

Paleoecological Significance of a Pre-mortem Crinoid-Coral Interaction from the Silurian of Southeastern Indiana

James R. Thomka¹ and Thomas E. Bantel²

¹Center for Earth and Environmental Science, State University of New York at Plattsburgh, Plattsburgh, New York 12901, USA

²Dry Dredgers, P.O. Box 210-013, Cincinnati, Ohio 45221, USA

E-mail: jthom059@plattsburgh.edu

Received 08/13/2020

Accepted for publication 11/11/2020

Published 03/15/2021

Suggested citation: Thomka, J. R., and Bantel, T. E., 2021, Paleoecological significance of a pre-mortem crinoid-coral interaction from the Silurian of southeastern Indiana: Indiana Geological and Water Survey, Indiana Journal of Earth Sciences, v. 3. DOI 10.14434/ijes.v3i1.31283



ABSTRACT

A noteworthy specimen recording a *syn vivo* interaction between a stalked echinoderm and a tabulate coral is described herein from the middle Silurian (Wenlock Series, Sheinwoodian Stage) Massie Formation of Ripley County, southeastern Indiana. Part of the column of the camerate crinoid *Eucalyptocrinites* Goldfuss, 1831 is encrusted around the entirety of its lateral margin by a favositid colony. The radially outward orientation of corallites of the colony show that the coral was elevated completely above the seafloor and, more importantly, that the crinoid column had to be vertical at the time of initial encrustation and subsequent coral astogeny. Hence, the crinoid host was most likely alive throughout the duration of this interaction. No evidence for a paleopathological reaction is present on the crinoid column, suggesting that the encruster did not adversely affect the host. This most likely reflects the long and inflexible column of *Eucalyptocrinites*, which could have supported encrusting secondarily tiered organisms—even relatively heavy ones—without interfering with the biological functions of the crown or weighing down the column.

INTRODUCTION

Paleozoic crinoids were involved in biotic interactions with a taxonomically and ecologically diverse suite of associated organisms (Meyer and Ausich, 1983; Donovan, 2015). During the Silurian Period, crinoids commonly served as encrusters of bioclasts as well as substrates for encrustation by other taxa (for example, Brett, 1984, 1991; Peters and Bork, 1998). Although discerning between a *syn vivo* interaction and *post mortem* encrustation of a bioclast in Paleozoic

assemblages can be difficult or equivocal (Boucot, 1990), the morphological complexity and taphonomic volatility of crinoid skeletons makes them atypically high-resolution sources of information on the timing of encrustation (for example, Brett and Eckert, 1982; Taylor and Brett, 1996; Peters and Bork, 1998). Consequently, Silurian crinoids that served as substrata or hosts while alive can be recognized, providing a clearer understanding of the nature, duration, and effects of the interaction (see Donovan and Tenny, 2015, for an

excellent example of discrimination between structures produced in living vs. dead Mississippian crinoid substrata).

The present contribution describes a noteworthy specimen that records a *syn vivo* interaction between an encrusting tabulate coral and its contemporary Silurian crinoid substrate. This specimen is significant because it represents a rarely encountered association in the highly fossiliferous unit from which it was collected; further, this is an atypically well-preserved example of such an association in general, in spite of the fact that both crinoids and tabulate corals are common in normal marine Silurian environments worldwide (for example, Brett, 1991). More importantly, this specimen provides information on the paleoautecology of the crinoid host, illustrating the paleobiological and paleoecological value of encrusted specimens that might be otherwise overlooked in favor of more pristine material.

MATERIALS AND METHODS

The specimen described herein was collected (by TEB) as float from the mudstone lithofacies of the Massie Formation (*sensu* Brett and others, 2012) at the New Point Stone quarry east of Napoleon, in northern Ripley County, Indiana (N39°12'31.39", W85°18'53.74"; fig. 1). This stratigraphic interval, formerly known as the "upper Osgood shale" (Foerste, 1897), consists of a poorly lithified medium-gray mudstone containing a rich invertebrate macrofauna indicative of a normal marine level-bottom softground environment (Frest and others, 1999). Taphonomic and faunal evidence suggest

a generally slow background sedimentation rate; however, this depositional setting was prone to episodic rapid burial events, most likely storms, resulting in the Massie Formation mudstone at the Napoleon quarry being internationally renowned for producing remarkably preserved trilobites and echinoderms (for example, Thomka and Brett, 2015). Such well-preserved fossils include intact specimens of the unusual spathacaly-menid trilobites that are known only from this site and thousands of articulated specimens of diploporitan echinoderms belonging to the enigmatic *Holocystites* Fauna (for example, Frest and others, 1999, 2011; Thomka and Brett, 2015; Thomka and others, 2016).

Because of the fine-grained, poorly lithified nature of the matrix sediment, minimal preparatory work was required for the specimen; it was washed using warm water and a brush and left to dry. The original orientation of the specimen relative to sedimentary bedding was not apparent at the time of collection, but the configuration of corallites indicate the original upward-facing direction at the time of coral growth (see below); there is no evidence that the colony changed orientation significantly throughout its existence.

DESCRIPTION AND INTERPRETATION

The specimen consists of a partial crinoid columnal that is encrusted on the entirety of its lateral circumference by a tabulate coral colony (fig. 2). The colony surrounds the crinoid column in a slightly ovoid configuration (fig. 2A,B), with the longer axis measuring 76 mm and the shorter axis measuring 61 mm. The

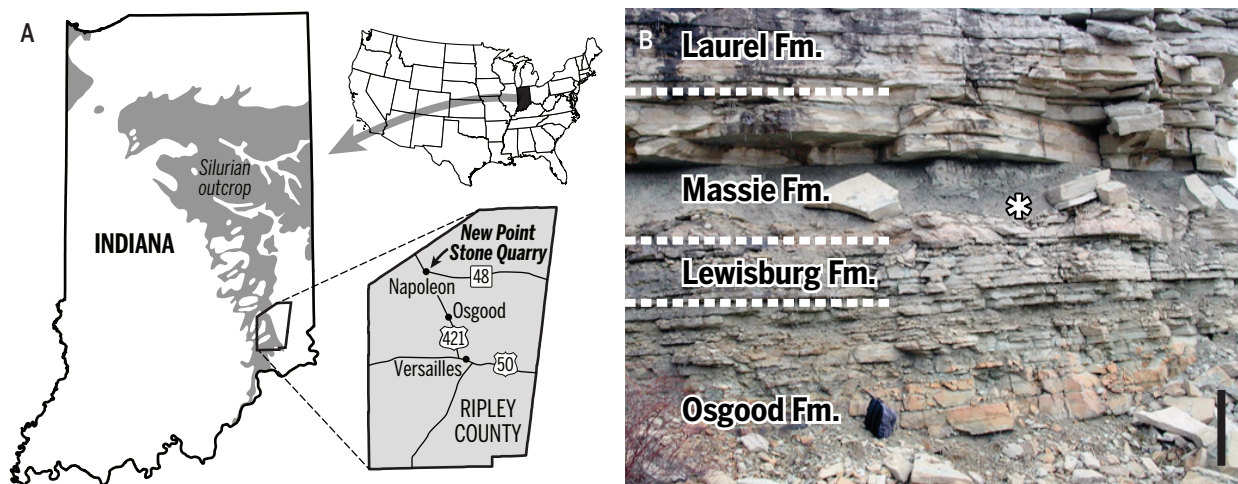


Figure 1. Locality and stratigraphic context of the studied material. A) Location of the Napoleon quarry, Ripley County, southeastern Indiana. From Thomka and others (2016). B) View of middle Silurian strata exposed at the Napoleon quarry, with formation-scale lithostratigraphic units labeled (lithostratigraphic nomenclature follows Brett and others, 2012). The specimen was collected from the basal 10 cm of the mudstone lithofacies of the Massie Formation (marked by asterisk). Scale bar = 1 m.

thickness of the coral colony ranges from 14 mm to 27 mm, with a distinctively depressed quadrant (fig. 2C). One side of the specimen is nearly flat, with all corallites oriented laterally, radiating away from the column (Fig. 2B); this was almost certainly the side of the colony facing down toward the substrate (Fig. 2B); this was almost certainly the side of the colony facing down toward the substrate. The opposite side (fig. 2A) displays some relief (fig. 2C), with corallites generally oriented vertically (parallel to the long axis of the column); this was almost certainly the upward-facing side of the colony. It is likely that the depressed portion of the upward-facing side (“min” in fig. 2A) represents the downcurrent direction, an interpretation that is supported by the decreased height of corallites (expected in the portion of the coral colony located in the “shadow” of the column; “max” in fig. 2A), as well as the maximum width and height of the colony being present nearly opposite (fig. 2A), as would be expected in the upcurrent direction.

The tabulate coral colony, which is light gray to greenish-gray in color, consists of strongly polygonal, pentagonal to sub-hexagonal corallites of approximately 2 mm in diameter. Corallites are in continuous contact with laterally adjacent corallites and no traces of septa are visible. This is clearly a favositid tabulate, most likely a species of *Favosites* Lamarck, 1816, possibly *F. forbesi* Milne-Edwards and Haime, 1851 (Stehl, 1978; see also Peters and Bork, 1998).

The crinoid column, which is dark brown in color and 7 mm in diameter, is oriented vertically, with lateral surfaces covered by the encrusting coral except for a 1–2 mm area where the coral is thinnest (fig. 2C). Articular surfaces of the through-going column are exposed on both sides of the specimen, being characterized by a centrally located pentalobate lumen comprising roughly 50 percent of the columnal diameter (fig. 2A,B). Based on comparison with more articulated material, this column can be confidently attributed to the monobathrid camerate *Eucalyptocrinites* Goldfuss, 1831 (for example, Halleck, 1973; Brett, 1984), a genus that is common within the Massie Formation at

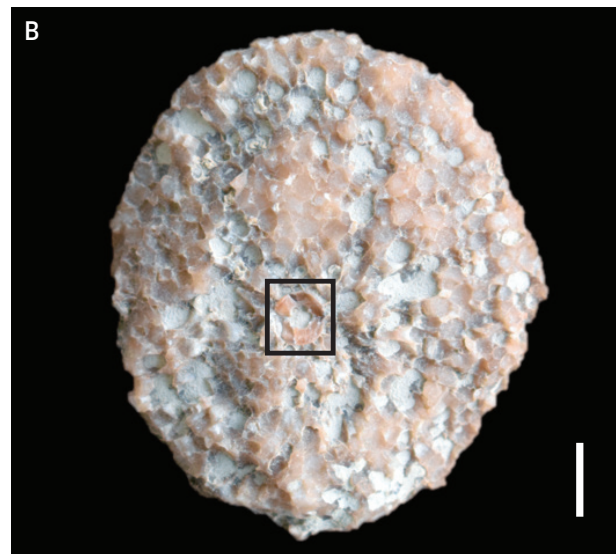
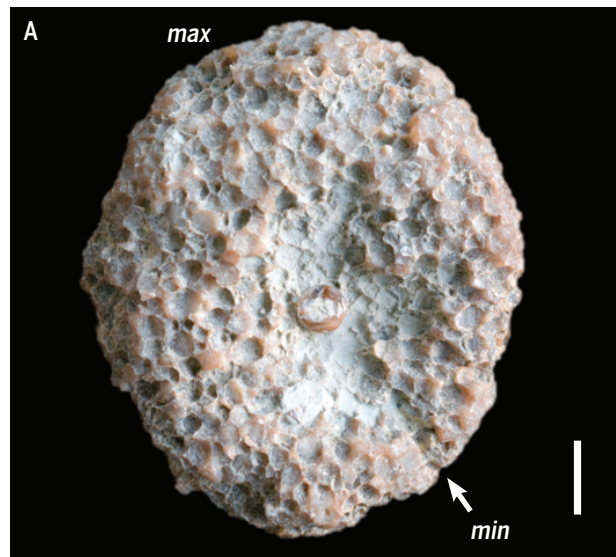


Figure 2. Partial column of the monobathrid camerate crinoid *Eucalyptocrinites* encrusted while alive by a colonial favositid tabulate coral (*Favosites*?). A) View of the upper surface showing the column surrounded by the encrusting coral colony. The arrow marks the area of minimal coral thickness (“min”). Opposite (“max”) represents the area of maximum coral thickness. B) View of the lower surface, showing the persistence of the column (marked by the box) in a central position, indicating a vertical orientation. C) Slightly oblique view, showing the thickness of the tabulate colony and the depressed quadrant. The arrow marks the position of the through-going column on the underside of the specimen, showing its vertical orientation. All scale bars = 10 mm.

the Napoleon quarry (Frest and others, 1999; Thomka and Brett, 2015).

Evidence that this represents encrustation of a living crinoid comes primarily from the holoperipheral outwardly radial orientation and distribution of corallites, which would have been possible only for astogeny around a vertically oriented column. There are no indicators of overgrowth of one portion of the coral by other parts, individual corallites are continuous on all sides, and the presumed lower surface is evenly flat whereas the presumed upper surface is upwardly domed around the column (fig. 2). Although crinoids are evidently capable of survival as stems following removal of crowns (Donovan and Pawson, 1997; Oji and Amemiya, 1998; Donovan and Schmidt, 2001), this explanation is less parsimonious than encrustation of a living crinoid, given the rarity of this phenomenon in both modern and especially Paleozoic environments and the relatively large size of the tabulate coral colony, which indicates a stable vertical column.

DISCUSSION

Discovery of a Paleozoic crinoid column that is encrusted by a coral in the manner described herein is not unprecedented (Meyer and Ausich, 1983). However, crinoid-tabulate coral biotic interactions are rare within the abundantly fossiliferous Massie Formation; most reports of coral-encrusted echinoderms from the study site consist of pelmatozoan thecae that were used, *post mortem*, as substrata for minute rugosans (Frest and others, 2011; Thomka and others, 2016). Indeed, in a larger sense, most of the recent published descriptions of noteworthy Paleozoic crinoid-coral associations involve interactions between crinoid hosts and solitary rugose corals (for example, Donovan and others, 2005; Głuchowski, 2005; Brett and others, 2007; Berkowski and Klug, 2012; Bohatý and others, 2012; Peel and McDermott, 2016) rather than tabulate coral colonies. Of the published examples of crinoid columns encrusted during life by tabulate corals (for example, Halleck, 1973; Brett and Eckert, 1982; Peters and Bork, 1998; Galle and Prokop, 2000; Głuchowski, 2005; Berkowski and Zapalski, 2014), few are as large and involve as complete a colony as the one described here (but see Hudson and others, 1966).

This specimen is also significant because of the absence of a pathologic response by the crinoid host to the interaction. Although swelling of the crinoid column in the area of encrustation is generally recognized as the most definitive evidence for a *syn vivo* interaction (Bohatý and others, 2012; see also Meyer and Ausich, 1983; Donovan, 2015), a living crinoid host that did not react to the interaction can nevertheless be inferred by the

taphonomic state of the crinoid (Brett and Eckert, 1982; Peters and Bork, 1998) and the orientation of the coral (Głuchowski, 2005; Berkowski and Zapalski, 2014; Peel and McDermott, 2016). The precise reason(s) that the crinoid did not respond pathologically to encrustation is unknown, but it should be noted that some other occurrences of Paleozoic crinoid-tabulate coral interactions are not associated with swelling (for example, Hudson and others, 1966; Berkowski and Zapalski, 2014), even in deposits where co-occurring crinoid columns infested by rugose corals consistently produced swellings (Głuchowski, 2005).

One potential explanation for the absence of a pathological response by the host in this instance involves the paleoautecology of the specific crinoid taxon involved. Live encrustation of the genus *Eucalyptocrinites* by tabulate corals in Silurian deposits has been documented by Halleck (1973), Brett and Eckert (1982), and Peters and Bork (1998), in addition to the present report, and none of these occurrences was associated with pathologically deformed host columns. The lack of a swelling response may indicate that these *Eucalyptocrinites* individuals were insufficiently affected by the interaction to trigger growth of secondary stereomic calcite in response to the encruster. Brett (1984) interpreted the column of *Eucalyptocrinites* as having been unusually long and inflexible relative to other Silurian crinoids. This structural rigidity—coupled with the unique ligamentary tissue in crinoid stems, which permits a fully upright position with little energy expenditure (Baumiller, 1997, 2008)—would have made *Eucalyptocrinites* capable of maintaining a vertical stem posture despite the weight generated by encrusting organisms on the column. Even the increased weight of the thickest portion of the coral colony, presumably representing the upcurrent-facing side, would have been sufficient to affect the posture of the crinoid (namely, the crinoid almost certainly was not tilted toward the upcurrent direction, but, rather, was vertically oriented or slightly tilted downcurrent, as in modern crinoids). The stiffness and length of *Eucalyptocrinites* columns fostered diverse secondarily tiered encrusting communities (Peters and Bork, 1998) without adversely affecting the biological functions of the crinoid itself. Hence, a relatively large and presumably heavy tabulate coral colony could persist for an extended duration around the erect column of *Eucalyptocrinites*, most likely benefitting from the elevation above the muddy seafloor during deposition of sediments of the Massie Formation.

In summary, an atypically informative example of a *syn vivo* interaction between the camerate crinoid *Eucalyptocrinites* and an encrusting tabulate coral colony (likely *Favosites* sp.) illustrates a number of paleoecological

phenomena. Not only does this represent a rare occurrence in a paleontologically important Silurian unit, but it also provides support for the interpretation that *Eucaelyptocrinites* was characterized by an inflexible vertically oriented stem that could support even relatively large encrusting organisms without appreciable negative effects.

ACKNOWLEDGMENTS

The Wanstrath family of Napoleon, Indiana, generously allowed access to the collection site. Our knowledge of the stratigraphy and paleontology of the Napoleon quarry has increased significantly through discussions with Carlton E. Brett (University of Cincinnati) and Donald L. Bissett (Dry Dredgers). Constructive reviews by Alyssa M. Bancroft (Indiana Geological and Water Survey) and Sarah A. Burgess (Indiana University) improved an earlier version of this paper.

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