Online ISSN 2435-0931 Print ISSN 0385-0900
DOI: 10.50897/bmfm.51.1_49

Bulletin of the Mizunami Fossil Museum, vol. 51, no. 1, p. 49–54, 2 figs.

Manuscript accepted on July 13, 2024; online published on August 23, 2024
http://zoobank.org/urn:lsid:zoobank.org:pub:41FF0BFC-9AB6-4393-9CFC-C3D56BCD6B01

Diploporitan 'cystoid' echinoderms as encrusters of Palaeozoic cephalopods: A brief comment

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Abstract

A recent article described an orthoceratid cephalopod from the Silurian of eastern midcontinental USA that is encrusted by two blastozoan echinoderms, with one attachment structure preferentially encrusting the attachment structure of the other. Discussion of the palaeoecological significance of this specimen centered around interactions between encrusting echinoderms, but as a note of secondary significance, it was reported that this occurrence supposedly represented the first published example of diploporitan encrustation of a cephalopod substratum that was not completely overgrown by the aboral region of the echinoderm. This claim is inaccurate, however, as two previously published examples have been documented. Nevertheless, the specimen represents the first published Silurian example of such a phenomenon, as both previously published examples were from other Palaeozoic systems. An additional Silurian cephalopod specimen (*Dawsonoceras annulatum*) displaying encrustation by a diploporitan echinoderm—the second example documented from Silurian strata—seemingly indicates that this relationship is less rare than the paucity of currently published descriptions suggests.

Key words: Echinodermata, Blastozoa, Silurian, orthoceratids, corrigendum

1. Introduction

Thomka and Bantel (2021) described an orthoceratid cephalopod from the middle Silurian (Wenlock: Sheinwoodian) of Indiana, USA, that is noteworthy in that it records a rare sequence of encrustation by blastozoan echinoderms. Specifically, one portion of the cephalopod was encrusted by the aboral thecal attachment structure of a holocystitid diploporitan (probably *Paulicystis*), with this attachment structure, in turn, being partially overgrown by a radicular attachment structure attributable to the hemicosmitid rhombiferan *Caryocrinites* (Fig. 1). Such an example of preferential encrustation of a cephalopod-encrusting blastozoan attachment structure by another blastozoan had not previously been documented, and the specimen was consequently described and analyzed in detail.

In addition to the blastozoan-on-blastozoan encrustation aspect, a secondary reason for the significance of the material described by Thomka and Bantel (2021) lies in the fact that this association represents an example of diploporitan encrustation of a cephalopod substratum that did not result in complete overgrowth of the encrusted bioclast. Instead, only a portion of the larger cephalopod was encrusted by the much smaller diploporitan (Fig. 1). This state is unusual because even though encrustation of cephalopods by diploporitan echinoderms is not, in general, a commonly encountered phenomenon, most of the described examples involve small, partial phragmocone material that was incorporated into the basal surface of the echinoderm and ultimately preserved as a mold (see Paul, 1971; Frest et al., 2011 for brief descriptions of substrata utilized by diploporitans at the specimen collection locality). In contrast, the specimen in Figure 1 was not preserved via substratum bioimmuration (*sensu* Taylor, 1990) and only a small portion of the cephalopod was overgrown by the diploporitan. Thomka and Bantel (2021, p. 58) claimed that the figured specimen represented the first published description of such an encrustation pattern. The primary purpose of this short paper is to correct the inaccuracy of this assertion, as two earlier published descriptions of incomplete overgrowth of cephalopod substrata by diploporitans were discovered after the publication of Thomka and Bantel (2021). A secondary purpose is description of supplemental material that improves documentation of diploporitan-cephalopod associations.

2. Published Examples of Diploporitan-Encrusted Cephalopods

In a review of criteria that can be used to distinguish between *syn vivo* and *post mortem* encrustation of Devonian and Carboniferous cephalopods, Klug and Korn (2001) described a specimen of *Chlupacites praeceps* from the late Emsian of Morocco that is encrusted by the diploporitan *Eucystis*. This study cited a previously published example of an Ordovician diploporitan-encrusted cephalopod described by Ganss (1937). Neither of the cephalopod substrata were completely overgrown by the encrusting diploporitan echinoderm, resulting in preservation similar to that of the specimen in Figure 1 (e.g. Klug and Korn, 2001, pl. 2, fig. H). Fortuitously, these earlier publications were brought to the attention of the senior author, allowing the present correction of an inaccurate assertion. Hence, the orthoceratid described by Thomka and Bantel (2021) was not the first published example of a cephalopod that was incompletely overgrown by a diploporitan 'cystoid,' as stated in the recent article, but the third.

Fig. 1. Orthoconic cephalopod (Orthoceratida indet.; CMC IP 87723) encrusted by two blastozoan echinoderm attachment structures (bottom right corner; the diploporitan thecal attachment structure is larger and further from the margin). This specimen, described by Thomka and Bantel (2021), was the first diploporitan-encrusted cephalopod reported from the Silurian System in which the cephalopod is not completely overgrown and preserved as a basal impression. It is the third overall example of such an encrustation relationship—not the first, as claimed by Thomka and Bantel (2021). Scale bar = 20 mm. From Thomka and Bantel (2021, fig. 1a).

The specimen described by Thomka and Bantel (2021)—CMC IP 87723 (Cincinnati Museum Center, Cincinnati, Ohio, USA)—is nevertheless the first reported example of such a faunal association from Silurian strata. The record of diploporitan encrustation of cephalopods therefore extends continuously, at least at the system level, from Ordovician (Ganss, 1937), through Silurian (Thomka and Bantel, 2021), to Devonian (Klug and Korn, 2001).

3. Discussion and Description of New Material

Given the extremely small number of published descriptions of cephalopod phragmocones encrusted and not fully overgrown by diploporitan echinoderms, any examples are worthy of documentation and interpretation. The apparent rarity of fossils bearing such encruster-substrate relationships may largely reflect a lack of attention to such material, particularly because isolated aboral thecal attachment structures typically do not allow identification of diploporitans to low taxonomic levels (Sheffield and Sumrall, 2019). Consequently, attachment structures that are separated from thecae receive less attention than intact thecae from researchers engaged in systematic study (Thomka and Brett, 2014a; see also Paul, 1988). In addition, the encrustation of larger cephalopod fossils may result in specimens being reposited in mollusk rather than echinoderm collections in museums.

Nevertheless, continued investigation of the collection of cephalopods that included the material described by Thomka and Bantel (2021) yielded another cephalopod that is similarly encrusted by a diploporitan echinoderm. This second Silurian-aged cephalopod encrusted by a partially overgrowing diploporitan is shown in Figure 2. It was recovered from the mudstone lithofacies of the Massie Formation (Wenlock: Sheinwoodian) as exposed at the Napoleon quarry of southeastern Indiana, USA. This is the same locality and stratigraphic interval from which the specimen described by Thomka and Bantel (2021) was collected, and the reader is directed to that study for more detailed information on the geographic and stratigraphic context of the described material. The newly discovered cephalopod described below is reposited at the Cincinnati Museum Center (Cincinnati, Ohio, USA) under specimen number CMC IP 97756.

The cephalopod is light grey in colour, measuring 81 mm in maximum length and 30 mm in maximum width. Neither the apex nor the body chamber is preserved and observable tapering is minimal, suggesting that a portion of the middle of the phragmocone is preserved (Figs. 2a–b). The specimen is slightly compressed, reflecting post-burial compaction, and one side displays slightly better shell surface quality (Fig. 2a), with the opposing side being somewhat degraded, seemingly reflecting damage from dissolution (Fig. 2b). The specimen can be confidently identified as *Dawsonoceras annulatum*, the most common cephalopod within the Massie Formation at the Napoleon quarry (Gunderson et al., 2024; see diagnostic criteria for identification in Foerste, 1928; Kröger and Isakar, 2006).

The *D. annulatum* shell is encrusted, as are the majority of cephalopod specimens from this collection site (Gunderson et al., 2024), with a few microconchid tentaculitoids and a small laminar trepostome bryozoan colony on the better-preserved surface (Fig. 2a); however, the most important encrusting structure is located on the less well-preserved side. Here, in a position near the lateral margin of the cephalopod shell (as defined by the axis of compression), is a brownish-gray discoidal structure measuring 15 mm in maximum diameter (Figs. 2b–d). It is circular in outline and composed of multiple plates surrounding a central circular depression with a diameter of 5 mm (Figs. 2c–d). The basalmost surface—which is cemented to the underlying cephalopod substratum—is slightly outwardly flared, comprising the widest part of the structure; above this area, the discoidal structure tapers upward to a flat-topped articular region surrounding the central depression (Fig. 2d). All plates contain numerous minute pores, the visibility of which are enhanced by slight weathering.

This encrusting discoidal structure represents the aboral thecal attachment of a holocystitid diploporitan echinoderm, probably a pentacystinid, trematocystinid, or holocystinid (*sensu* Frest et al., 2011). Specifically, the morphology and dimensions of this structure identically match the indeterminate holocystitid attachment structures of Thomka and Brett (2014a) and "type 2 holdfasts" of Thomka and Brett (2014b). These were initially described from a hardground surface immediately underlying the mudstone lithofacies of the Massie Formation at the study site (see Thomka and Brett, 2015). The attachment structure morphology shown in Figure 2 is substantially more common on the hardground surface than the *Paulicystis* attachment structure encrusting the orthoceratid cephalopod shown in Figure 1 and described by Thomka and Bantel (2021).

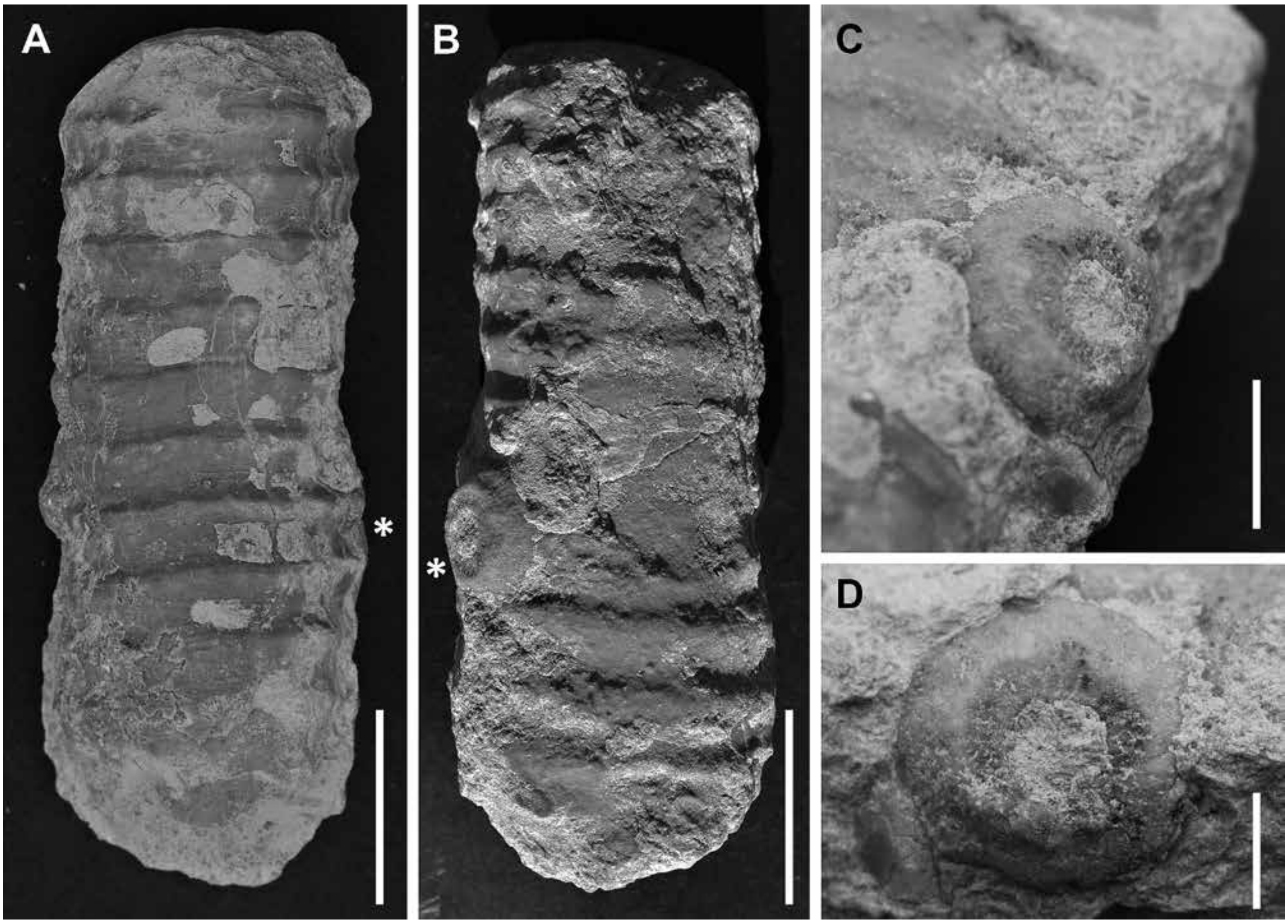

Fig. 2. Nautiloid cephalopod (*Dawsonoceras annulatum*) from the middle Silurian of southeastern Indiana, USA, that is encrusted by the aboral thecal attachment structure of a holocystitid diploporitan echinoderm (CMC IP 97756). This is the second diploporitan-encrusted cephalopod reported from the Silurian System that preserves the style of echinoderm overgrowth displayed in Figure 1. **A,** View of the more well-preserved surface of the specimen. The encrusting attachment structure is not directly visible, but its position is marked by the asterisk. Scale bar = 20 mm. **B,** View of the more poorly preserved, encrusted surface of the specimen. The encrusting attachment structure, near the lateral margin, is marked by the asterisk. Scale bar = 20 mm. **C,** Oblique view of the diploporitan attachment structure, which can be attributed to an indeterminate holocystitid, probably a pentacystinid, trematocystinid, or holocystinid taxon. Scale bar = 10 mm. **D,** Close-up view of the diploporitan thecal attachment structure, showing the flat articular region surrounding the central inter-stelar depression. Note the presence of numerous minute pores and the faintness of sutures between adjacent component plates. Scale bar = 5 mm.

In comparing the diploporitan-encrusted cephalopod specimen shown in Figure 2 to that described by Thomka and Bantel (2021; Fig. 1), it is worth noting that the identities of both the cephalopod substrata and the encrusting diploporitan echinoderms differ. Nevertheless, in both associations, attachment structure morphologies are identical to corresponding structures encrusting the underlying hardground surface (Thomka and Brett 2014a, 2014b, 2015). This demonstrates that holocystitid diploporitans were characterized by a commonly underestimated degree of morphological plasticity in their aboral regions: they were capable of modifying the attachment area in order to adopt the same strategy used in occupation of laterally continuous hardgrounds as well as large bioclasts within softground settings. This may have contributed to the success of this echinoderm group within the Massie Formation.

In a larger sense, however, the most significant aspect of the *D. annulatum* phragmocone encrusted by an indeterminate holocystitid diploporitan (Fig. 2) lies in the fact that it represents only the second documented association of this kind from the Silurian System. As discussed above, the (perceived) rarity of this biotic association in Silurian and other strata may reflect a simple lack of attention or documentation. Given that the second Silurian-age specimen was discovered as soon as focused effort was devoted to searching for it, the prospect of additional material being documented from other Ordovician, Silurian, and/or Devonian deposits is promising.

4. Acknowledgements

The Wanstrath Family of Napoleon, Indiana, USA, allowed access to the study site for both the Thomka and Bantel (2021) article and new material described in the present study. Reposition of the new specimen at the Cincinnati Museum Center was facilitated by Cameron E. Schwalbach. An earlier version of this paper was read and commented on by Sarah L. Sheffield (State University of New York at Binghamton) and Peter A. Jell (University of Queensland). The present article was improved by the constructive review provided by Stephen K. Donovan (Manchester, UK).

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