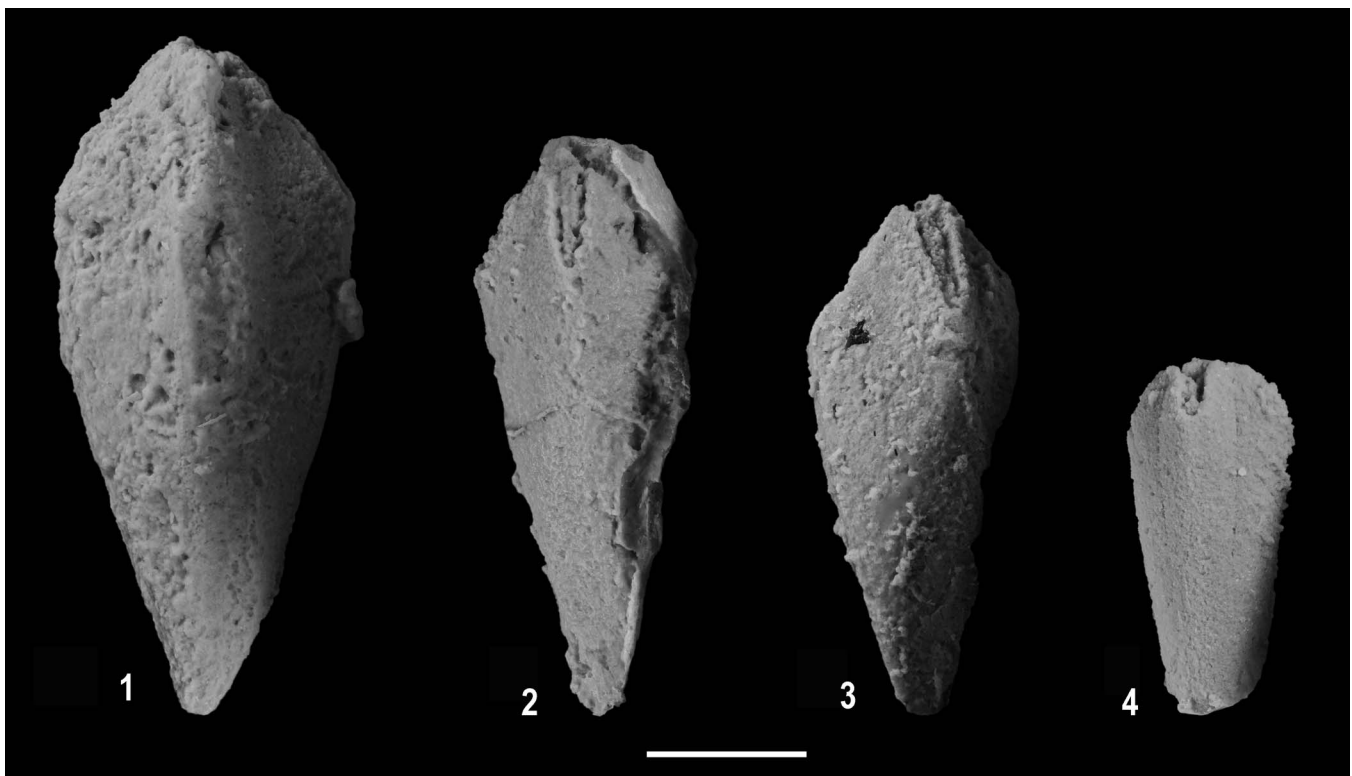
in the normal position, tapering into a triangular outline (Fig. 5.3).

**Materials.**—OSU 558801–558811.

**Measurements.**—OSU 558802: TH 38.0, TW 15.0; OSU 558803: TH 41.8, TW 17.7; OSU 558804: TH 32.4, TW 13.3; OSU 558805: TH 21.4\*, TW 10.5.

**Remarks.**—Specimens previously described were all internal casts, making the current description necessary to understand this species. Gerontic specimens become more convex in profile (Fig. 7.1). The earliest clear example of ontogenetic variation in blastoids (Fig. 7) is in *Troosticrinus subcylindricus*, which is the second oldest described species of *Troosticrinus*. *Troosticrinus sanctipaulensis* Foerste, 1920 is the oldest species of *Troosticrinus* and is most closely related to *Troosticrinus subcylindricus* (Fig. 8). Specimens used in this study occurred as a localized colony, associated with a significant bryozoan colony. The bryozoans formed a 50–75 mm layer that is quite obviously in cross section. The bryozoans were poorly preserved and were most likely a fenestellid. The best specimens were collected just above the bryozoans and surrounded by sediment. Specimens occurred directly in the bryozoans but were typically difficult to collect because they were more dolomitized and fragmented from compaction. Crinoids and ‘cystoids’ also occurred in the colony but were fewer in number. Silurian blastoids were typically preserved as isolated specimens and were typically rare elements of a large echinoderm fauna. The specimens in this colony represent a broad ontogenetic range, suggesting that it was a longer-lasting colony and represents many spatfalls.

Another example of a blastoid/bryozoan colony occurs in the Silurian Waldron Shale. The bryozoan *Trematopora* sp. indet. occurs with the blastoid *Decaschisma pulchellum* (Miller and Dyer, 1878). Bulk sampling resulted in a yield of two or three blastoids per cubic foot of matrix (using #10 sieve size), with a total yield of > 60 specimens. The colony consisted of



**Figure 7.** Growth series of *Troosticrinus subcylindricus* (Hall and Whitfield, 1875) in lateral view: (1) OSU 558803; (2) OSU 558804; (3) OSU 558805; (4) OSU 558806. Scale bars = 10.0 mm; latex casts coated with ammonium oxide sublimate for photography.

Series	Stage	<i>Troosticrinus</i>	<i>Polydeltodeus</i>	<i>Decaschisma</i>	gen. sp. indet.
Pridoli	Pridolian	<i>T. reinwardti minimus</i> (Bainbridge Fm.)	<i>P. enodatus</i> (Decatur Ls.) <i>P. plasovae</i> (Pridoli Beds)		
Ludlow	Ludfordian	<i>T. reinwardti</i> (Beech River Mbr.) <i>T. concinna</i> (Bob Fm.) <i>T. sp. indet.</i> (Lobelville Fm.)	<i>P. enodatus</i> (Henryhouse Fm.)		
	Gorstian				
Wenlock	Homerian	<i>T. sp. indet.</i> (Racine Dol.) <i>T. sp. indet.</i> (reported, not confirmed) (Louisville Ls.)		<i>D. pulchellum</i> (Waldron Sh.)	
	Sheinwood.	<i>T. subcylindricus</i> (Cedarville Dol.) <i>T. sanctipaulensis</i> (Laurel Ls.)		<i>D. sp. indet.</i> (Massie Sh.)	
Llandovery	Telychian				<i>incertae sedis</i> (Hopkinton Fm.)  <i>Blastoid</i> reported <i>incertae sedis</i> (Estill Sh.)
	Aeronian				
	Rhuddan.				

**Figure 8.** Stratigraphic distribution of Silurian blastoid genera and species. Taxa not otherwise discussed in the text are *Troosticrinus reinwardti minimus* (Foerste, 1920), *Troosticrinus concinna* Reinmann, 1945, *Polydeltodeus enodatus* Reinmann and Fay, 1961, *Polydeltodeus plasovae* Prokop, 1962.

multiple spat falls, also indicating a longer-lived colony. Most Waldron localities have a low abundance of blastoids, typically in the single digits or none (Ausich, 1975). The association of blastoids and bryozoans also occurs in the Devonian Silica Shale, unit 13 (Brint Road Member) of Ohio, where

*Hyperblastus reimani* (Kier, 1952) occurs with the bryozoan *Sulcoretopora deissi* (McNair, 1937). These colonies tend to form limestone lenses with blastoids preserved on bedding surfaces. At Sylvania, Ohio, the blastoids were accompanied by a diverse crinoid association (Kesling, 1975). However, at



Pauling, Ohio, crinoids very rarely occurred with crinoids. More than 1,000 blastoids have been collected from the Silica Shale.

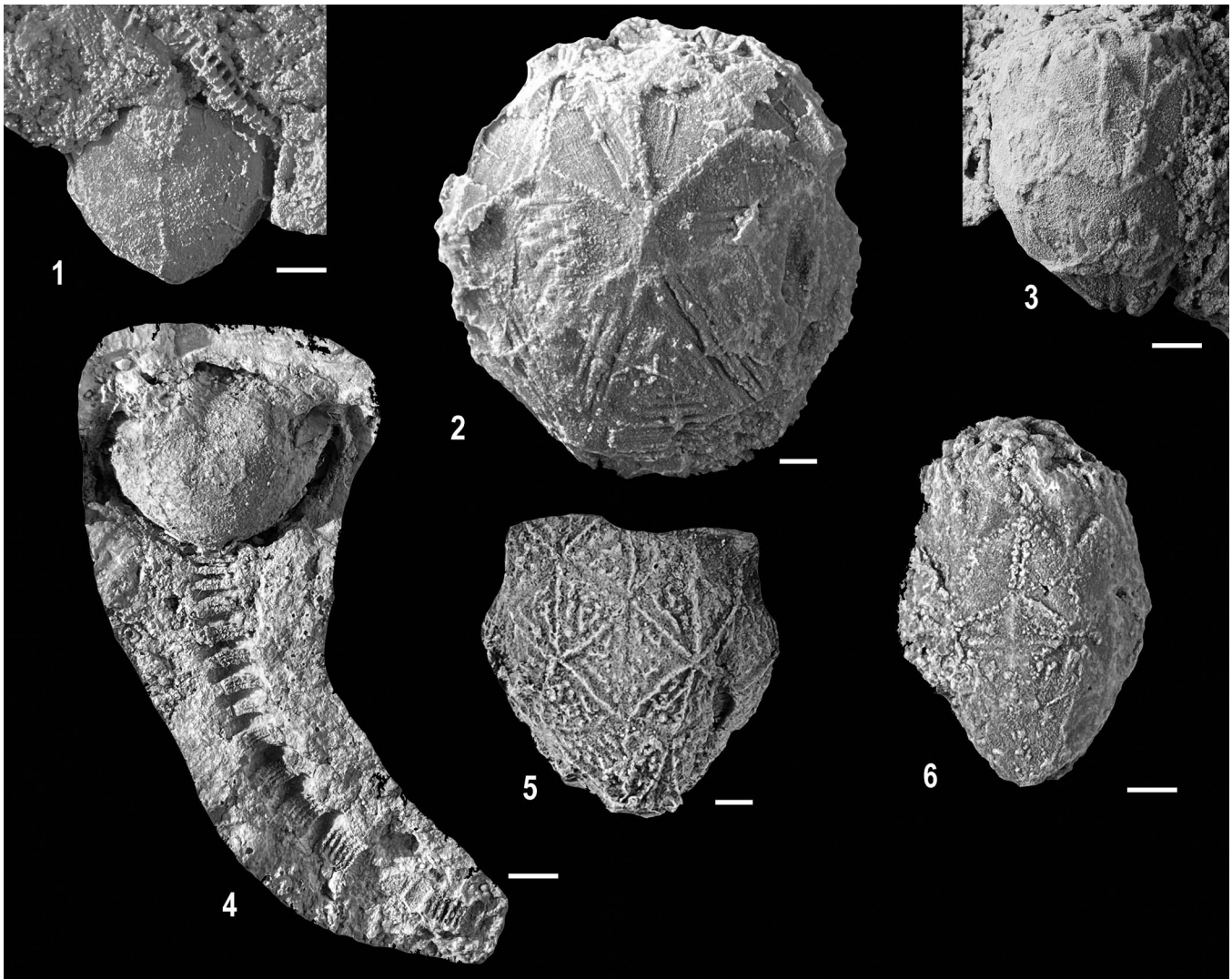
Class Rhombifera von Zittel, 1879  
 Superfamily Hemicosmitoidea Jaekel, 1918  
 Family Caryocrinidae Bernard, 1895  
 Genus *Caryocrinites* Say, 1825

*Type species.*—*Caryocrinites ornatus* Say, 1825.

*Caryocrinites* sp. indet.  
 Figure 9.2, 9.3, 9.5, 9.6

*Measurements.*—OSU 558812 (external mold): TW 25.4\*; OSU 558813 (internal mold): TH 47.2\*, TW 42.1\*; OSU 558814 (internal mold): TH 35.5\*, TW, 22.2\*; OSU 558815 (internal mold): TH 43.8\*, TW 28.3\*; OSU 558816 (internal mold): TH 30.2\*, TW 23.0\*.

*Remarks.*—Five specimens of *Caryocrinites* sp. indet. are known from the Cedarville Member fauna. These include one external mold and four internal molds. The external mold (OSU 558812) is approximately the lower half of a specimen, and the entire shape of the theca cannot be determined (Fig. 9.5). OSU 558813 is only a portion of a very large theca (Fig. 9.2), and a single radial plate is the only plate completely preserved. OSU 558814–558816 are internal molds with a high-globe shape, with OSU 558816 somewhat more spherical rather than an elongate ovoid shape (Fig. 9.3). The external mold preserves a striking pattern of plate sculpturing unlike that in other known species of *Caryocrinites* (Fig. 9.5). Each preserved plate has six stellate ridges connecting to like ridges of adjoining plates. The spaces between the radiating ridges are completely filled with coarse nodes that do not form a pattern. Other species with nodes between stellate ridges either have nodes aligned (e.g., *Caryocrinites ornatus*) or the spaces between radiating ridges are incompletely filled with nodes.



**Figure 9.** *Caryocrinites* and a diplobathrid camerate from the Pepcon Cement Quarry: (1, 4) Internal molds of Diplobathrida indet.: (1) OSU 558819, lateral view of internal mold, note mold of pluricolumnal along the upper right margin of the calyx; (4) OSU 558820, calyx with column attached, note the increasing number of internodals distally. (2, 3, 5, 6) *Caryocrinites* sp. indet.: (2) OSU 558813, internal mold of a very large partial specimen with one large radial plate intact; (3) OSU 558816, internal mold in matrix; (5) OSU 558812, external latex cast of half of distal half of a specimen, not striking thecal plate sculpturing; (6) OSU 558814, internal mold preserving pore canals. Scale bars = 5.0 mm; specimens coated with ammonium chloride sublimate for photography.

The internal molds preserve radiating ridges and growth lines, as well as preserving remnants of pore canals (Fig. 9.6).

Unfortunately, it is not possible to determine whether the internal and external molds are conspecific, and even the internal molds have some contrasting features. So, despite the fact that the plate sculpturing on OSU 558812 is unlike any other species in *Caryocrinites*, this taxon is left in open nomenclature until its morphology can be more fully understood.

Class Crinoidea Miller, 1821  
Subclass Camerata Wachsmuth and Springer, 1885  
Infraclass Eucamerata Cole, 2017  
Order Diplobathrida Moore and Laudon, 1943

Diplobathrida indet.  
Figure 9.1, 9.4

*Occurrence*.—Cedarville Member of the Laurel Formation (Silurian, Wenlock, Homerian) from the Pepcon Cement Quarry near Bradford, Ohio.

*Description*.—Calyx low- to medium-globe shape; basal concavity absent (Fig. 9.1). Calyx plate sculpturing unknown. Infrabasal cirlet ~7% of calyx height, small, very low cone-shaped, visible in lateral view; five infrabasal plates. Basal cirlet ~26% of calyx height; radial cirlet ~18% of calyx height.

Regular interarray plating 1-2-?, in wide contact with tegmen; interradial plates hexagonal, decreasing in size distally. First interradial plate higher than wide. CD interarray unknown.

Two fixed primibrachials, both higher than wide. Fixed brachials continue into tertibrachials, but number of fixed tertibrachials unknown.

Tegmen and free arms unknown.

Columnals circular with a convex latus; column pattern is N-5 at distal end of preserved column, from base of calyx to end of preserved column progressively more internodals between nodals. Nodals ~4 times higher and ~1.4 times wider than internodals (Fig. 9.4).

*Material*.—OSU 558819 and 558820.

*Measurements*.—OSU 558819 (internal mold): CaH 19.0, CaW 23.0; OSU 558820 (internal mold): CaH 12.0, CaW 22.0, ColW 50.0\*.

*Remarks*.—Two internal molds are described above as Diplobathrid indet. Both have a globe-shaped calyx with grouped arms, and interarrays widely connected with the tegmen. OSU 558819 is a low-globe shape, whereas OSU 558820 is a medium-globe shape. OSU 558819 has calyx plating partially preserved, and the calyx description is based largely on this specimen. The column description is based on OSU 558820.

These two specimens are too poorly preserved to verify with certainty that they are the same taxon and are too incompletely preserved to even assign to a known genus. Regardless, they are a very distinctive taxon from the Cedarville Member and are included for completeness.

Order Monobathrida Moore and Laudon, 1943  
Suborder Compsocrinina Ubaghs, 1978  
Family Periechocrinidae Bronn, 1849  
Genus *Periechocrinus* Morris, 1843

*Type species*.—*Periechocrinus costatus* Austin and Austin, 1842.

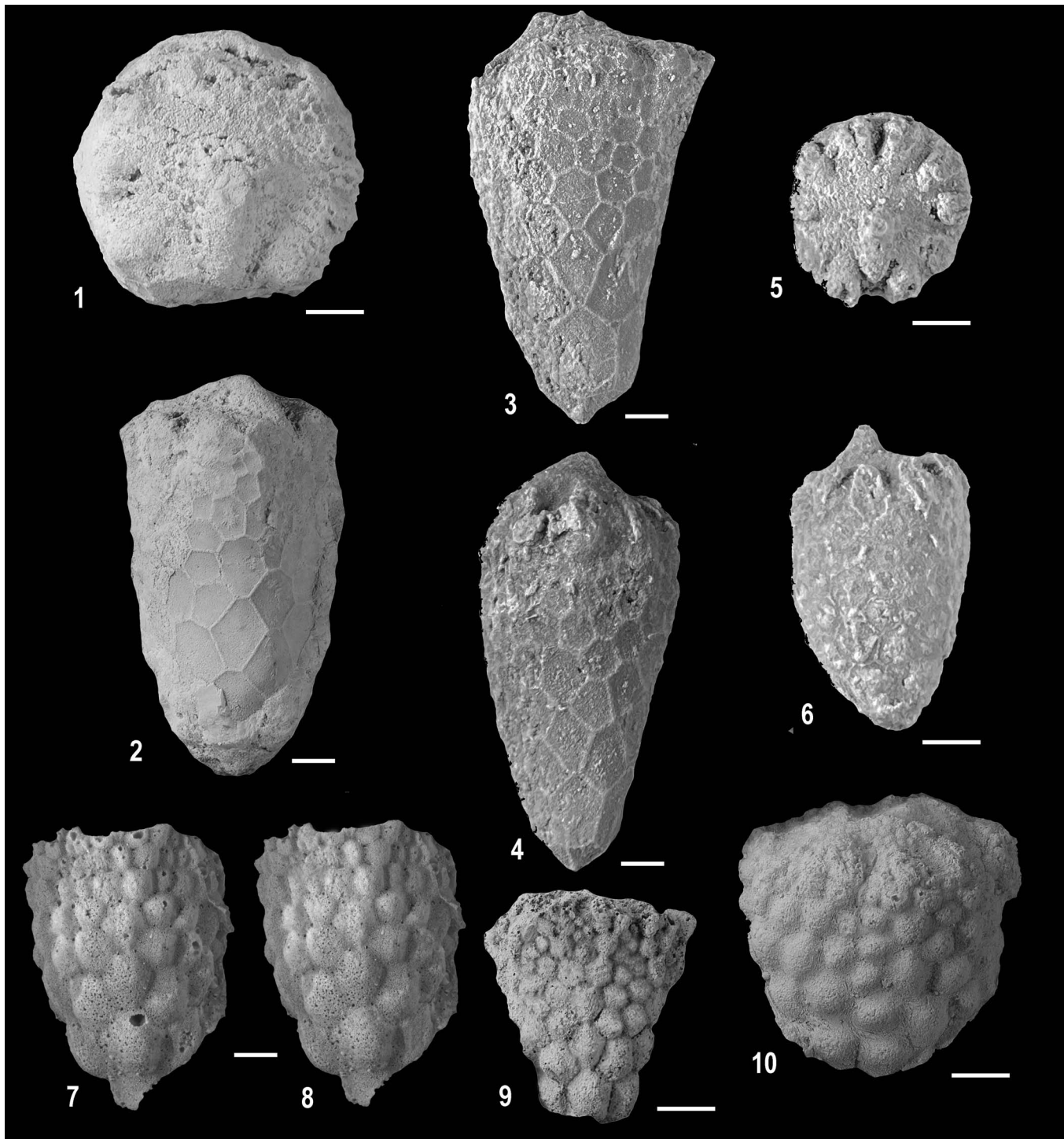
*Included species*.—*Periechocrinus annulatus* Angelin, 1878; *Periechocrinus articulatus* Austin and Austin, 1842; *Periechocrinus baylii* (de Verneuil, 1850); *Periechocrinus brevimanus* (Angelin, 1878); *Periechocrinus bulbous* Ramsbottom in Donovan et al., 2012; *Periechocrinus costatus* Austin and Austin, 1842; *Periechocrinus cuspidatus* (Springer, 1926); *Periechocrinus cylindricus* Foerste, 1917; *Periechocrinus dubius* (Troost in Wood, 1909); *Periechocrinus egani* (Miller, 1881); *Periechocrinus geometricus* Angelin, 1878; *Periechocrinus gorbyi* (Miller, 1891); *Periechocrinus grandiscutatus* Angelin, 1878; *Periechocrinus hamiltonensis* (Goldring, 1923); *Periechocrinus infelix* (Winchell and Marcy, 1865); *Periechocrinus interradiatus* Angelin, 1878; *Periechocrinus laevis* Angelin, 1878; *Periechocrinus limonium* Salter, 1873; *Periechocrinus lindstromi* Wachsmuth and Springer, 1881; *Periechocrinus longidigitalis* (Angelin, 1878); *Periechocrinus longimanus* (Angelin, 1878); *Periechocrinus marcouanus* (Winchell, and Marcy, 1866); *Periechocrinus moniliformis* (Miller, 1821); *Periechocrinus multicostatus* Angelin, 1878; *Periechocrinus natatiformis* Milicina, 2000; *Periechocrinus necis* (Winchell and Marcy, 1866); *Periechocrinus nubilis* (Angelin, 1878); *Periechocrinus ornatus* (Hall and Whitfield, 1875); *Periechocrinus prumiensis geometricus* (Schultz, 1866); *Periechocrinus pulcher* (M'Coy, 1854); *Periechocrinus scanicus* Angelin, 1878; *Periechocrinus schultzi* (Angelin, 1878); *Periechocrinus shaveri* Lane and Ausich, 1995; *Periechocrinus simplex* Salter, 1873; *Periechocrinus speciosus* (Hall, 1852); *Periechocrinus tennesseensis* (Hall and Whitfield, 1875); *Periechocrinus umbrosus* (Miller and Gurley, 1895); *Periechocrinus undulatus* Angelin, 1878; *Periechocrinus urniformis* (Miller, 1881); *Periechocrinus whitfieldi* (Hall, 1864).

*Occurrence*.—Silurian (Llandovery, Telychian) to Ludlow (Ludfordian) of Canada, UK, Estonia, Russia, Sweden, and USA; and Devonian (Emsian to Givetian) of Germany, Spain, and USA (see Ausich et al., 2012; Webster, 2014).

*Periechocrinus tennesseensis* (Hall and Whitfield, 1875)  
Figure 10.1–10.8

*Type specimens*.—Specimens labelled as types in the Hall and Whitfield (1875) collection in the Orton Geological Museum are OSU 3297a–f and 8743a–b. However, none of these specimens correspond to the illustration of this species by Hall and Whitfield (1875, pl. 6, fig. 10). Thus, we are left with the interpretation that the illustration is a composite with some artistic license. OSU 3297a is designated herein as the lectotype, and OSU 3297b–f and 8743a–b are designated herein as paralectotypes.





**Figure 10.** *Periechocrinites* from the Cedarville Member from the Pepcon Cement Quarry: (1, 2) *Periechocrinites tennesseensis* (Hall and Whitfield, 1875), internal mold of OSU 558821: (1) tegmen view; (2) D-ray lateral view of calyx. (3) *Periechocrinites tennesseensis*, OSU 558823, B-ray lateral view of internal mold. (4) *Periechocrinites tennesseensis*, OSU 558822, C-ray lateral view of internal mold. (5, 6) *Periechocrinites tennesseensis*, OSU 558824, internal mold of a juvenile specimen: (5) oral view of tegmen; (6) BC interrady view of calyx. (7, 8) External silicone cast of *Periechocrinites tennesseensis*?, OSU 558848: (7) unretouched photograph; (8) retouched photograph to eliminate air bubbles in cast. (9) *Periechocrinites egani*? (Miller, 1881), OSU 558851, external plaster cast of partial specimen. (10) *Periechocrinites egani*?, OSU 558850, external plaster cast of partial specimen. Scale bars = 5.0 mm; specimens coated with ammonium chloride sublimate for photography.

**Diagnosis.**—*Periechocrinites* with a high bowl-shaped or high cone-shaped calyx, conical basal circlet, sides of the distal calyx parallel or slightly expanding, (presence or absence of ray ridges not known), radial plates higher than wide or as high as wide, first primibrachials higher

than wide, first secundibrachials as wide as high, first interradyial in regular interrays higher than wide, first interradyial plate larger than first primibrachial, 12 or more interradyial plates in regular interrays, flat cone tegmen shape, and 20 arms.



**Occurrence.**—*Periechocrinus tennesseensis* was previously known from the Cedarville Dolomite (Wenlock, Homerian) of southwestern Ohio, the Louisville Limestone (Wenlock, Homerian) to Ludlow, Gorstian) of north-central Kentucky, and the Brownsport Formation (Ludlow, Ludfordian) of western Tennessee. In the present study, it is described from the Cedarville Member of the Laurel Formation (Silurian, Wenlock, Homerian) from the Pepcon Cement Quarry, near Bradford, Ohio.

**Description.**—Calyx large, high-bowl to high-cone shape with sides of the distal calyx parallel or slightly expanding; basal concavity absent (Fig. 10.3). Calyx plate sculpturing unknown. Basal circling ~7% of calyx height, conical; basal plates presumably three, visible in lateral view; radial circling ~15% of calyx height (Fig. 10.4), interrupted in only CD interray; radial plates large, five, hexagonal, 1.2 times wider than high.

Regular interray plating 1-2-2-2 with plates in two offsetting columns; in narrow contact with tegmen (Fig. 10.2), interradial plates typically hexagonal, decreasing in size distally. First interradial plate higher than wide. CD interray P-3-?, poorly known.

Fixed brachials at least through the first or second tertibrachial. Fixed brachials ~65% of calyx height; two fixed primibrachials, two fixed secundibrachials, and one or two fixed tertibrachials; fixed intrabrachials medially between second fixed secundibrachials.

Tegmen flat cone (Fig. 10.2–10.4, 10.6), comprised of numerous very small plates (Fig. 10.1, 10.5). Anal tube beginning as a bulge of the outer margin of the CD interray and tegmen; continuing to expand slightly across the tegmen to near the center of the tegmen, becoming a vertical, narrow, probably short anal tube.

Free arms 40; other details unknown. Column unknown.

**Additional material.**—OSU 558821–558845; OSU 5558846–558849 questionably assigned to *Periechocrinus tennesseensis*.

**Measurements.**—OSU 558821 (internal mold): CaH 39.9, CaW (distal) 23.4, BH 4.8, BW 5.0, RH 9.3, RW 7.8, TH 4.0; OSU 558822 (internal mold): CaH 40.5, CaW (distal) 23.1, BH 3.8, BW 4.4, RH 8.4, RW 5.8, TH 9.0; OSU 558823 (internal mold): CaH 39.2, CaW (distal) 25.4, BH 4.3, BW 4.4, RH 9.4, RW 7.3, TH 9.8; OSU 558824 (internal mold): CaH 19.8, CaW (distal) 15.4, BH 2.5, RH 4.4, RW 3.8, TH 6.4.

**Remarks.**—As with most taxa in the Cedarville Member, species identification is difficult because it can be difficult to compare molds and casts of this new material to species definitions in other faunas that were based on either external morphology, internal casts, or rarely both. Specimens assigned herein to *Periechocrinus tennesseensis* with confidence are all internal molds, and a few external molds are questionably assigned to *Periechocrinus tennesseensis* (e.g., Fig. 10.7). The latter specimens have smooth, very convex calyx plates with depressed sutures, and it is not certain that these exterior plate characteristics were present on specimens only known from internal molds. Portions of plates are attached to a few internal

molds. These incomplete plates are preserved in dolostone and are not well enough preserved to determine details of plate surfaces.

North American, Silurian species of *Periechocrinus* are distinguishable on the basis of calyx shape, profile of the distal calyx, calyx plate sculpturing, presence or absence of ray ridges, shape of the radial plates, shape of the first primibrachials, shape of the first secundibrachials, size of the first interradial plate compared to the first interradial plate, number of interradial plates fixed in regular interrays, tegmen shape, and arm number. *Periechocrinus tennesseensis* has a high bowl-shaped or high cone-shaped calyx, conical basal circling, sides of the distal calyx parallel or slightly expanding, (presence or absence of ray ridges not known), radial plates higher than wide or as high as wide, first primibrachials higher than wide, first secundibrachials as wide as high, first interradial in regular interrays higher than wide, first interradial plate larger than first primibrachial, 12 or more interradial plates in regular interrays, flat cone tegmen shape, and 20 arms. This contrasts with *Periechocrinus egani?*, which also occurs in the Cedarville Member, because *Periechocrinus egani?* has a medium cone-shaped calyx, (basal circling not known), the sides of the distal calyx expanding through the distal calyx, defined ray ridges absent but increased convexity of ray plates demarcating the rays, radial plates probably as high as wide, first primibrachials higher than wide, first secundibrachials higher than wide or as high as wide, first interradial plates in regular interrays higher than wide, first interradial plates in regular interrays larger than the first primibrachial plate, < 12 interradial plates, flat cone-shaped tegmen, and 20 arms.

Two juvenile specimens of *Periechocrinus tennesseensis* were recovered from the Cedarville Member (OSU 558814, 558844). These specimens have the same plating as adults, but the plates are more equidimensional when compared to adult specimens (compare Fig. 10.4 and 10.6).

*Periechocrinus egani?* (Miller, 1881)  
Figure 10.9, 10.10

**Holotype.**—Not located.

**Diagnosis.**—*Periechocrinus* with a medium cone- to medium bowl-shaped calyx, (basal circling not known), sides of the distal calyx expanding through the distal calyx, defined ray ridges absent but increased convexity of ray plates demarcating the rays, radial plates probably as high as wide, first primibrachials higher than wide, first secundibrachials higher than wide or as high as wide, first interradial plates in regular interrays higher than wide, first interradial plates in regular interrays larger than the first primibrachial plate, < 12 interradial plates, flat cone-shaped tegmen, and 20 arms.

**Occurrence.**—*Periechocrinus egani?* was initially described from the Racine Dolomite of northeastern Illinois, and the precise position of this rock unit within the Silurian is uncertain. In the present study, *Periechocrinus egani?* is described from the Cedarville Member of the Laurel Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

*Description.*—Calyx small, medium-cone to medium-bowl shape (Fig. 10.9, 10.10). Calyx plate sculpturing smooth; plates very convex with depressed sutures. Basal cirlet not preserved. Radial cirlet ~25% of calyx height; interrays only interrupted in the CD interray. Radial plates largest plates in calyx, five, hexagonal, ~1.2 higher than wide.

Regular interray plating 1-2-2-2 in two alternating rows, in narrow contact with tegmen (Fig. 10.9); interradial plate sizes decreasing distally, hexagonal. First interradial plates as high as wide. CD interray not known.

Fixed brachials through second or third tertibrachial (two fixed primibrachials and two fixed secundibrachials); variable convexity of plates giving impression of ray ridges, but no defined ridges present.

Tegmen flat cone with small plates, raised radial regions separated by depressed interradial regions.

Free arms 20 but other details unknown. Column unknown.

*Additional material.*—OSU 558850–558851.

*Measurements.*—OSU 558850 (external mold): CaH 20.0\*, CaW (distal) 14.9, RH 4.4\*, RW 3.5, TH 2.5\*.

*Remarks.*—Two external molds are questionably assigned to *Periechocrinus egani*. No corresponding internal modes can be assigned to *Periechocrinus egani*. This taxonomic placement was made with some question because neither mold exposes a complete side of a calyx from the proximal basal cirlet to the tegmen. However, these specimens are similar in having more equidimensional calyx plates, unlike *Periechocrinus tennesseensis* and most other species of *Periechocrinus*. This taxon is compared to *Periechocrinus tennesseensis* in the remarks section of the latter species.

#### Genus *Stiptocrinus* Kirk, 1946

*Type species.*—*Stiptocrinus spinosus* Kirk, 1946.

*Included species.*—*Stiptocrinus carinatus* (Kirk, 1946); *Stiptocrinus chicagoensis* (Weller, 1900); *Stiptocrinus farringtoni* (Slocum, 1908); *Stiptocrinus howardi* (Miller, 1892); *Stiptocrinus nodosus* (Springer, 1926); *Stiptocrinus spinosus* Kirk, 1946.

*Occurrence.*—Silurian (Wenlock, Homerian) to Devonian (Lochkovian), USA (see Webster, 2014).

*Stiptocrinus farringtoni* (Slocum, 1908)  
Figure 11.9

*Type species.*—Holotype, FMNH P 8474.

*Diagnosis.*—Medium cone-shaped calyx; flat outer surface of calyx plates, smooth sculpturing; deep, widely impressed calyx plate sutures; basal cirlet visible in lateral view, not in basal concavity; arms grouped; short arm lobes present.

*Occurrence.*—In the present study, *Stiptocrinus farringtoni* is described from the Cedarville Member of the Laurel

Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

*Description.*—Calyx small, medium-cone shaped without basal concavity; arm openings grouped with very short arm lobes (Fig. 11.9). Calyx plate sculpturing smooth; plates flat and separated by wide sutural depressions. Basal cirlet ~15% of calyx height; three basal plates, visible in lateral view. Radial cirlet ~40% of calyx height, radial cirlet interrupted in the CD interray; radial plates largest plates in calyx, five, hexagonal, twice as high as wide.

Regular interray plating 1-2-3-?, in contact with tegmen (Fig. 11.9); interradial plates small, hexagonal. First interradial plate largest; subsequent interradial plates decreasing in size distally. CD interray P-3-?, wider than regular interrays.

Two fixed primibrachials and two fixed secundibrachials. Intraradial plates between secundibrachials within a ray.

Tegmen unknown.

Free arms 10; details unknown. Column unknown.

*Additional material.*—A single external mold was available for study from the Cedarville Member of the Laurel Formation (OSU 558852).

*Measurements.*—OSU 558852 (external mold): CaH 16.9, CaW (distal) 16.3\*, BH 3.0, BW 3.8, RH 4.5, RW 4.4, TH 3.8\*.

*Remarks.*—A single specimen of *Stiptocrinus farringtoni* is known from the Cedarville Member. It is an external mold that yielded an excellent cast from the basals to the arm lobes, but the plating above the arm lobes is poorly defined. The flat calyx plates with wide and deeply impressed sutures are diagnostic for this species.

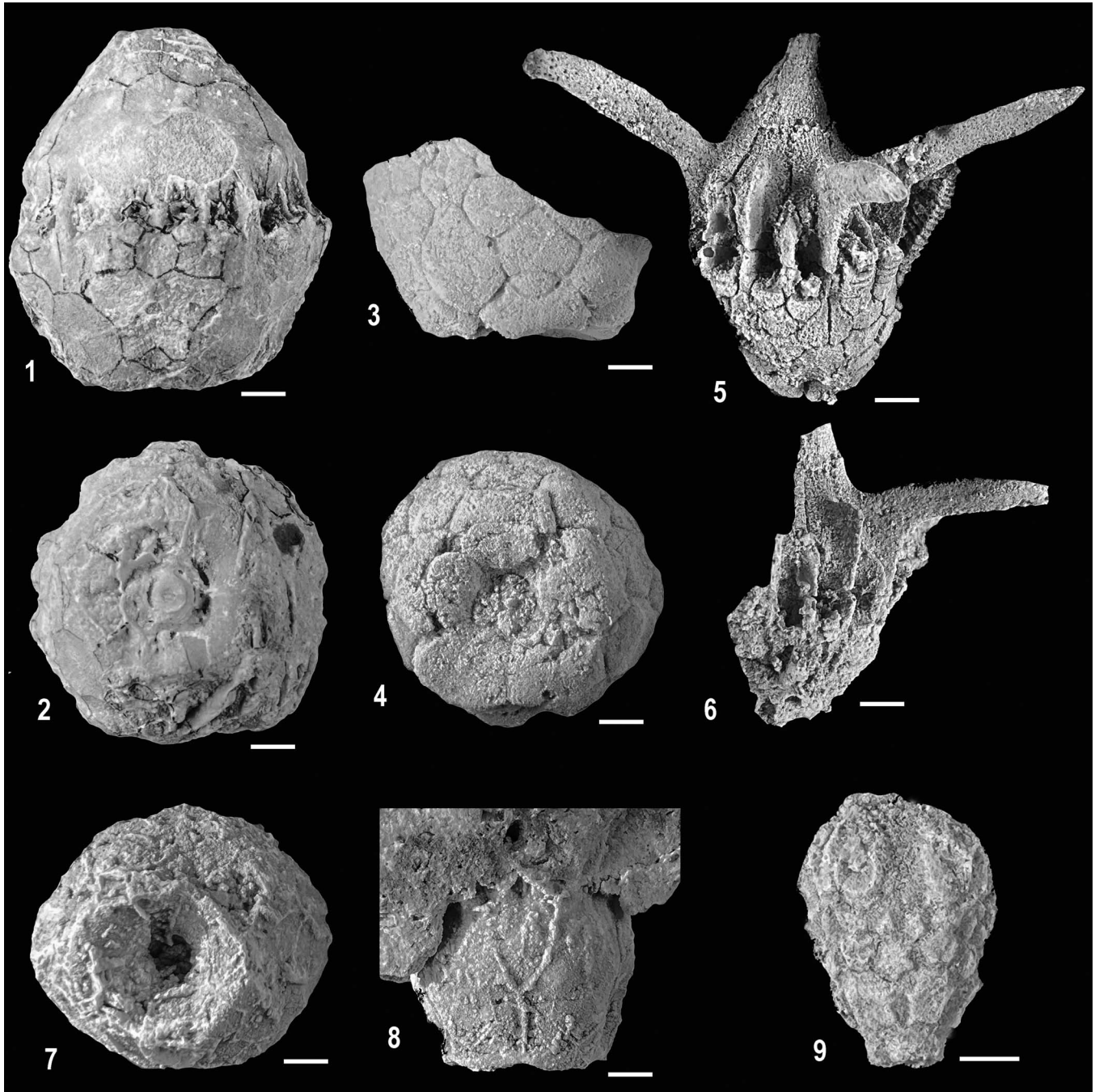
#### Suborder Glyptocrinina Moore, 1952

Superfamily Eucalyptocrinitoidea Austin and Austin, 1842

Family Eucalyptocrinidae Roemer, 1855

*Remarks.*—The Eucalyptocrinidae is an iconic Silurian–Devonian crinoid family known from Australia, Canada, Czech Republic, England, Germany, Russia, Sweden, UK, and USA. Ubaghs (1978a) only recognized two genera in the Eucalyptocrinidae: *Eucalyptocrinites* Goldfuss, 1831 and *Calliocrinus* d’Orbigny, 1850. However, Witzke and Strimple (1981) recognized two additional genera, *Archaeocalyptocrinus* Witzke and Strimple, 1981 and *Chicagocrinus* Weller, 1900, the latter of which was synonymized with *Calliocrinus* by Ubaghs (1978a). Finally, *Aclistocrinus* Eckert and Brett, 2001 was described from the Telychian of New York, USA.

Diagnostic characters for differentiation of *Eucalyptocrinites* and *Calliocrinus* have varied historically, and the Cedarville Member eucalyptocrinids add further inconsistency among previously stated genus-level characters. Springer (1926) distinguished *Eucalyptocrinites* and *Calliocrinus* because *Calliocrinus* typically possessed a broader basal concavity; the tegmen ‘decanter-shaped’; the partition plates not as long as the arms; and large spines could be present from the basal plates, interradial plates, and tegmen plates. Ubaghs (1978a) supported these distinctions and added that



**Figure 11.** *Calliocrinus* and *Stiptocrinus* from the Cedarville Member from the Pepcom Cement Quarry: (1, 2) *Calliocrinus primibrachialis* Busch, 1943, internal mold of OSU 19259: (1) radial view of calyx, plate boundaries marked by Busch (1943), uncoated; (2) basal view. (3, 4) *Calliocrinus primibrachialis*, OSU 558853, external silicone cast: (3) lateral view of partial calyx; (4) basal view of calyx. (5, 6) *Calliocrinus poepplemanni* n. sp., OSU 558856, external silicone cast (compare with Fig. 4.1); photographed without a highlight to avoid shadows covering some spines: (5) lateral view of tegmen, note conical, asymmetrical anal tube and long, flat spines extending away from the theca; (6) oblique view showing the lateral extent of the middle spine in Figure 11.5. (7) Internal mold of *Calliocrinus primibrachialis*, OSU 558854. (8) Internal mold of *Calliocrinus poepplemanni* n. sp., OSU 558857. (9) *Stiptocrinus farringtoni* (Slocum, 1908), OSU 558852, lateral view of external silicone cast, specimen retouched to remove air bubbles on cast. Scale bars = 5.0 mm; specimens coated with ammonium chloride sublimate for photography.

*Eucalyptocrinites* had the first interradial plates approximately the same size as the two plates combined in the second range of interradial plates; 10 partition plates approximately as high as the arms forming recesses into which arms retracted when the crinoid was in a trauma posture (see Messing et al., 2021); spinose plates confined to the tegmen; and fixed rays invariably with two primibrachials in Silurian species.

Witzke and Strimple (1981) defined all four genera. *Eucalyptocrinites* and *Calliocrinus* were distinguished because *Eucalyptocrinites* has one or two fixed primibrachials per ray; the base of the calyx flat or with a small basal concavity; 10 partition plates approximately as large as the arms; in some species, an elongated anal tube with flattened spines projecting laterally; and no spines on calyx plates. In contrast, *Calliocrinus* has



two fixed primibrachials per ray; basal plates and proximal portions of radial plates in a small to large basal concavity; 20 partition plates much shorter than the arms; in some species, elongated conical spines or flattened spines from the distal tegmen; and in some species, long, conical spines from radial plates and/or the first interradial plates.

Cedarville Member eucalyptocrinitids do not conform to these traditional diagnoses. For example, *Calliocrinus* specimens in the Cedarville Member have either only one primibrachial (first primibrachial is axillary) or a small first primibrachial that does not extend the full width of the radial facet. We follow Witzke and Strimple (1981) in recognizing four genera in the Eucalyptocrinitidae and redefine generic concepts. Genus-diagnostic characters include the presence or absence of spines on calyx plates, shape of the base of the calyx, size of basal plates, number of primibrachials, size of first primibrachial plates relative to the length of the distal suture of the radial plate, shape of the primaxil, relative sizes of plates in the regular interrays, presence or absence of first secundibrachials in sutural contact medially, number of tegmen partition plates, relative height of tegmen partition plates, relative size of tegmen, and presence or absence of flattened summit spines from the anal tube (Table 1).

Unexpectedly, *Calliocrinus* is the only eucalyptocrinitid recognized in the Cedarville Member at the Pepcon Cement Quarry. *Eucalyptocrinites* is a common faunal element in many Silurian faunas in the USA and Western Europe (e.g., Springer, 1926; Bassler and Moodey, 1943, p. 42–56; Frest et al., 1999). It is present in siliciclastic facies, such as the Waldron Shale of Indiana (Hall, 1882); in mixed siliciclastic and carbonate facies, such as the Brownsport Formation of Tennessee (Springer, 1926); in dolomite strata in Illinois, Indiana, Ohio, and Wisconsin (see Weller, 1900); and the Cedarville Dolomite Member of the Laurel Formation elsewhere in Ohio (Foerste, 1920). Future work on dolomite faunas and/or more precise application of Eucalyptocrinitidae generic diagnoses (see Witzke and Strimple, 1981; and below) are needed to determine whether the Pepcon eucalyptocrinitids are typical or unusual for dolomite, reef-associated faunas.

Genus *Calliocrinus* d’Orbigny, 1850

*Type species.*—*Eugeniocrinites? costatus* Hisinger, 1837.

*Included species.*—*Calliocrinus acanthinus* Ringuéberg, 1890; *Calliocrinus beachleri* Wachsmuth and Springer, 1892; *Calliocrinus beyrichianus* Angelin, 1878; *Calliocrinus bifurcatus* Weller, 1900; *Calliocrinus bilobus* (Weller, 1897); *Calliocrinus cornutus* (Hall, 1864); *Calliocrinus cornutus excavatus* (Hall, 1865); *Calliocrinus corrugatus* (Weller, 1897); *Calliocrinus costatus* (Hisinger, 1837); *Calliocrinus desideratus* Weller, 1900; *Calliocrinus diadema* Angelin, 1878; *Calliocrinus digitatus* (Weller, 1897); *Calliocrinus hydei* (Weller, 1897); *Calliocrinus koninckianus* Angelin, 1878; *Calliocrinus longispinus* Weller, 1900; *Calliocrinus minor* Angelin, 1878; *Calliocrinus murchisonianus* Angelin, 1878; *Calliocrinus pentangularis* Weller, 1900; *Calliocrinus primibrachialis* Busch, 1943; *Calliocrinus roemerianus* Angelin, 1878; *Calliocrinus rugiferus* Ramsbottom in

Table 1. Generic diagnostic characters for the Eucalyptocrinitidae.

	Spines on calyx plates	Basal concavity of calyx	Size of basal plates	Number of primibrachials	First primibrachial full width of ray	Primaxil shape	Regular interrays	First secundibrachials in sutural contact medially	Number of tegmen partition plates	Partition plates relative height	Tegmen size	Flattened spines from anal tube
<i>Aclistocrinus</i>	absent	moderately developed, includes only basal plates	visible in lateral view and extend up sides of calyx	2	present	pentagonal	first interradial similar in size or smaller than combined size of two interradials in second range	present	10	as high as arms or higher	high to very high	present
<i>Archaeoacalyptocrinus</i>	absent	absent or weakly developed	visible in lateral view and extend up sides of calyx	2	present	pentagonal	first interradial larger than combined size of two interradials in second range	present	10	shorter than arms	relatively low	absent
<i>Calliocrinus</i>	present or absent	deep, includes basal and some of radial plates	small, not visible in lateral view	1 or 2	present or absent	pentagonal	first interradial larger than combined size of two interradials in second range	absent	20	shorter than arms	high to very high	present or absent
<i>Chicagocrinus</i>	absent	deep, includes basal and some of radial plates	small, not visible in lateral view	2	absent	triangular	first interradial similar in size or smaller than combined size of two interradials in second range	absent	20	shorter than arms?	unknown	unknown
<i>Eucalyptocrinites</i>	absent	narrow and shallow or absent with base flat	small, not visible in lateral view	1 or 2	present or absent	pentagonal	first interradial similar in size to combined size of two interradials in second range	absent	10	as high as arms or higher	high to very high	present or absent

Donovan et al., 2012; *Calliocrinus sedgwickianus* Angelin, 1878; *Calliocrinus uralicus* Tschernyschew, 1893.

**Diagnosis.**—Spines on calyx plates present or absent; basal concavity deep and wide; basal plates and proximal radial plates in basal concavity; basal plates small, not visible in lateral view. One or two primibrachials; if two, first primibrachial might or might not be full width of radial suture; primaxil pentagonal; first interradial in regular interrays larger than combined size of two interradials in second range; first secundibrachials not in sutural contact medially; 20 tegmen partition plates; tegmen partition plate shorter than arms; tegmen high to very high; flattened summit spines from anal tube present or absent.

**Occurrence.**—Silurian: Llandovery (Telychian) to Wenlock (Homerian), USA, and UK; Wenlock (Sheinwoodian) to Pridoli, Estonia, and Sweden; early Devonian, Russian Republic (see Ausich et al., 2012; Webster, 2014).

**Remarks.**—A comprehensive list of species-diagnostic characters for North American species assigned to *Calliocrinus* is not possible (see Supplementary Table 1) because several species were defined only on the basis of flattened spine shapes with no known calyx characters. These include *Calliocrinus bifurcatus*, *Calliocrinus bilobus*, *Calliocrinus corrugatus*, *Calliocrinus desiderata*, *Calliocrinus digitalis*, and *Calliocrinus hydei*. In contrast, *Calliocrinus acanthinus*, *Calliocrinus beachleri*, *Calliocrinus cornutus*, *Calliocrinus longispinus*, *Calliocrinus pentagularis*, and *Calliocrinus primibrachialis* were described on features of the thecae, with the latter known primarily from interior molds.

Four *Calliocrinus* taxa are described below. These include *Calliocrinus primibrachialis*, *Calliocrinus poeppelmani* n. sp., *Calliocrinus hadros* n. sp., and *Calliocrinus* sp. indet. The distinctive aspect of Cedarville Member *Calliocrinus* is that species have only one primibrachial or either one or two primibrachials, and *Calliocrinus primibrachialis* has two primibrachial plates but the first primibrachial only occupies ~33–71% of the distal radial plate suture. *Calliocrinus* sp. indet. is an isolated, incomplete summit spine plate.

As listed in Supplementary Table 1, species diagnostic characters for *Calliocrinus* known from the thecae include calyx shape, shape of the base of the calyx, presence or absence of spines on the radial plates, other sculpturing on radial plates, presence or absence of spines on the first interradial plates, presence or absence of additional spines on the calyx plates, calyx outline at the position of arm openings, number of first primibrachials, and summit spine shape.

*Calliocrinus primibrachialis* Busch, 1943  
Figure 11.1–11.4, 11.7

**Type specimens.**—The type specimens of *Calliocrinus primibrachialis* (OSU 19256–19260) are all internal molds and were reported from the Cedarville Dolomite at the Moore Lime Company Quarry and the Jenkins Quarry, each 1.6 km southwest of Springfield, Clark County, Ohio and from the Cedarville Quarry in Cedarville, Green County, Ohio. Herein,

OSU 19259 is designated as the lectotype, and paralectotypes are OSU 19256–19258 and 19260.

**Diagnosis.**—Low to very low cone-shaped calyx; base of calyx subpentagonal; convexity of calyx plates unknown; presence or absence of spines on radial plates unknown; other sculpturing on radial plates unknown; sculpturing on other calyx plates unknown; presence or absence of spines on first interradial plates unknown; presence or absence of other spines unknown; calyx outline at arm openings subcircular; two primibrachials with first primibrachial not occupying full width of radial plate distal suture; summit spine shape unknown.

**Occurrence.**—Busch (1943) originally described this species from the lower 18.3 m of the Cedarville Dolomite (of his day) in the Moore Lime Quarry and the Jenkins Quarry, both one mile southwest of Springfield, Ohio and from the Cedarville Quarry at Cedarville, Ohio. New specimens described herein are from the Cedarville Member of the Laurel Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

**Description.**—Calyx large, low-cone shape with a deep, wide pentagonal to pentalobate basal concavity; angles of pentagonal basal concavity in a radial position (Fig. 11.2, 11.4, 11.7). Calyx plates moderately convex, sculpturing smooth, and calyx sutures impressed. Basal cirlet small, completely in basal concavity but not completely covered by proximal columnal. Radial cirlet ~15% of calyx height in lateral view, in contact in all interrays. Radial plates large, five, hexagonal, ~4 times wider than high in lateral view of calyx; approximately equal height of radial plate on the interior of the basal concavity as visible in lateral view from the outside.

Regular interray plating 1-2. Regular interrays in contact with tegmen (Fig. 11.1). First fixed interradial plates large, octagonal, ~1.5 times higher than wide, supported beneath by radial plates, extending as high as the lower half of the first secundibrachials, two elongate plates in second range of regular interray plates. CD interray undifferentiated.

Fixed brachials at least through the first tertibrachial; first primibrachial occupying ~44–63% of upper suture of radial plate (Fig. 11.1, 11.3); second primibrachial axillary in sutural contact with the radial plate on either side of the narrow first primibrachial; second secundibrachials axillary, much smaller than first secundibrachials; details of tertibrachials unclear. Ray ridges absent on exterior of plates, but ridge along rays present on well-preserved internal molds, which might trace nerve canals.

Regular interray plating 1-2; first interbrachial plate supported beneath by shoulders of adjacent radial plates; in each half-ray, fixed intrabrachial plate supported by adjacent first secundibrachials; one intraradial in each half-ray supported beneath by two first tertibrachials.

Tegmen low to medium inverted-bowl or vase shape. Twenty partition plates positioned with bases at approximately the same height. Other details of partition plates unknown.

Free arms 20; further details unknown. Column unknown.

**Additional material.**—OSU 558853–558855.

**Measurements.**—Lectotype: OSU 19259 (internal mold): CaH 17.0, CaW (distal) 34.5, RH 4.0, RW 10.4, RFW 6.0, Pbr1H 2.5, Pbr1W 3.8, TeH 20.6\*. Paralectotype: OSU 19257 (internal mold): CaH 15.7, CaW (distal) 37.7, RH 5.0, RW 11.4, RFW 7.9, Pbr1H 2.8, Pbr1W 2.6. Paralectotype: OSU 19258 (internal mold): CaH 14.3, CaW (distal) 26.3\*, RH 3.3, RW 8.1, RFW 4.1, Pbr1H 1.5, Pbr1W 2.1, TH 19.9\*. Paralectotype: OSU 19260 (internal mold): CaH 16.3, CaW (distal) 35.2, RFW 7.1, Pbr1H 3.0, Pbr1W 3.1, TH 21.5\*. OSU 558854 (internal cast): CaH 17.5, CaW 31.1, RFW 5.75, Pbr1H 2.6, Pbr1W 4.3.

**Remarks.**—*Calliocrinus primibrachialis* is differentiated from other North American *Calliocrinus* species as outlined in Supplementary Table 1. It is differentiated from other *Calliocrinus* spp. in the Cedarville Member by calyx shape, shape of the base of the calyx, convexity of plates above the base, sculpturing on radial plates, sculpturing on other calyx plates, spines from tegmen partition plates, calyx outline at position of arm openings, and number of first primibrachials. *Calliocrinus primibrachialis* has a low- to very low-cone calyx shape, a subpentagonal-shaped base of the calyx, (convexity of calyx plates above the base unknown), (other sculpturing on radial plates unknown), (sculpturing on other calyx plates unknown), (presence or absence of spines unknown), calyx outline at arm openings subcircular, and two first primibrachials with first not full width of distal radial plate suture. In contrast, *Calliocrinus poepplemanni* n. sp. has a low-bowl calyx shape, subpentagonal-shaped base of the calyx, slightly convex to slightly concave calyx plates above the base, faint ray ridge on radial plates, faint ray ridge on fixed brachials, long flat spine projecting outward from interradially positioned tegmen partition plate, calyx outline at arm openings subcircular, and one first primibrachial. *Calliocrinus hadros* n. sp. has a low-vase calyx shape with constriction at level of radial plate-first primibrachial suture, circular- to subpentalobate-shaped base of the calyx, gently to very convex calyx plates above the base, single central ridge from proximal end of radial (within basal concavity) to radial first primibrachial suture, subtle ridges from radial plates to first interradial plates that merge centrally and form a single subtle ridge to distal suture of plate, spines absent as known, calyx outline at arm openings circular, and one or two first primibrachials.

*Calliocrinus poepplemanni* new species  
Figures 4.1, 11.5, 11.6, 11.8

**Type specimens.**—Holotype, OSU 558856; paratype, OSU 558857.

**Diagnosis.**—Calyx low bowl-shaped; subpentagonal base of calyx; calyx plate slightly concave to slightly convex; spines absent on radial plates; radial plates with faint ray ridges; faint ray ridges along fixed brachials; spines absent on first interradial plates; long, flat spine projecting outward from interradially positioned tegmen partition plate; calyx outline at arm openings subcircular; one primibrachial; summit spines absent.

**Occurrence.**—*Calliocrinus poepplemanni* n. sp. is described from the Cedarville Member of the Laurel Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

**Description.**—Calyx medium-sized, low-bowl shape presumably with a moderately sized basal concavity (both in outline size and depth); tegmen higher than calyx; subcircular calyx outline at position of free arm openings; subpentagonal calyx base (Fig. 11.5). Calyx plates slightly convex, flat, or slightly concave (this variability could be a consequence of dolostone preservation), sculpturing presumably smooth (pattern on molds of plates presumed to be a consequence of the texture of the dolostone mold), faint ray ridges on fixed ray brachials, and calyx sutures impressed. Basal circling small, completely in basal concavity. Radial circling ~3% of calyx height in lateral view, in contact in all interrays. Radial plates large, presumably five, hexagonal, ~4 times wider than high in lateral view of calyx.

Regular interray plating 1-2. Regular interrays in contact with tegmen (Fig. 11.1). First fixed interradial plates small, octagonal, approximately as high as wide, supported beneath by radial plates, extending as high as the lower two-thirds of the first secundibrachials; two elongate plates in second range of regular interray plates. CD interray undifferentiated.

Fixed brachials through first tertibrachial; ray ridges present on fixed secundibrachials through fixed tertibrachials. First primibrachial axillary, full width of distal radial plate suture; second secundibrachials axillary, much smaller than first secundibrachials; one fixed tertibrachial after which arms are free. Ray ridges on first secundibrachials through first tertibrachial.

Regular interray plating 1-2; first interradial plate supported beneath by shoulders of adjacent radial plates; in each half-ray, fixed intrabrachial plate supported by adjacent first secundibrachials; one intraradial in each half-ray supported beneath by two first tertibrachials.

Tegmen low to medium, inverted bowl or vase shaped (Fig. 11.1). Twenty partition plates positioned interradially, mid-ray, and mid half-ray. The base of partition plates can be stepped with the interradial partition plate positioned highest and the mid-ray partition plate positioned lowest. All partition plates less than one half the height of tegmen. Inter radially positioned partition plate flat, projecting upward and with an outward projecting, flattened spine that is longer than the anal tube is high (Fig. 11.5, 11.6). Half-ray partition plate projecting upward only and extending for approximately half the height of the adjacent partition plates. Mid-ray partition plate projecting upward, flat, similar to the interray partition plate; based on the external mold, it also had a spine that projected outward as a flattened spine but its length is unknown.

Anal tube high, asymmetrical inverted cone.

Free arms 20; proximal free arms uniseriate pinnulate; characters of more distal arms unknown. Column unknown.

**Etymology.**—The species name recognizes Jim Poeppleman, who generously allowed access to the Pepcon Cement Quarry for collecting.

**Measurements.**—OSU 558856 (external mold): CaH 19.1, CaW 27.7\*, RH 3.1, RW 9.4, TH 25.2\*; OSU 558857 (internal mold): CaH 20.8, CaW 28.6.



*Remarks.*—The holotype of *Calliocrinus poeppelmani* n. sp. (OSU 558856) is an external mold and a corresponding cast. The paratype (OSU 558857) is an internal mold (e.g., Fig. 11.8). Two distinctive features of this species are the prominent, long spines that project outward from the interradially positioned tegmen partition plate and the rapidly tapering conical anal tube from which there does not appear to be summit spines. *Calliocrinus poeppelmani* n. sp. is compared with sympatric species of *Calliocrinus* in the remarks under *Calliocrinus primibrachialis* and to other North American species in Supplementary Table 1.

*Calliocrinus hadros* new species  
Figures 4.2, 12.1–12.4

*Type specimens.*—Holotype, OSU 558858; paratypes, OSU 558859–558861.

*Diagnosis.*—Calyx low-vase shaped; circular to subpentalobate base of calyx; calyx plate gently concave to gently convex; spines absent on radial plates; single, central ridge from proximal radial plates (within basal concavity) to distal suture of radial plates; subtle ridges from radial plates onto first primibrachials that merge centrally and continue to the distal suture of the first primibrachials; spine on first interradial plate absent; spines on other calyx plates absent; calyx outline at arm openings circular; one or two primibrachials; summit spines unknown.

*Occurrence.*—*Calliocrinus hadros* n. sp. is described from the Cedarville Member of the Laurel Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

*Description.*—Calyx large, low-vase shaped with width constriction at level of radial plate–first primibrachial suture (Fig. 12.1); a deep, wide circular to subpentalobate basal concavity; angles of pentagonal basal concavity in radial positions (Fig. 12.4). Calyx plates gently to very convex, sculpturing smooth, and calyx sutures impressed. Basal circling small, completely in basal concavity covered by proximal columnal (Fig. 12.2). Radial circling ~30% of calyx height in lateral view, in contact in all interrays. Radial plates large, five, hexagonal, ~2.0 times wider than high in lateral view of calyx. Radial plates projecting upward into basal concavity; as a radial plate wraps around from the basal concavity, it forms a sharply convex to flat, upward sloping base to the calyx. From basal concavity, a single ridge bisects the radial plate, wraps around to outside of the radial, divides, and connects to like ridges/folds on superjacent first interradial plates (Fig. 12.1, 12.2).

Regular interray plating 1-2. Regular interrays in contact with tegmen (Fig. 12.1, 12.3). First fixed interradial plates large, octagonal, ~1.5 times higher than wide, supported beneath by radial plates, extending to more than lower half of the first secundibrachials; two elongate plates in second range of regular interray plates. CD interray undifferentiated.

Fixed brachials through first or second tertibrachial; first or second primibrachial axillary; if two primibrachials, first

primibrachial much smaller than second primibrachial; node at center proximal portion of plate on the proximal end.

Regular interray plating 1-2; first interbrachial plate supported beneath by shoulders of adjacent radial plates; in each half-ray, fixed intrabrachial plate supported by adjacent first secundibrachials; one intraradial in each half-ray supported beneath by two first tertibrachials; broad folding near base where ridges from radial plates converge, might or might not have a single low fold projecting distally to proximal end of first primibrachial.

Tegmen shape and height unknown. Twenty partition plates positioned interradially, mid-ray, and mid half-ray. Base of partition plates stepped with mid-ray partition plate highest and interradial partition plate lowest. As known, partition plate height less than calyx height and outward spinose projections absent; interradial and mid-ray partition plates approximately same height; half-ray partition plate lower. Other details of tegmen unknown.

Free arms 20; further details unknown. Column unknown.

*Etymology.*—*hadros*: Gr., thick, bulky, stout, strong; referring to the robust calyx on this new crinoid.

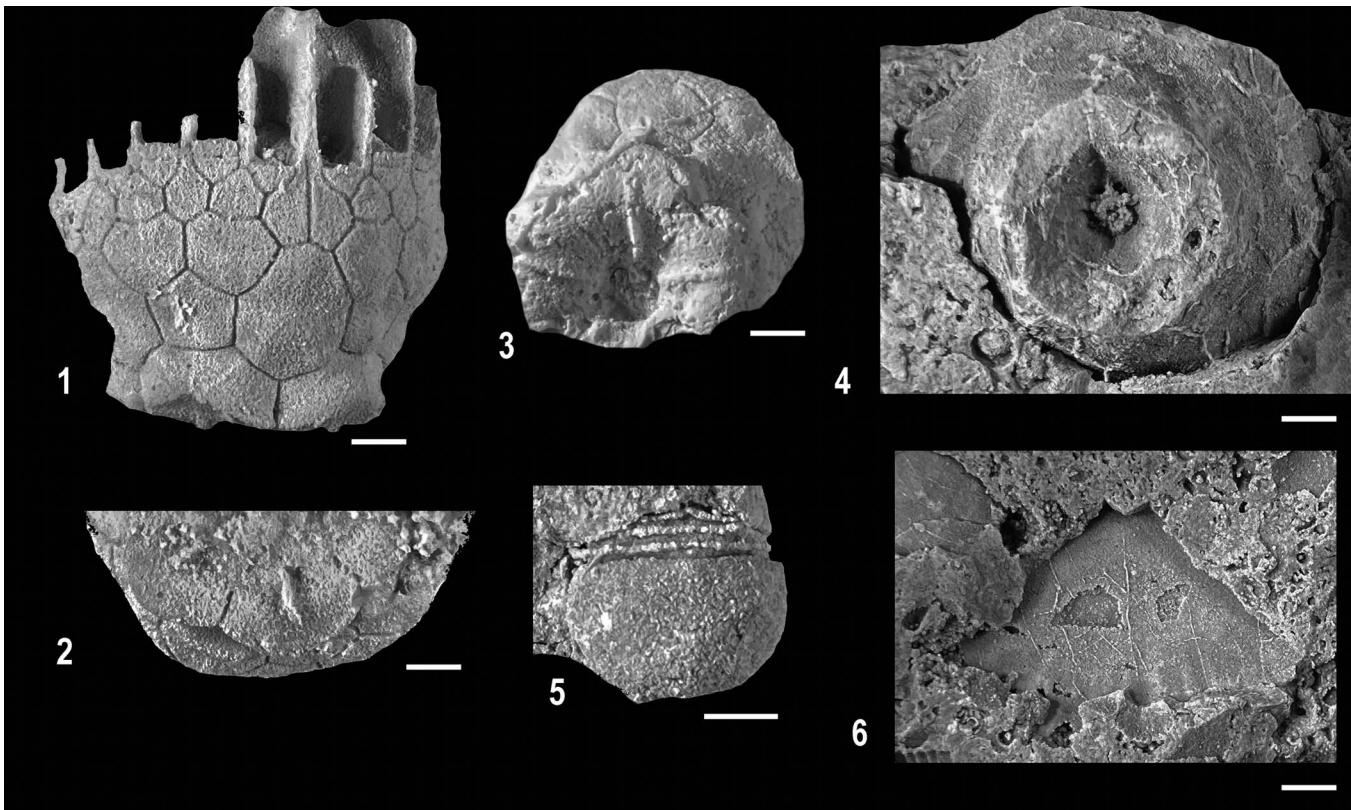
*Additional material.*—OSU 558862, 558863.

*Measurements.*—Holotype: OSU 556658 (external mold): CaH 21.6, CaW 30.7, RH 6.3, RW 10.4, TH 16.4\*. OSU 558860 (internal mold): CaH 23.8, CaW 29.9; OSU 558861 (external mold): CaH 22.6, CaW 41.4.

*Remarks.*—The holotype of *Calliocrinus hadros* n. sp. (OSU 558858) is an external mold and a corresponding cast, and one of the paratypes (OSU 558859) is an external mold of the basal portion of a calyx. Other paratypes and additional specimens are internal molds. The large vase-shaped calyx and very wide subpentalobate basal concavity are the most distinctive features of this new species. *Calliocrinus hadros* n. sp. is compared with sympatric species of *Calliocrinus* in the remarks under *Calliocrinus primibrachialis* and to other North American species in Supplementary Table 1.

*Calliocrinus* sp. indet.  
Figure 12.6

*Remarks.*—A single, large, flat, fan-shaped summit spine plate (OSU 558864) is assigned to *Calliocrinus* sp. indet. The maximum length and width of this plate is 27.0 and 47.0 mm, respectively (Fig. 12.6). The inner portion of this plate is attached to what appears to be a pentagonal structure, and the outer rim is not preserved. This plate is interpreted to be from a *Calliocrinus* summit spine plate that would have been attached to the distal end of the anal tube. However, for several reasons, this plate cannot be assigned to a species of *Calliocrinus*. First, none of Cedarville Member calyces of *Calliocrinus* are preserved with attached or associated summit spine plates. Second, species designations based on summit plates are based on the overall size and shape of the plates, as well as the details of the outer rim of these plates, the latter of which is not preserved on this Cedarville Member specimen. Further, in published illustrations of *Calliocrinus* summit



**Figure 12.** *Calliocrinus* and *Lecanocrinus* from the Cedarville Member from the Pepcom Cement Quarry: (1, 2) *Calliocrinus hadros* n. sp., external silicone cast of OSU 558858: (1) lateral view of calyx, note short tegmen partition plates (compare with Fig. 4.2); (2) basal view, center of calyx base near center of upper part of photograph. (3) *Calliocrinus hadros* n. sp., OSU 558859, external silicone cast of partial basal concavity, note distinct ridges on radial plates coming out of basal concavity. (4) *Calliocrinus hadros* n. sp., OSU 558861, internal mold. (5) *Lecanocrinus* sp. indet., OSU 558873, internal mold, lateral view of aboral cup and proximal arms, note third primibrachial axillary. (6) *Calliocrinus* sp. indet., OSU 558864, external mold of flat tegmen spine, note undulating surface abaxially and adaxial suture apparently on a pentagonal plate. Scale bars = 5.0 mm.; specimens coated with ammonium chloride sublimate for photography.

plates, the central attachment of flattened spines is a tetragonal structure, whereas in OSU 558864, it is presumably pentagonal. It is highly likely that this summit spine plate belongs to one of the species of *Calliocrinus* described herein, however it is not possible to confidently assign this to either *Calliocrinus poeppelmani* n. sp. or *Calliocrinus hadros* n. sp. Thus, it is placed in open nomenclature.

In addition to the *Calliocrinus* specimens noted above, additional *Calliocrinus* specimens that are not assigned to a species are present. These specimens include OSU 558865–558872.

Subclass Pentacrinioidea Jaekel, 1894  
 Infraclass Inadunata Wachsmuth and Springer, 1885  
 Parvclass Cladida Moore and Laudon, 1943  
 Magorder Eucladida Wright, 2017  
 Superorder Flexibilia von Zittel, 1895  
 Order Sagenocrinida Springer, 1913  
 Superfamily Lecanocrinoidea Springer, 1913  
 Family Lecanocrinidae Springer, 1913  
 Genus *Lecanocrinus* Hall, 1852

*Type species.*—*Lecanocrinus* (*Lecanocrinus*) *macropetalus* Hall, 1852.

*Other species.*—*Lecanocrinus anna* (Tansey, 1924); *L. breviarticulatus* Chapman, 1935; *L. elongatus* Springer, 1926;

*L. hanusi* Prokop and Petr, 1993; *L. invaginatus* Strimple, 1952; *L. lawsonae* McIntosh, 1981; *L. (Alnecocrinus)* *angulatus* (Springer, 1920); *L. (Alnecocrinus)* *erectus* (Strimple, 1952); *L. (Lecanocrinus)* *bacchus* (Salter, 1873); *L. (Lecanocrinus)* *billingsi* Angelin, 1878; *L. (L.) facietatus* Angelin, 1878; *L. (L.) huntonensis* Strimple, 1952; *L. (L.) lindenensis* Strimple, 1952; *L. (L.) lindstroemi* Springer, 1920; *L. (L.) macropetalus* Hall, 1852; *L. (L.) magniradialis* (Weller, 1903); *L. (L.) meniscus* Springer, 1920; *L. (L.) pusillus* (Hall, 1863); *L. (L.) solidus* Ringueberg, 1886; *L. (L.) soyei* Oehlert, 1882.

*Occurrence.*—Silurian, Australia, Canada, Czech Republic, Sweden, UK, USA; and Devonian (Lockhovian–Emsian), Czech Republic, France, USA (Webster, 2014)

*Remarks.*—*Lecanocrinus* sensu lato is a cosmopolitan Silurian to Devonian flexible crinoid. Moore (1978) included four genera (*Lecanocrinus*; *Geroldicrinus* Jaekel, 1918; *Miracrinus* Bowsher, 1953; *Mysticocrinus* Springer, 1918) in the Lecanocrinidae. Also in 1978, Frest and Strimple revised *Lecanocrinus* by creating three subgenera—*L. (Lecanocrinus)*, *L. (Alnecocrinus)*, and *L. (Miracrinus)*—and by designating a new genus, *Nummicrinus* Frest and Strimple, 1978. Frest and Strimple (1978) did not place all known species of *Lecanocrinus* into subgenera, and Webster (2014) did not

follow the revision of assigning *Miracrinus* to subgenus status. It is not the purpose of the present study to revise the Lecanocrinidae, so assignment of species to higher taxonomic ranks follows Webster (2014).

*Lecanocrinus?* sp. indet.  
Figure 12.5

**Occurrence.**—Cedarville Member of the Laurel Formation (Silurian, Wenlock [Homerian]) from the Pepcon Cement Quarry, near Bradford, Ohio.

**Description.**—Aboral cup medium-sized, low-bowl shaped, with subcircular outline at distal aboral cup, (unclear whether a basal concavity is present). Plate sculpturing unknown; aboral cup plates presumably moderately convex; any evidence of ridges on internal cast of aboral cup plates absent. Infrabasal circlet ~12.4% of aboral cup height, visible in lateral view, presumably three. Basal circlet ~46.3% of aboral cup height; basal plates hexagonal. Radial circlet ~41.3% of aboral cup height; radial plates pentagonal; radial facets plenary. CD interray unknown.

Proximal brachials very thin, ~17.5 times wider than high, third primibrachial axillary (in one ray) (Fig. 12.5). Column unknown.

**Materials.**—OSU 558873 and 558874.

**Measurements.**—OSU 558873 (internal mold): CaH 7.5, CaW 11.3, IH 1.25, BH 4.6, BW 6.5, RH 4.1, RW 8.8.

**Remarks.**—Two specimens are assigned to *Lecanocrinus* sp. indet. OSU 558873 is an internal mold with relatively well-preserved aboral cup plate sutures. However, the details of the posterior interray, base of the aboral cup, and arms are not preserved and preclude assignment of this specimen to a species. It is placed in *Lecanocrinus* because the distal portion of the infrabasals is visible, the aboral cup is not conical, and the primibrachials are very thin. *Lecanocrinus* sp. indet. is similar to *L. (L.) lindenensis* and *L. (L.) pusillus* because of its globe-shaped aboral cup and infrabasals visible in lateral view; and it is similar to *Nummicrinus waukoma* Hall, 1864 with three primibrachials (Fig. 12.5).

OSU 558874 is only questionably assigned to *Lecanocrinus*. Although the size and shape of this second specimen is similar to OSU 558873, the aboral cup plate boundaries are very poorly preserved.

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## Declaration of competing interests

The authors declare none.

## Data availability statement

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sn02v6x8v>.

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