Silurian Diploporitans as Substrata: Paleoecological Observations and Patterns of Encrustation by Eucalyptocrinites (Crinoidea) in Southeastern Indiana

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ABSTRACT
The middle Silurian Massie Formation of southeastern Indiana contains a rich stalked echinoderm fauna, of which diploporitan “cystoids” are a significant component. A small number of diploporitan thecae are encrusted by the dendritic radicular attachment structures of the monobathrid camerate crinoid Eucalyptocrinites. Recently, several encrusted specimens of the diploporitan Holocystites scutellatus were described from the Massie Formation of the Napoleon quarry (Ripley County) that are unusual in that the encrusting holdfasts display pronounced asymmetry with respect to radicle development. Due to settlement near the margin of the thecae, long, well-developed radicles are present on the side of the attachment structure where they could extend over the entire lateral surface of the theca, and short, poorly developed radicles are present on the side facing the margin of the theca. The anomalous nature of this attachment structure morphology is herein highlighted by comparison to more typical Eucalyptocrinites-encrusted diploporitan thecae from the same locality and stratigraphic interval. These display a much more radially symmetrical configuration of radicles due to a more central settlement position on the thecal lateral surface. Several additional morphological and paleoecological aspects of crinoid encrustation of diploporitans are described and illustrated, including an apparently bilaterally symmetrical radicle growth pattern and a rare occurrence of an encrusted Paulicystis.

INTRODUCTION
Recently, Thomka and others (2021) described thecae of the holocystitid diploporitan “cystoid” Holocystites scutellatus that were encrusted by terminal dendritic radicular attachment structures of the monobathrid camerate crinoid Eucalyptocrinites. These specimens, which were collected from the Silurian of southern Indiana, were unusual because the encrusting
attachment structures displayed strong asymmetry with respect to radicle length on opposite sides of the radix structure. More specifically, radicles were long and relatively well-developed (for example, displaying dichotomous branching) on one hemisphere of the radix but short, poorly developed, and unbranched on the opposite hemisphere. Thomka and others (2021) attributed this pattern to the initial settlement of *Eucalyptocrinites* larvae near the margin of the theca (following the death of the diploporitan), which permitted long radicles to grow on the side of the radix facing the lateral surface of the theca, whereas radicles on the opposite side of the radix could only extend for a few millimeters before reaching the edge of the theca and encountering the siliciclastic mud surrounding the encrusted bioclast. This asymmetry in attachment structure development serves as an indicator of the degree of morphological plasticity inherent to *Eucalyptocrinites* distal attachments (see also Halleck, 1973; Brett, 1981; Thomka and Brett, 2015a).

Unfortunately, recognition of the atypical specimens’ significance is somewhat diminished by the absence of published descriptions of more typical morphologies. Although encrustation of holocystitid diploporitan thecae by *Eucalyptocrinites* attachment structures in certain Silurian deposits in southern Indiana have been referenced repeatedly (for example, Frest and others, 2011; Thomka and others, 2016), they are quite rare, with at most a few dozen collected out of the tens of thousands of diploporitan thecae collected from the Napoleon quarry (Bissett, 2017; see also Thomka and others, 2016); hence, very few examples have been figured or described in detail. This is probably because *Eucalyptocrinites* is not particularly common in the Massie Formation, particularly when compared to the slightly younger Waldron Formation, from which attachment structures and encrusted calyaxes of this genus are famously abundant (Frest and others, 1999). The purpose of the present study is to fill this gap in the literature on Paleozoic echinoderm paleosyneclology by illustrating, describing, and interpreting *Eucalyptocrinites* radix-encrusted specimens of Silurian diploporitans that are more typical than those analyzed by Thomka and others (2021). In addition, several noteworthy and previously undescribed features on certain atypical specimens were recognized, and these are documented and interpreted as well.

**MATERIAL**

All studied material was collected from the middle Silurian (Wenlock: Sheinwoodian) Massie Formation, specifically from the lower portion of the mudstone lithofacies (formerly known as the “upper shale” of the Osgood Formation prior to the lithostratigraphic revisions by Brett and others, 2012). Specimens were collected from the active New Point Stone quarry just east of Napoleon, Ripley County, southeastern Indiana (N39°12’31.39” W85°18’53.74”; WGS84, Mercator projection), a site that is famous for the abundance and quality of stalked echinoderm and trilobite fossils recovered from the Massie Formation (Bissett, 2017). This is due to both the depositional conditions, in which organisms were rapidly buried by episodic storm-deposited muds, and the fact that this small area of southern Indiana managed to escape regionally extensive late-diagenetic dolomitization (Thomka and Brett, 2015b).

The fine-grained, poorly indurated lithology of the mudstone lithofacies of the Massie Formation allowed relatively intact specimens to be removed from matrix with little preparation, as the fossils readily weathered free from the surrounding sediment. When needed, preparation entailed immersing loose specimens in a solution of RockQuat—29.57 ml per 946.25 ml of water (2 tablespoons per quart of water)—for 24 hours at room temperature, which removed any adhering mud, followed, if necessary, by light air abrasion with 25-micron aluminum oxide abrasive powder. For specimens collected in association with surrounding sedimentary matrix, this same procedure was employed, but occurred after the specimen was carefully removed from the matrix and was followed by returning the specimen to its original position in matrix.

With one exception, diploporitan “cystoid” thecae analyzed in this study belong to the holocystitid species *Holocystites scutellatus*, which is the dominant component of the echinoderm fauna in this stratigraphic interval at the Napoleon quarry (Frest and others, 1999, 2011; Thomka and others, 2016). Brachioles are absent, but diploporitan thecae are otherwise intact (Thomka and others, 2016). Encrustation of diploporitan thecae by crinoid attachment structures occurred after the death of the “cystoid” but prior to final burial (Thomka and others, 2016); during this phase in the fossils’ taphonomic history, exposed portions of thecae served as “benthic islands” surrounded by soft muds, readily utilized as substrata by organisms that preferred hard substrates over softground sediments (Thomka and others, 2021).

**TYPICAL SPECIMEN DESCRIPTIONS**

A sample of diploporitan thecae encrusted by *Eucalyptocrinites* attachment structures (collected by DLB and TEB) was analyzed for this study, with an emphasis on fairly typical examples (Fig. 1). The encrusting structures are classified as terminal dendritic radix structures composed of multiple, distally tapering, branching radicles (appendages) extending radially outward from a central, vertically oriented column (see
Donovan and others, 2007; Donovan, 2016). Diagnostic features of radix structures attributable to *Eucalyptocrinites* include a relatively small pentalobate lumen, minute pentalobate or circular lumina within radi- cles, and radicles composed of discrete ossicles, sometimes surrounded by an amorphous cortex of calcite (Halleck, 1973; Brett, 1981, 1984; Thomka and Brett, 2015a, 2019; Plotnick and others, 2016; Poschmann, 2020). These features allow *Eucalyptocrinites* radices to be confidently differentiated from similar attachment structures, such as the dendritic radix structures of the hemicosmitid rhombiferan *Caryocrinites*, which has a larger, trilobate lumen and radicles that lack lumina. Instead, *Eucalyptocrinites* radices are solid rods of unsegmented calcite (Brett, 1978, 1981, 1984; Thomka and Brett, 2015a, 2015b, 2019).

In all examples shown in Figure 1, radicles are present in a roughly radial configuration, typically with five or so primary radicles. All radicles are relatively long, generally extending across the lateral surface of the encrusted theca until reaching the margin. Radicles taper distally, and branching, where observed, is dichotomous; the distal tapering may be enhanced to some degree by overgrowth of the proximal portions of radicles by a cortex of secondary skeletal material (Fig. 1). In some instances, this led to amalgamation of the proximal portions of two or more adjacent radicles, resulting in difficulty in discerning the number of primary radicles (for example, Fig. 1B).

The morphology of these attachment structures is strongly influenced by their location on the lateral surface of the encrusted theca, in addition to the amount of thecal surface area exposed and available for encrustation. Because initial settlement occurred near the middle of the upward-facing surface of the diploporent thecae, outward growth of radicles could proceed in all directions for substantial lengths before reaching the edge of the theca (Fig. 1). This settlement position fostered a radially symmetrical radix structure regardless of number of radicles, degree of secondary overgrowth of radicles, and other factors. This morpho- logical attribute comprises the major contrast between the typical specimens shown in Figure 1 and the atypical specimens described by Thomka and others (2021), in which radicles were only well developed on one side of the structure. Thus, both the more typical specimens described here (Fig. 1) and the atypical specimens described by Thomka and others (2021) testify to the capacity of *Eucalyptocrinites* to modify the morphology of its attachment structure in response to local substrate conditions. Physical or chemical detection of a preferred substratum resulted in outward growth and branching.
of radicles, whereas less preferable material—in this instance, the muds surrounding the “benthic islands” of diploporitan thecae—caused radicles to stop growing, change direction, and/or not develop branches.

In other comparable muddy softgrounds, such as the Rochester Shale (Brett, 1978, 1981) and Waldron Shale (Halleck, 1973; Plotnick and others, 2016), radices commonly grow via initially encrusting a macrofossil, then extending into the surrounding muds, overgrowing and incorporating any additional macrofossils that are encountered. It is unclear why the specimens from the Massie Formation were so incapable of extending radicles beyond the edge of the encrusted thecae. One potential explanation is that these Eucalyptocrinites radices were simply smaller and did not need to extend beyond their preferred substratum. Another possibility, which is more speculative, is that the radices in other units developed in areas of the seafloor where macrofossils were clustered, so radicles only needed to extend a short lateral distance before encountering another solid bioclast that could improve their support. In this scenario, these diploporitan thecae may have been more widely separated from other bioclasts.

ATYPICAL SPECIMEN DESCRIPTIONS

Although the primary purpose of this study is to describe and show figure relatively typical examples of holocystitid diploporitans that are encrusted by Eucalyptocrinites radix structures, the sample also contained several atypical specimens with noteworthy features. Specifically, four radices on diploporitan thecae are worthy of discussion: (1) a radix with well-developed radicles only in two opposing quadrants of the structure; (2) a radix with well-developed radicles on one hemisphere of the structure and poorly developed radicles on the opposite side, where they approached a laminar bryozoan colony; (3) a radix that preferentially encrusted a small patch of bryozoan that was already present on the theca; and (4) a rare example of a radix encrusting the holocystitid genus Paulicystis.

The Holocystites scutellatus theca shown in Figure 2 is encrusted by a Eucalyptocrinites attachment structure characterized by radicles that are long, well-developed, and tightly aligned in only two directions. One set of four to five radicles is oriented roughly 45° from the long axis of the encrusted theca (at approximately the 7 o’clock position as shown on Fig. 2), with the other set of five to six radicles oriented nearly 180° across the radix axis (at approximately the 2 o’clock position as shown on Fig. 2). There are no radicles, even poorly developed examples, extending in any other direction, leaving two quadrants of the radix devoid of appendages. This is a highly unusual morphology given the position of the radix toward the center of the lateral surface of the thecae, which would be expected to result in a radially symmetrical structure such as those in Figure 1. This bilateral symmetry suggests an additional influence on the growth of radicles beyond position on the encrusted substratum. Plotnick and others (2016) reported somewhat bilaterally symmetrical Eucalyptocrinites radices and interpreted the directions of radicle growth as parallel to current flow; this was based on calculations demonstrating that radicular growth parallel to strong currents would reduce shear forces acting upon the crinoid. This seems plausible for the specimen described here (Fig. 2); however, the radices studied by Plotnick and others (2016) were in softground muds rather than encrusting a solid macrofossil. Perhaps this particular encrusted theca was unstable to some extent (for example, rocking back and forth rather than being firmly impressed into the underlying and surrounding sediment), necessitating bilaterally symmetrical radicle growth.
Another unusual *H. scutellatus* theca (Fig. 3) is similar to those described by Thomka and others (2021) in that radicles are long and branching on only one hemisphere of the *Eucalyptocrinites* radix. However, the cause of this asymmetry is quite different: whereas the radicles described by Thomka and others (2021) reflected settlement near the margins of encrusted thecae, the radix in Figure 3 is more centrally located. In fact, the long, well-developed radicles are on the side of the radix that is closest to the edge of the theca (at roughly the 5 o’clock position in Fig. 3), in contrast to the short and poorly developed radicles on the opposite side of the structure (at roughly the 10 o’clock position in Fig. 3). This unexpected pattern is most likely related to the presence of a thin, laminar, stenolaemate bryozoan colony encrusting a portion of the diploporitan theca (Fig. 3). Although it is possible that the radicles of the attachment structure were somehow unable to overgrow a dead bryozoan colony, this seems highly unlikely given the frequency of bryozoans encrusted by *Eucalyptocrinites* in the Massie Formation (Thomka and Brett, 2015b). Rather, it is more likely that both encrusters were alive concurrently, with growth of the bryozoan inhibiting growth of the crinoid radicles that extended toward it. Interactions between stalked echinoderms and bryozoans have been reported from the hardground surface underlying the mudstone interval of the Massie Formation at the study site (Thomka and Brett, 2014, 2015b), but there was no evidence that growth of one organism interfered with growth of the other; perhaps the more limited space available for encrustation on the lateral surface of an individual diploporitan theca compared to a laterally continuous hardground resulted in more aggressive strategies by certain encrusting organisms. Regardless, this specimen is highly atypical and represents a different mechanism for strongly asymmetrical radicle development in *Eucalyptocrinites* radices beyond settlement position on a substratum bioclast, as invoked by Thomka and others (2021).

The encrusted *H. scutellatus* theca shown in Figure 4 represents a crinoid-bryozoan association of a different sort. In this instance, the encrusting *Eucalyptocrinites* radix did not avoid a bryozoan colony encrusting the same substratum, but rather preferentially settled upon it. The crinoid radix is minute and present near the margin of the oral region of the theca (Fig. 4A). Recent weathering has damaged the radix structure, so the hemisphere directed toward the aboral region of the theca has been removed (Fig. 4B). The remaining structure consists of four to five slender radicles, each extending for a few millimeters. Importantly, the entire attachment structure is restricted to a laminar bryozoan colony (Fig. 4B) that had encrusted the diploporitan theca prior to settlement by *Eucalyptocrinites*. This clearly represents encrustation of a dead bryozoan colony, in contrast to the association described above (Fig. 3). Preferential encrustation of the bryozoan is evidenced by the length and orientation of radicles, which correspond identically with the extent of the underlying bryozoan (Fig. 4B). The reason for this substratum preference is unknown. It is possible that the orientation of the diploporitan made the bryozoan-encrusted area a preferable settling place (for example, if that area represented the most elevated position of a partially buried theca); this explanation might best account for the extremely limited extent of encrustation (Fig. 4A). The small size of the crinoid radix structure may also be related to the relative smoothness of the flat bryozoan, which might have been easier to encrust than the irregular, ornamented (pustulose) surface characteristic of *H. scutellatus* thecal plates.
The only encrusted diploporan analyzed in this study that does not belong to *H. scutellatus* is shown in Figure 5. This intact theca, which is still embeded in matrix, belongs to the holocystitid diploporan genus *Paulicystis*, a taxon that is a subordinate echinoderm component of the lower mudstone lithofacies of the Massie Formation at the Napoleon quarry (Frest and others, 1999, 2011), as it is exponentially rarer than *H. scutellatus*. This specimen is encrusted by a *Eucalyptocrinites* radix comprising at least four primary radicles arranged evenly around the structure, one of which shows well-developed dichotomous branching (Fig. 5). The attachment structure is close to the center of the lateral surface of the theca, making the configuration of radicles logical, as also shown by the examples in Figure 1. Relative to *H. scutellatus*, which is commonly encrusted (Thomka and others, 2016), *Paulicystis* is not known to frequently serve as a substratum; the compendium of echinoderm encrustation relationships in Frest and others (2011) lists only bryozoans as encrusters of *Paulicystis*. The only published documentation of *Paulicystis* having been encrusted by another stalked echinoderm comes from Thomka and Bantel (2021), who described a thecal attachment structure tentatively assigned to *Paulicystis* that was overgrown by a radix belonging to the rhombiferan *Caryocrinites*. The presence of an attachment structure attributable to *Eucalyptocrinites* (Fig. 5) demonstrates that this diploporan genus was capable of serving as a substratum to multiple organisms, including crinoids as well as blastozoans.

Figure 4. Theca of *Holocystites scutellatus* that is encrusted by a small laminar stenolaemate bryozoan colony that is, itself, preferentially encrusted by a minute *Eucalyptocrinites* radix. A) Lateral surface of the theca with the position of the bryozoan-crinoid attachment structure association marked by the asterisk. Scale bar = 1 cm. B) Close-up view of the crinoid radix showing its restriction to the underlying bryozoan. The reason for preferential encrustation of a bryozoan is unclear. Scale bar = 2 mm.

Figure 5. Theca of the holocystitid diploporan *Paulicystis* that is encrusted by a typical *Eucalyptocrinites* attachment structure. Note the dichotomous branch on the radicle extending to the left of the image. This relatively rare diploporan genus has not previously been reported as a substratum for encrusting crinoids. Scale bar = 1 cm.
DISCUSSION

These specimens contribute substantially to the knowledge of *Eucalyptocrinites* radicular attachment structures on blastozoan thecae, a relatively rare and unusual paleoecological phenomenon. Typical examples of encrusting radices are described and illustrated in hitherto unprecedented detail, and new examples of informative atypical examples are discussed. The mudstone lithofacies of the Massie Formation at Napoleon, Indiana, continues to be among the best sources of material capable of providing information on the paleoecology of Paleozoic stalked echinoderms, particularly involving crinozoan-blastozoan interactions.

In a larger sense, study of this material highlights the morphological plasticity of *Eucalyptocrinites* attachment structures, which contrasts with the more fixed and consistent nature of the other parts of the crinoid skeleton. The plating of the crown and stem (aside from heteromorphy) tend to be far less variable. Although an underlying genetic control dictates development of some form of radix, the specific morphology of any given attachment structure is highly dependent upon a combination of multiple factors. Such controls include the consistency of the substrate; the predominant current direction(s) and strength; the size, texture, and amount of exposed surface of bioclastic substrata; the initial settlement position on encrusted bioclasts; the presence, distribution, and morphology of other encrusters on the surface of bioclasts; and the behavior of any living encrusters sharing the same surface. This complexity makes attachment structures valuable sources of information on paleoenvironmental processes and biotic associations.

ACKNOWLEDGMENTS

The Wanstrath Family of Napoleon, Indiana, allowed access to the quarry from which the studied specimens were collected. Constructive reviews provided by Bradley Deline (University of West Georgia) and Gary J. Motz (Yale University) improved an earlier version of this paper.
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