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# Crinoid encrustation of holocystitid diploporitan echinoderms: strongly asymmetrical Silurian dendritic attachment structures with palaeobiological implications

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## Abstract

Articulated thecae of the holocystitid diploporitan echinoderm *Holocystites scutellatus* from the middle Silurian (Wenlock: Sheinwoodian) Massie Formation of southeastern Indiana, USA, are encrusted by distinctive structures belonging to another echinoderm. A dendritic attachment structure consisting of multiple slender, branching radices, attributable to the camerate crinoid *Eucalyptocrinites*, is present on one side of each of the diploporitan thecae. However, the development of radices is remarkably asymmetrical, with all radices—including one more than 25 mm in length—being present exclusively on one side of the attachment structure. This reflects initial settlement by the encrusting crinoids near the oral or marginal regions rather than the central portion of the diploporitan thecae, which were on their sides; this essentially prohibited further outward growth of radices toward the oral area or edges, but allowed radices oriented in the opposite direction to extend over nearly the entire length of the lateral surface of the theca. Although crinoid encrustation of holocystitid diploporitan thecae is moderately common in the Massie Formation, no previously described specimens display such pronounced asymmetry with respect to radice development. More importantly, these specimens convincingly illustrate the degree to which *Eucalyptocrinites* attachment structure morphologies could be modified in response to local substrate variations; such skeletal modules were, indeed, highly dynamic, probably contributing to the success of taxa bearing such adaptable attachment structures.

**Keywords:** Echinodermata, Wenlock, *Eucalyptocrinites*, *Holocystites*, Indiana, Massie Formation

## Introduction

Silurian pelmatozoan echinoderms evolved a diverse suite of attachment structures that were used to occupy laterally continuous hardgrounds, isolated hard substrata such as shells and cobbles, relatively coarse and rubby bioclastic sediments such as crinoidal gravels, and muddy to sandy softground substrates (e.g., Brett, 1981, 1984, 1991). Among the most ecologically successful of such

Silurian organisms, at least as measured by geographic distribution and diversity of environments occupied (e.g., Frest et al., 1999), were pelmatozoans that possessed a dendritic attachment structure. This strategy of substrate affixation readily allowed modification in response to the properties of underlying or immediately surrounding material (Brett, 1984).

Two famous examples of widespread, long-ranging, and locally abundant pelmatozoan echinoderms that employed “root-like” attachment structures are the monobathrid camerate crinoid *Eucalyptocrinites* and the hemicosmitid rhombiferan *Caryocrinites*—both of which are characterized by terminal dendritic structures comprised of multiple, radially oriented, branching

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radices (sensu Donovan in press; see this paper for a review of radicular attachment structure terminology). The increased surface area provided by the array of laterally directed radices was effective at permitting stability in soft, water-rich muds (e.g., Brett, 1978; Halleck, 1973; Plotnick et al., 2016; Poschmann, 2020), and the tendency toward initial settlement upon solid particles was effective at permitting colonization of bioherms and bioclast-rich firmgrounds and hardgrounds (e.g., Brett, 1978, 1991; Thomka & Brett, 2015a, 2019).

An additional aspect of this attachment strategy, emphasized most strongly by Brett (1978) for *Caryocrinites*, is the capacity to modify the total number of radices as well as the length, thickness and growth direction of individual radices in response to variations in local sediment properties. For example, an otherwise slender, single radice may locally swell to cement itself to and incorporate a discrete bioclast, or might cease growth after encountering an obstacle (Brett, 1978, 1984; Halleck, 1973). Although many radicular attachment structures are comparatively regular, bearing a radial array of fairly uniform radices, the preferential growth of one or more radices relative to others can produce a more irregular or asymmetrical structure.

The present study describes dendritic attachment structures (belonging to *Eucalyptocrinites*) that are characterized by remarkable asymmetry in radice development. Detailed analysis of these specimens provides information on the palaeobiological process of radice growth, as well as information on the properties of the underlying substrate.

#### Locality, stratigraphic setting and studied material

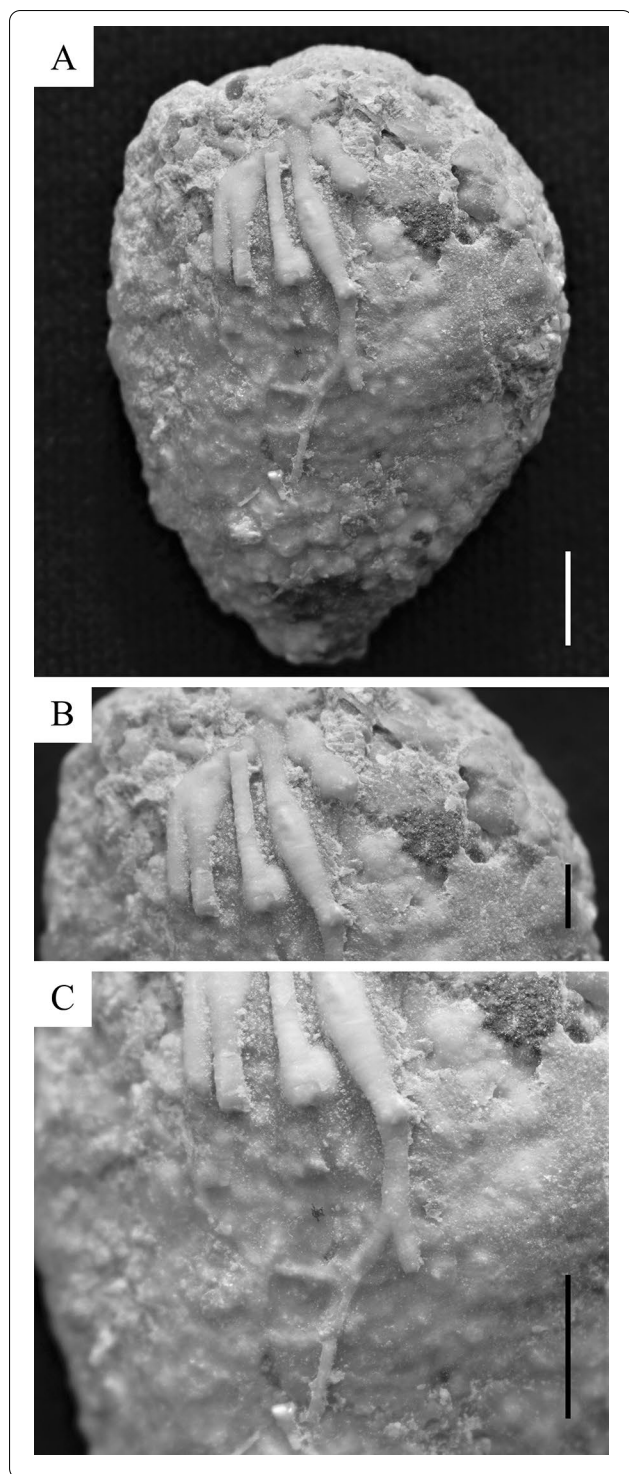
The two specimens studied here were collected from the New Point Stone quarry immediately outside of Napoleon, Ripley County, southeastern Indiana, USA (N39° 12' 31.39", W85° 18' 53.74"). This active quarry is renowned for the abundance, diversity and exceptional preservation of invertebrate macrofossils collected from stratigraphic units that are more strongly dolomitized and typically sparsely fossiliferous in coeval sections throughout the region (e.g., Thomka & Brett, 2015b; Thomka et al., 2016). Middle Silurian-age stratigraphic units exposed at this locality include, in ascending order, the Osgood, Lewisburg, Massie, and Laurel formations (Brett et al., 2012), of which the lower decimeter of the Massie Formation is most productive in terms of articulated echinoderm material (Frest et al., 1999, 2011; Thomka et al., 2016). This interval consists of a grey, poorly lithified mudstone with evidence for episodic rapid burial by storm events (e.g., Thomka & Brett, 2015b), in addition to reworking and exhumation of shallowly buried skeletons (Thomka et al., 2016).

Studied material was collected (by TEB) from close to the base of the mudstone lithofacies of the Massie Formation. This unit, long known as the 'upper Osgood shale' (Foerste, 1897; Frest et al., 1999, 2011), is Wenlock (early Sheinwoodian) in age (Brett et al., 2012). Pelmatozoan echinoderms are abundant and diverse from this interval, and holocystitid diploporitans comprise the dominant faunal elements (Frest et al., 1999, 2011). Macrofossils from the lower Massie Formation mudstone readily weather-free from the surrounding matrix and are collected as float, as is true of the presently considered specimens. The specimens are deposited in the invertebrate palaeontology collection of the Cincinnati Museum Center (Cincinnati, Ohio, USA), recorded under Catalogue numbers CMC IP 88496-88497.

#### Descriptions

The two studied specimens consist of articulated thecae of the holocystitid diploporitan *Holocystites scutellatus* (Figs. 1, 2), characterized by an oblate shape and a short, stubby stele (Frest et al., 2011). There are no brachioles or brachiolar plates attached to the thecae, nor are any oral or anal cover plates present in either specimen. Thecae are light grey to pinkish-grey in colour, with one (CMC IP 88496; Fig. 1) 43 mm in height and 32 mm in maximum width, the other (CMC IP 88497; Fig. 2) 38 mm in height and 29 mm in maximum width. Both are slightly compressed (sensu Thomka et al., 2016) perpendicular to the oral-aboral axis. Where exposed, exterior features of thecal ossicles such as plate sutures and pustulose sculpturing are clearly visible and well-preserved, at least on one side (Figs. 1, 2).

One *H. scutellatus* theca—CMC IP 88496 (Fig. 1)—is encrusted by several organisms, including a laminar fistuliporoid bryozoan colony over the oral region, but the largest and most prominent encruster is a dendritic radicular attachment structure belonging to a pelmatozoan echinoderm. The attachment structure is present on the lateral surface of one side of the diploporitan, with the distalmost column (from which radices extend) occurring near the proximal region, only a few millimeters from the oral summit (Fig. 1A). Five radices, comprised of numerous component ossicles not surrounded by a substantial cortex of secondary calcite (Brett, 1981; Plotnick et al., 2016), extend outward from a central, vertically oriented columnal, bearing a minute, centrally located, pentalobate lumen (Fig. 1B). Radices also contain minute, centrally located, circular to subtly pentalobate lumina. All radices are parallel, running along the lateral surface of the theca, extending from the oral region toward the aboral region (Fig. 1A); there are no radices extending in other directions (i.e., overgrowing the oral surface (Fig. 1B)). Four

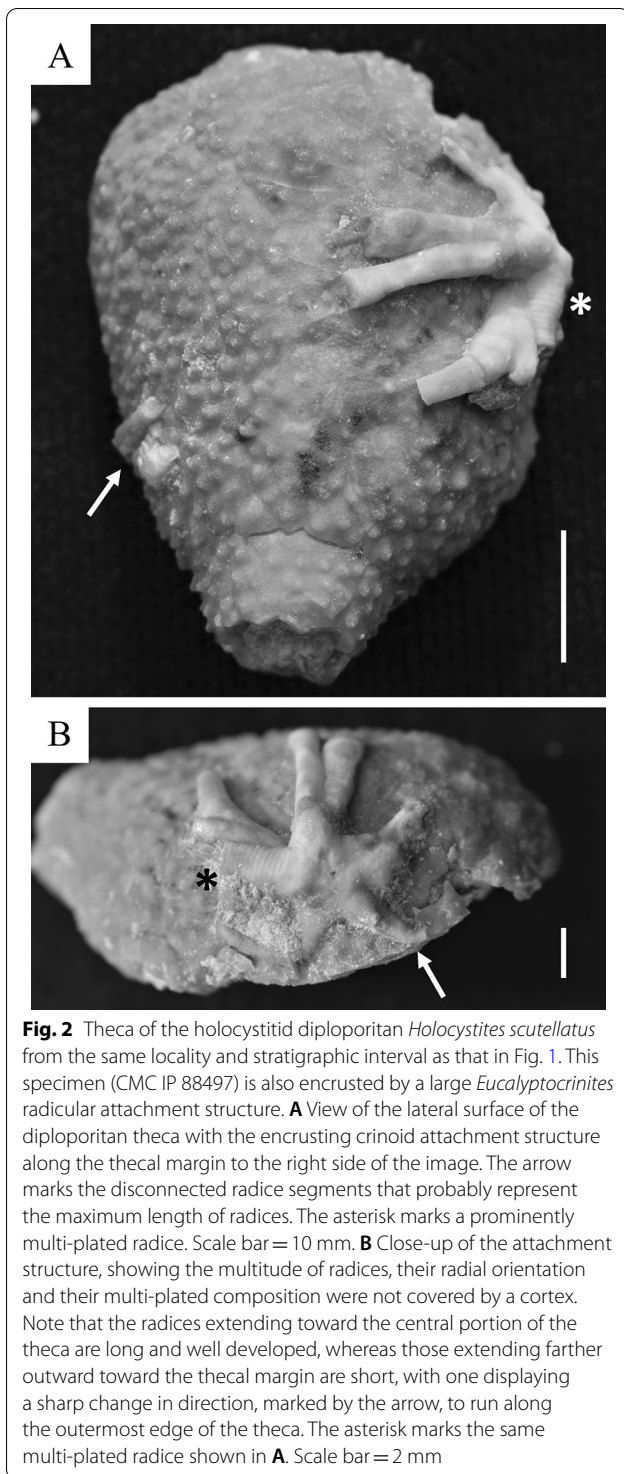


**Fig. 1** Theca of the holocystitid diploporean *Holocystites scutellatus* from the middle Silurian Massie Formation of southeastern Indiana, USA (CMC IP 88496), encrusted by a dendritic radicular attachment structure belonging to the camerate crinoid *Eucalyptocrinites*. **A** View of the lateral surface of the diploporean theca with the encrusting crinoid attachment structure near the oral pole (at the top of the specimen in this image). Note that the radices extending down along the surface of the theca are relatively long. Scale bar = 10 mm. **B** Close-up of the encrusting attachment structure, showing the well-developed radices extending from the oral region toward the aboral region and the essentially invisible radices extending toward the oral pole. Scale bar = 2 mm. **C** View of the longest radice, displaying dichotomous branching and tapering. This radice extends over most of the lateral surface of the theca. Scale bar = 5 mm

The other *H. scutellatus* specimen—CMC IP 88497 (Fig. 2)—has fewer encrusters but is missing most of the plates on the opposite, un-encrusted side of the theca. One large dendritic attachment structure is present on the upper hemisphere of the theca, located along the thecal margin (right side of specimen in Fig. 2A). At least seven radices extend outward from a central area, although determining the exact number of radices is complicated due to anastomosing and/or partial overgrowth of proximal portions of several radices (Fig. 2B). Radices are comprised of discrete lumen-bearing columnals. That the radices consist of multiple ossicles rather than solid rods of calcite is shown particularly clearly by one radice that extends toward the aboral region of the theca (marked by asterisks in Fig. 2); however, most radices are covered by a cortex of amorphous stereom calcite. The most prominent radices extend from the center of the attachment structure, located along the outer margin of the theca, toward the central portion of the lateral surface of the theca (Fig. 2A). These radices average 13.8 mm in length. It is worth noting that there are two small segments of crinoid radice encrusting the aboral portion of the theca, opposite the longest radices of the primary attachment structure (marked by arrows in Fig. 2A). Given the distal terminations of these radices, which have evidence of breakage, it is probable that radices originally extended across the entirety of the lateral surface of the theca, resulting in a maximum radice length of approximately 29 mm. Two radices extend toward the outermost edge of the theca (i.e., in the opposite direction of the larger, more well-developed radices directed toward the center of the lateral thecal surface). These two radices are relatively thin and are only a few millimeters in length (Fig. 2B), reflecting the fact that this portion of the theca would have been resting against the substrate. One of these thin, poorly developed radices appears to change direction sharply, displaying a

of the radices are shorter, averaging 8.1 mm in length, with the fifth radice being significantly longer (Fig. 1B), achieving a maximum length of 25 mm (Fig. 1C). The longer radice displays strong distal tapering and a prominent branch point (Fig. 1C).





shift from extending toward the outermost edge of the theca to running along the outermost edge of the theca (marked by arrow in Fig. 2B). This suggests that the radice was unable to extend into the soft muds surrounding the encrusted theca.

The overall morphology of the attachment structures, the pentalobate configuration of columnal lumina and presence of radice lumina, and the fact that radices are comprised of discrete ossicles rather than solid rods of undifferentiated calcite allow the encrusting specimens to be attributed to *Eucalyptocrinites* (see Halleck, 1973; Brett, 1981, 1984; Thomka & Brett, 2015a, 2019; Plotnick et al., 2016). This taxon is common in the mudstone lithofacies of the Massie Formation (Frest et al., 1999, 2011) as well as the immediately underlying carbonate lithofacies, which is capped by a hardground that is encrusted by morphologically similar *Eucalyptocrinites* attachment structures (Thomka & Brett, 2015a).

### Discussion

Encrustation of diploporitan theca by the *Eucalyptocrinites* radix structures described here is noteworthy for two major reasons: it demonstrates that the strongly asymmetrical radice development was related to position on the encrusted substrate, and it attests to the articulated state of the diploporitan theca during encrustation. The development of relatively long radices, including one with a dichotomous branch and pronounced tapering, on only one side of a radix structure is made possible by initial settlement by the crinoid near the oral or lateral areas of the diploporitan theca. Given these positions, radices could grow outward in one direction to encrust the entire lateral surface of the diploporitan theca, but radices growing in the other direction could only extend for a few millimeters or less before reaching the oral apex of the theca (for CMC IP 88496; Fig. 1) or the lateral edge of the theca (for CMC IP 88497; Fig. 2). The presence of well-developed radices on only one side of each radial attachment structure illustrates the extent to which the development of relatively complex pelmatozoan attachment structures is influenced by local substrate conditions. Brett (1978) documented changes in *Caryocrinites* radice morphology in response to encountering bioclasts in muddy softgrounds (see also Thomka & Brett, 2019), and Plotnick et al. (2016) interpreted growth of longer radices in two opposing directions in softgrounds as a response to prevailing current direction; however, the present specimens probably represent the most strongly asymmetrically developed radicular attachment structures described in the body of literature on stalked echinoderms. The fact that they occur as encrusting structures on diploporitan thecae indicates that the hard skeletal substratum was preferable to extending radices into fine, soft sediment surrounding this “benthic island,” probably because of greater stability relative to the nearby bioturbated sediments (see Kauffman, 1978). The development of a dichotomous branch in one of the radices reflects an increase in attachment structure

surface area—not to increase stability, but rather to more securely bind the encrusting crinoid to the substrate.

The occurrence of *Eucalyptocrinites* attachment structures on holocystitid diploporitan thecae clearly demonstrates that diploporitan material was capable of remaining articulated while remaining near the sediment–water interface for a sufficient interval to permit settlement and growth of the radicular structure. Diploporitans are generally considered as being taphonomically comparable to most cladid and articulate crinoids, prone to rapid skeletal disarticulation into isolated ossicles within hours to a few days in the absence of rapid burial by sediment (Brett et al., 1997). However, Thomka et al. (2016) recently proposed that the ligament-bound, sac-like thecae of diploporitans might have been capable of remaining articulated for longer intervals than previously recognized, citing the occurrence of articulated diploporitan thecae in high-energy carbonate shoal deposits (e.g., Bassler, 1915; Bockelie, 1981; Brett, 1985; Paul & Bockelie, 1983; Sumrall et al., 2009) in addition to more than 45% of diploporitan thecae having at least one encrusting organism in the Massie Formation. The results of the present study contribute additional evidence suggestive of greater resistance to disarticulation for diploporitan thecae than long recognized. Using the generalized taphonomic grade spectrum developed for Mississippian (Lower Carboniferous) crinoids (Ausich, 2001; Ausich & Sevastopulo, 1994; Meyer et al., 1989), it seems that the holocystitids in the Massie Formation mudstone exhibit a preservation potential less like cladids and more similar to disparids and thinner-plated monobathrid camerates.

## Conclusions

In summary, two specimens of the middle Silurian holocystitid diploporitan *Holocystites scutellatus* are reported to be encrusted, *post-mortem*, by dendritic radicular attachment structures attributable to the monobathrid camerate crinoid *Eucalyptocrinites*. The radices of the attachment structure are only developed on one side of the structure, reflecting the initial settlement position of the encrusting crinoids on the diploporitan thecae, which were oriented parallel to the sediment–water interface (i.e., perpendicular to their oral-aboral axis). Settlement occurred near the oral pole of one theca, precluding further outward growth of radices in the oral direction but permitting extension of radices for substantial lengths along the lateral surface of the diploporitan in the aboral direction. Settlement occurred along the lateral margin of the other theca, precluding outward growth of radices toward the edge of the diploporitan but permitting extension of radices for substantial lengths toward the central portion of the lateral surface of the theca. This pattern is a direct reflection of the palaeobiology of

*Eucalyptocrinites*, which was capable of precisely modulating growth of radices in dendritic attachment structures in response to local substrate properties. The ability of *Eucalyptocrinites* to detect which directions would provide preferable materials for overgrowth, encrustation and/or penetration, and which directions were more poorly suited for radice growth many have contributed to the success of this taxon in Palaeozoic marine environments. Attachment structure growth strategy is an easily overlooked but nevertheless ecologically important aspect of crinoid existence, persistence, and success.

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## Authors' contributions

JRT analyzed the material and prepared most of the manuscript; TEB collected, prepared, and analyzed the material; CEB analyzed the material and assisted with manuscript preparation. All authors read and approved the final manuscript.

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## Availability of data and materials

There are no associated datasets for this study, and the studied material is deposited at the Cincinnati Museum Center (Cincinnati, Ohio, USA) under specimen numbers CMC IP 88496-88497.

## Declarations

## Competing interests

There are no competing interests to declare.

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