


Symbiotic embedment structures in Silurian *Caryocrinites* (Echinodermata, Rhombifera, Hemicosmitida)

James R. Thomka,¹  Carlton E. Brett,² and Donald L. Bissett³

¹Center for Earth and Environmental Science, State University of New York at Plattsburgh, Plattsburgh, New York 12901, USA <jthom059@plattsburgh.edu>

²Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA <brettce@ucmail.uc.edu>

³Dry Dredgers, P.O. Box 210013, Cincinnati, Ohio 45221, USA <donbissett@gmail.com>

Abstract.—A variety of pits representing symbiotic embedments, sometimes associated with pathological deformation in the host, are known from the skeletons of Paleozoic stalked echinoderms. These structures are well known from multiple genera of crinoids and a limited number of blastozoans but have not previously been described in detail from the skeletons of rhombiferans. This is surprising given the abundance of rhombiferans in certain deposits, the co-occurrence of rhombiferans with frequently infested taxa, including diploporitans, in multiple assemblages, and the morphological similarity between certain rhombiferan taxa and coeval infested crinoids. The common hemicosmitid rhombiferan *Caryocrinites* Say, 1825 is widespread throughout the middle Silurian of eastern North America and is herein reported to contain symbiotic (potentially parasitic) embedment structures. Specimens were collected from the lower portion of the mudstone lithofacies of the Massie Formation (Wenlock, Sheinwoodian) at the Napoleon quarry of southeastern Indiana, USA. Strong host specificity is indicated by the absence of pits in *C. ornatus* Say, 1825 and exclusive infestation of a smaller co-occurring species of *Caryocrinites*. Thecae with embedment structures are consistently smaller than thecae without such structures, with pitted specimens being restricted to a narrow range of thecal heights (20–24 mm). All embedment structures are present only on the proximal portion of thecae, with individual specimens containing between one and 30 pits. No elevated rims or significant swelling were observed on any specimens, and all pits are relatively small (~1 mm in diameter). The presence of symbiotic embedment structures represents an additional example of a crinoid-like aspect to the ecology of *Caryocrinites*.

Introduction

One of the most widely distributed, long-ranging, and distinctive blastozoan echinoderms in the Paleozoic fossil record is the hemicosmitid rhombiferan *Caryocrinites* Say, 1825. This taxon is a particularly conspicuous component of numerous carbonate and mudrock deposits in the middle Silurian of eastern and midcontinental North America and is the dominant echinoderm in some assemblages (Frest et al., 1999). Despite the abundance and long history of study of *Caryocrinites*, it is noteworthy that no specimens containing symbiotic pits have hitherto been described in detail. Stalked echinoderms displaying a paleopathological response to symbiotic (possibly parasitic) infestation are quite common in the Silurian (e.g., Franzén, 1974; Brett, 1978b; Eckert, 1988; Eckert and Brett, 2001; Widdison, 2001; Donovan, 2015; Vinn et al., 2015), and the supposed absence of such structures in *Caryocrinites* is particularly surprising given the common co-occurrence of this genus with stalked echinoderms that display high frequencies of symbiotic pits. Such infested associated echinoderms include cladid, camerate, and flexible crinoids from the Rochester Shale of western New York and Ontario (Brett, 1978c, 1985) and diploporitan ‘cystoids’ from the Massie Formation of southeastern Indiana (Paul, 1971; Frest et al., 1977, 2011; Thomka and Brett, 2014b).

Herein we describe symbiotic embedment structures in thecae of *Caryocrinites* from the middle Silurian of the Cincinnati Arch region of eastern midcontinental Laurentia. Hence, pits are present in three Silurian pelmatozoan classes. Moreover, aspects of echinoderm host specificity and paleoecology (of both host and pit-forming organism) are indicated by this occurrence.

Materials and methods

Locality and stratigraphy.—Specimens described here were recovered from the lower decimeter of the mudstone lithofacies of the Massie Formation at the New Point Stone quarry just east of Napoleon, Ripley County, southeastern Indiana, USA (39°12′31.39″N, 85°18′53.74″W; Fig. 1). Before the lithostratigraphic revisions of Brett et al. (2012), this interval was known as the base of the ‘upper shale’ of the Osgood Formation (Foerste, 1897). It represents the most productive horizon for collection of articulated echinoderms and trilobites (e.g., Paul, 1971; Frest et al., 1999, 2011; Thomka and Brett, 2015b; Thomka et al., 2016). An abundant and diverse echinoderm fauna has been collected from this interval, and articulated and partial thecae, isolated thecal plates, and pluricolumnals and columnals of *Caryocrinites* are abundant within the poorly indurated mudstone and thin wackestone interbeds (Frest et al., 1999; Thomka and Brett, 2015b).

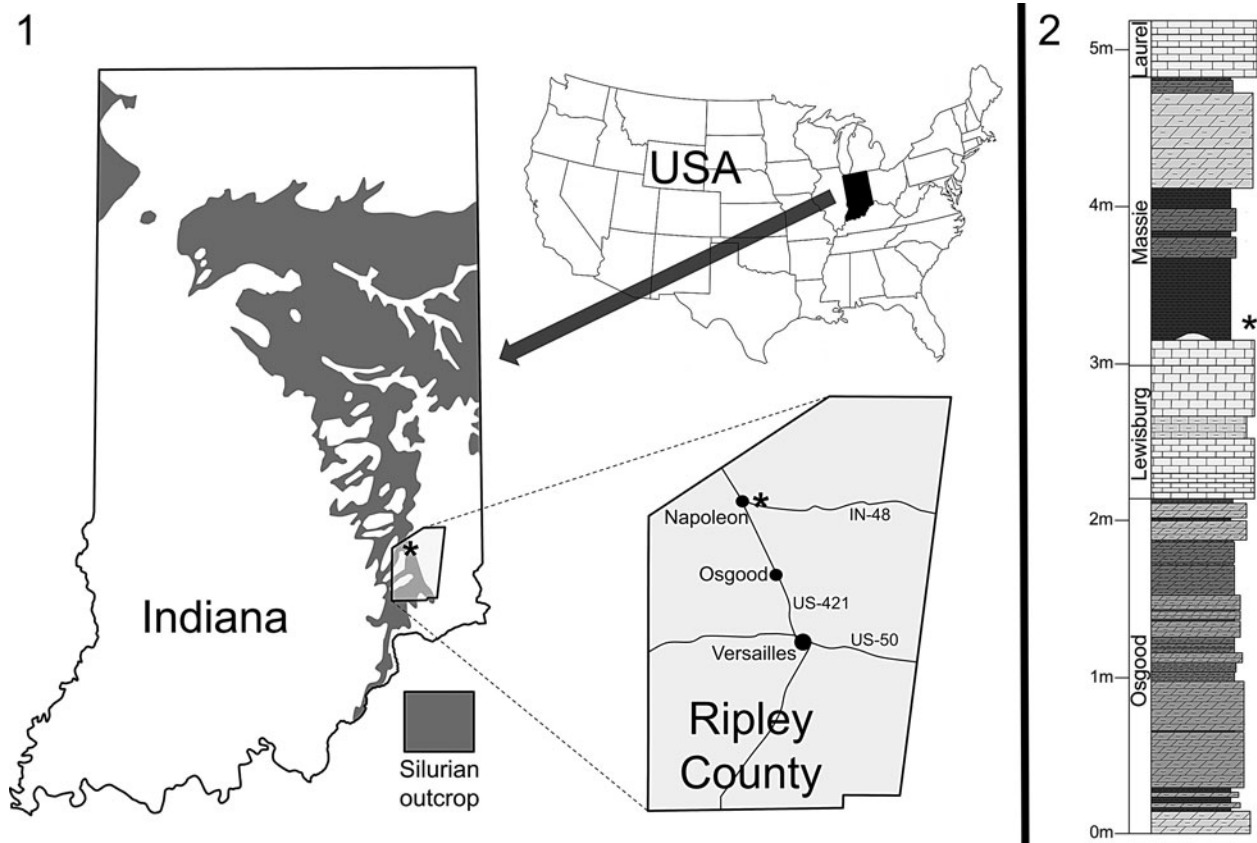


Figure 1. Locality and stratigraphy of the site from which the studied specimens were collected. (1) Location of the New Point Stone quarry (marked by asterisk) to the east of Napoleon, northern Ripley County, southeastern Indiana. (2) Stratigraphy of a portion of the Silurian section exposed at the study site, with the approximate position of the studied specimens marked by the asterisk. Note that this interval corresponds to the base of the ‘upper Osgood shale’ of Foerste (1897), a famous echinoderm-bearing unit. Figures modified from Thomka and Brett (2014a).

Exhaustive field collection of the Massie Formation at the Napoleon quarry over more than three decades by one of us (DLB) has thus far produced an estimated total of several hundred intact *Caryocrinites* thecae, a number far lower than that of the prolific diploporitan assemblage from this locality (Frest et al., 2011; Thomka et al., 2016). A representative sample of 106 *Caryocrinites* thecae, including *C. ornatus* and *C. sp. indet. A*, a diminutive species that is distinct from *C. ornatus*, was collected and analyzed for this study. Differentiation between *C. ornatus* and *C. sp. indet. A* is based on the absence of granular sculpturing, characteristic of *C. ornatus*, on thecal plates of *C. sp. indet. A*; although *C. sp. indet. A* is smaller (with respect to thecal height) than *C. ornatus*, recognition of these as separate entities is based on thecal ossicle properties rather than the size difference. Each specimen was identified as precisely as possible, measured with respect to thecal height, and carefully inspected for embedment structures; if any pits were present, the number, location, and size(s) were documented.

Repository and institutional abbreviation.—A total of six specimens were discovered with symbiotic embedment structures, all in thecae belonging to *C. sp. indet. A* (Fig. 2). These specimens, repositated at the Cincinnati Museum Center (Cincinnati, Ohio, USA) under specimen numbers CMC IP 87833–87838 (relevant specimen numbers beginning with

CMC are also provided in the figure captions), are the basis for this study and are described and interpreted below.

Description of symbiotic pits

Pits are circular in outline and oriented perpendicular to thecal plates. There is no evidence that any structures penetrated completely through the affected ossicle(s) to reach the interior of thecae, and there is no visible damage to stereom at the bottom of pits. Pit width is greater than depth. There are no discrete raised rims or concentric structures surrounding pits, and swelling due to precipitation of secondary stereom in the vicinity of pits is amorphous and minor, grading into unaffected portions of the theca (Fig. 2). Pits are smoothly parabolic in cross section, and there is no evidence for regrowth of pore structures or other fine surficial details of plates within excavated pits. The pit size is consistent, with a diameter of approximately 1 mm for all specimens (Fig. 2).

The number of pits on a single theca ranges from 1 to 30 with an average of 14 pits per individual (Figs. 2, 3). Pits are found both at plate sutures and in the central portions of plates, with no detectable preference for pit development as pits commonly occur in both locations on the same theca. No linear arrangements or prominent clusters of pits are discernable, aside from all being found in the lower hemispheres of thecae (further discussion follows). In thecae displaying numerous

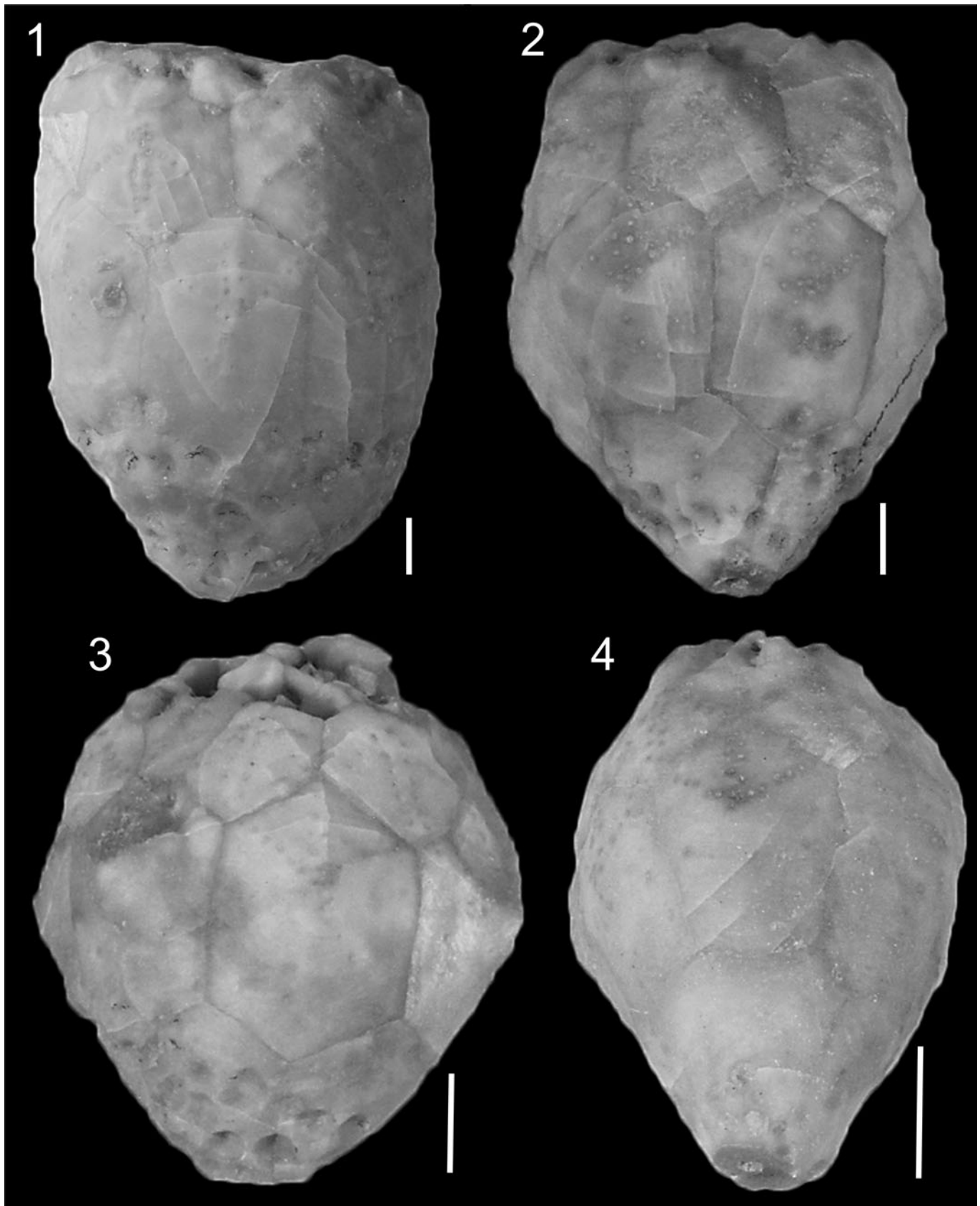


Figure 2. Examples of *Caryocrinites* sp. indet. A with symbiotic embedment structures (pits). These are representative of all pit-bearing specimens recovered from the Massie Formation of the Napoleon quarry. Note that pits are restricted to the lower hemisphere of thecae, in most instances being present only in the lowest one or two plate circlets. (1) CMC IP 87833 with numerous overlapping pits on the lower third of theca. (2) CMC IP 87834 with multiple relatively large pits, many of which occur along sutures between basal plates. (3) CMC IP 87835 with numerous prominent pits in the basal plates. (4) CMC 87836 with small number of less conspicuous pits present along the very base of the theca. Note that swelling in association with pits has resulted in some asymmetrical deformation at the site of columnal articulation to the theca. Scale bars = 5 mm.

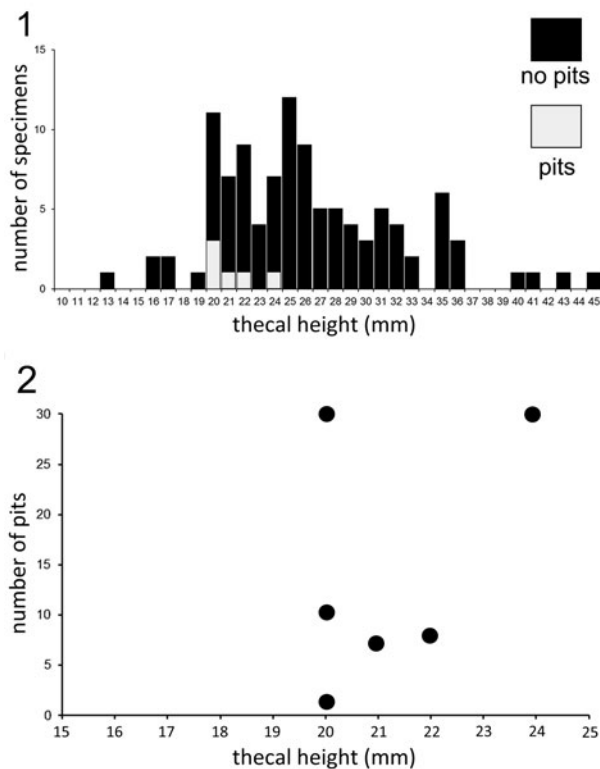


Figure 3. Data on the relationship between thecal size and the presence and number of pits. *Caryocrinites ornatus* and *Caryocrinites* sp. indet. A are pooled together in this master dataset. (1) Histogram showing *Caryocrinites* thecal heights, which range from 13 to 45 mm and display a roughly bell-shaped distribution. The average thecal height for all specimens is 26.1 mm. Specimens with pits are restricted to a range between 20 and 24 mm, with an average of 21.1 mm in thecal height. (2) Scatterplot showing the number of pits on each theca relative to thecal height. Note that there is no discernible relationship between the size of pitted thecae and the number of pits.

pits, closely spaced pits display overlapping borders (Fig. 2), which can sometimes complicate determining the precise number of pits on certain thecae.

All embedment structures are present in the lower (proximal) portion of articulated *Caryocrinites* sp. indet. A thecae (Fig. 2). In specimens with numerous pits, they are distributed around the entire basal region rather than being concentrated on one side of the theca. A narrow size range of individuals shows evidence of infestation as all specimens fall between 20 and 24 mm in thecal height (Fig. 3), with an average thecal height of 21.1 mm (compared with an average thecal height of 26.1 mm for all individuals and an average thecal height of 28.2 mm for uninfested individuals).

Discussion

Paleoecological implications.—To date, symbiotic embedment structures have been documented in the skeletons of Paleozoic crinoids (e.g., Franzén, 1974; Brett, 1978b, 1985; Eckert, 1988; Donovan, 2015), eocrinoids (Rozhnov, 1989), and diploporitans (Paul, 1971; Frest et al., 1977, 2011; Thomka and Brett, 2014b). This account represents the first published description of symbiotic pits in rhombiferan echinoderms. Hence, four Paleozoic pelmatozoan classes are known to be

hosts to pit-forming organisms; it is also noteworthy that the Massie Formation of southeastern Indiana is the only known interval to contain three different classes of infested echinoderms (crinoids, diploporitans, and rhombiferans).

Two paleoecological aspects of this occurrence are particularly worthy of discussion: the abundance and consistent location of pits on the proximal (lower) portion of thecae and the decreased average thecal height of pit-bearing specimens relative to those lacking pits. The presence of numerous pits exclusively on the lower hemisphere of *Caryocrinites* is similar to an infested Mississippian camerate crinoid described by Donovan et al. (2006). The absence of pits on the distal (upper) portion of the crinoid calyx was attributed to the sweeping activity of podia, which may have removed settling organisms (Donovan et al., 2006); however, the likely absence of podia in blastozoans (Sprinkle, 1973) precludes this interpretation as an explanation for the nearly identical distribution of pits on Silurian specimens described here. Although the exact reason for the restriction of pits to the lower hemisphere of *Caryocrinites* remains unclear, a more likely factor is the orientation of the host theca relative to current direction. If the long axis of the theca was oriented parallel to current flow, with the distal theca pointed toward the down-current direction as is the typical feeding posture for Paleozoic pelmatozoans (e.g., Brett, 1984), then the basal theca would have been exposed to stronger or more persistent currents, which may have been preferable to suspension-feeding symbiotic organisms. This concept is supported by the radial distribution of pits around the proximal region being even (Fig. 2) rather than being concentrated on a single side of the theca.

Nature of the biotic interaction.—Although multiple potential interpretations for the origin of embedment structures such as those described herein can be supported (see Donovan, 2015), we submit that parasitism by pit-forming organisms on echinoderm hosts is most logical. This follows some of the earliest interpretations of pitted Paleozoic echinoderms (Moodie, 1918), which were expanded upon by later researchers (e.g., Franzén, 1974; Brett, 1985). Despite an absence of evidence that pit-forming symbionts penetrated thecal plates to access and directly feed upon viscera within thecae, a net adverse effect on pelmatozoan hosts can be recognized. First, there is abundant evidence that the pit-forming organisms were primarily immobile suspension feeders (see Brett, 1978b, 1985; Donovan, 2015). The presence of suspension-feeding organisms in the vicinity of pelmatozoan thecae may have resulted in the diversion of potential food away from hosts and toward embedded symbionts, as argued by Donovan (1991, 2015). In addition to the possible stealing of food, the pathological response of echinoderm hosts—resulting in swelling by secondarily precipitated calcite surrounding pits—would have added weight to the host skeleton and required expenditure of energy to produce the secondary skeletal material. Further, and perhaps most important, some evidence for true boring (i.e., removal of pre-existing stereom) in association with pits has been reported by Brett (1985; see also Paul, 1971). Finally, it is important to consider the fact that *Caryocrinites*, as well as other blastozoan echinoderms, were characterized

by the presence of exothecal respiratory structures on the exterior of thecal plates. Symbionts present on the surface of blastozoan thecae for extended intervals likely interfered with the development of respiratory structures, as indicated by damage to, and reorientation of, humatipores in pit-bearing diploporitans from the Massie Formation (Paul, 1971) and similar interference with, and modified growth of, ambulacra in younger pit-bearing echinoid tests (Donovan, 2015).

Hence, utilization of stalked echinoderms, including the *Caryocrinites* thecae described here, provided benefits to the enigmatic pit-forming, suspension-feeding symbiotic organisms, and the host echinoderms most likely experienced negative effects as consequences of this prolonged interaction. Although this relationship between echinoderm hosts and embedment-structure-producing organism(s) may not meet the most traditional definition of parasitism (see discussions in Zapalski, 2011; Donovan, 2015), it nevertheless seems more appropriate to view the nature of this biotic association as parasitic rather than commensalistic.

An additional aspect potentially of interest to the discussion of the nature of the relationship between pits and pitted caryocrinitids involves the decreased size of infested versus uninfested host specimens (average thecal heights of 21.1 and 26.1 mm, respectively), which may attest to the detrimental effects of this relationship on *Caryocrinites*. A statistically significant difference in calyx size was documented between populations of Paleozoic crinoids that were hosted to parasitic platyceratid gastropods (smaller) and those devoid of parasites (larger) in several studies (e.g., Rollins and Brezinski, 1988; Baumiller and Gahn, 2002; Baumiller, 2003; but see Baumiller and Gahn, 2018). The small sample size of pit-bearing *Caryocrinites* limits the application of statistical tests on this assemblage, but these data nevertheless provide suggestive evidence that symbiosis (possibly reflecting a form of parasitism) of rhombiferans can result in decreased size. However, it must be noted that without larger pit-bearing specimens of *C. sp. indet. A*, the consistently smaller thecal size may reflect a taxonomic difference rather than an ecological effect of infestation.

Hemicosmitid paleobiology and evolution.—The rhombiferan *Caryocrinites* has long been recognized as a relatively unusual blastozoan, primarily because of this taxon's morphological similarities to camerate crinoids. Distinctly crinoid-like features include: (1) a dendritic radicular attachment structure (Brett, 1978c) that is more complex than that of most Silurian blastozoans and more similar to that of the monobathrid camerate *Eucalyptocrinites* (Brett, 1981, 1984; Thomka and Brett, 2015a, b); (2) a relatively long column compared with those of most Silurian blastozoans (Brett, 1984); (3) a theca composed of large plates arranged into organized circlets rather than a mosaic pattern and an oral region resembling the tegmen of a camerate crinoid (Kluessendorf, 1983; Brett, 1984); and (4) relatively long, branching brachioles similar to pinnulate crinoid arms (Sprinkle, 1975). These skeletal features resulted in a number of paleoecological interactions that are unique or rare among coeval blastozoans. *Caryocrinites* is the only noncrinoid echinoderm in the middle Paleozoic that serves as a host to commensalistic/parasitic platyceratid gastropods (Kluessendorf, 1983; Brett, 1984),

presumably because of morphological similarities and/or ecological convergence with the more commonly infested camerate crinoids. The data presented here indicate that *Caryocrinites* is also the only Silurian rhombiferan that was infested by the pit-forming organism(s) that also produced traces on several types of crinoids in the Massie Formation and coeval deposits (Brett, 1978b, 1985; Frest et al., 1999; Brett et al., 2018). This suggests an additional component to the distinctiveness of *Caryocrinites* among Silurian blastozoans as this is the only taxon to serve as host to both of the common potentially parasitic organisms infesting pelmatozoans. The morphology of the pits on *Caryocrinites* is quite similar to that of pits found on certain middle Silurian crinoids (e.g., ichthyocrinids; Brett, 1985), including some from the Massie Formation (Frest et al., 1999, 2011), but differs substantially from pits found on other crinoid hosts (e.g., dendrocrinids, eucalyptocrinitids; Brett, 1978b; Brett et al., 2018).

Brett (1978b) initially documented strong host specificity among pit-forming organisms in the crinoid fauna of the Rochester Shale of western New York and Ontario, with later data indicating that host lineages continued to show infestation over long spans of geologic time (Brett, 1985), suggesting strong evolutionary linkage between symbionts and their preferred echinoderm host(s). The data presented here indicate that host specificity is also apparent in the record of infestation of rhombiferans. The presence of symbiotic pits exclusively on the smaller species of *Caryocrinites* (*C. sp. indet. A*) rather than *C. ornatus* is not expected given the much greater abundance and increased size of *C. ornatus*. Nonselective settling by pit-forming organisms would have favored development of pits on the host taxa that were most prevalent and/or capable of providing the greatest area for settlement. The preference for other *Caryocrinites* species over *C. ornatus* seemingly explains the total absence of pits in the more than 700 thecae analyzed from the Rochester Shale of western New York and Ontario by Brett (1978a). Although the Rochester Shale is roughly correlative to the Massie Formation (McLaughlin et al., 2008; Thomka and Brett, 2015a), the former contains a hemicosmitid assemblage consisting entirely of *C. ornatus* (Brett, 1978a; Frest et al., 1999), which was evidently avoided despite an abundance of pits in some contemporary crinoids in the Rochester Shale.

Glyptocystid rhombiferans are not yet known to have served as hosts to pit-forming symbiotic organisms, even in communities where they outnumber hemicosmitids or are the only rhombiferans present (e.g., Frest et al., 1999). However, specimens of *Hemicosmites* von Buch, 1840 from Middle Ordovician (Darriwilian) strata of the St. Petersburg region of Russia that currently await detailed description (S. Nikolay, personal communication, 2017) have been discovered with multiple pits of a similar morphology to those on *Caryocrinites*. The *Hemicosmites* thecae containing symbiotic embedment structures show that hemicosmitid rhombiferans were utilized as hosts for potentially parasitic symbiosis by pit-forming organisms, with this relationship persisting at least from Middle Ordovician to middle Silurian time. Further attention should be devoted to searching for pits in lower Paleozoic rhombiferan assemblages to determine the degree to which hemicosmitids

were selectively infested relative to other pelmatozoans and the specific hemicosmitid taxa that served as hosts. If it can be determined that hemicosmitids were the only rhombiferans to contain symbiotic pits (as opposed to taphonomic biases favoring preservation of articulated hemicosmitid thecae, for example), then the taxa that were preferentially infested through time may reflect co-evolutionary linking between symbiont and host lineages and can therefore provide a potential paleoecological test of systematic hypotheses.

Ichnotaxonomy.—Description of embedment or bioerosion structures in skeletal substrates is most accurate when ichnotaxonomic nomenclature is applied (Donovan, 2017). The ichnogenus *Tremichnus* Brett, 1985 was initially established to describe circular-parabolic pits, sometimes associated with swelling, in stalked echinoderm endoskeletons (Brett, 1978b, 1985). The pits present on Silurian *Caryocrinites* specimens are typical examples of *T. paraboloides* Brett, 1985, the type ichnospecies (Brett, 1985). Diagnostic features include a circular outline that is gradational with the surrounding, unaffected skeletal material of the host echinoderm plate(s); pit dimensions indicating significantly greater width than depth; and a lack of total penetration through plates (Brett, 1985; Wisshak et al., 2015). Additional noteworthy, though not ichnotaxonomically diagnostic, features that are relatively consistently associated with *T. paraboloides* include the presence of multiple pits on individual host thecae and pit margins that are slightly swollen by precipitation of secondary stromatolite (Brett, 1978b, 1985).

However, recent and ongoing debate has centered around the validity of *Tremichnus* as an ichnogenus, with some researchers arguing that *Tremichnus* should be synonymized with either *Sedilichnus* Müller, 1977 (Bromley, 2004; Zonneveld and Gingras, 2014) or *Oichnus* Bromley, 1981 (Pickerill and Donovan, 1998; Donovan and Pickerill, 2002, 2017), while others have presented strong evidence that *Tremichnus* is a valid ichnogenus and should be retained (Vinn et al., 2015; Wisshak et al., 2015). Fully resolving this ichnotaxonomic issue is beyond the scope of the present study and is best treated elsewhere; in fact, the use of an ichnogenus name has purposefully been avoided thus far in favor of the generalized term ‘pits.’ The primary foci of this paper are the description of this new occurrence and paleoecological interpretation of the nature of this biotic interaction; ichnotaxonomy is a secondary aspect here. However, we feel that it is worth noting our support for retaining *Tremichnus* as the proper ichnogenus (and *T. paraboloides* as the proper ichnospecies) for these symbiotic embedment structures, as initially outlined by Brett (1985) and more recently modified and redefined by Wisshak et al. (2015).

Conclusions

Symbiotic embedment structures (pits) are herein reported on rhombiferan echinoderms for the first time. Thecae of the hemicosmitid rhombiferan *Caryocrinites* from the middle Silurian (Wenlock, Sheinwoodian) Massie Formation generally contain multiple pits per specimen (average of 14; range of one to 30), with pits restricted exclusively to the lower portion of thecae.

Pits are morphologically identical to structures found in crinoids and diploporitans from this unit and are attributable to *Tremichnus paraboloides*. The restriction of pits to the basal region of thecae likely reflects the living posture of *Caryocrinites*, with the feeding appendages pointed downstream and the basal region exposed to currents. Thecae with pits are smaller than uninfested thecae, potentially reflecting the detrimental effects of infestation; however, the small sample size of infested specimens limits the robustness of statistical analyses.

This occurrence represents the first formal description of symbiotic pits on rhombiferans and indicates that at least four pelmatozoan classes (Crinoidea, Diploporita, Eocrinoidea, Rhombifera) were infested by pit-forming organisms. Symbiotic pits are thus far known only from hemicosmitid rhombiferans, suggesting host specificity evolving in the Middle Ordovician and persisting through the middle Silurian. *Caryocrinites* is characterized by multiple physical attributes that more closely resemble camerate crinoids than they do other rhombiferans; this likely contributed to the infestation of this blastozoan, providing an additional ecological consequence of morphological convergence on crinoids.

Acknowledgments

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References

- Baumiller, T.K., 2003, Evaluating the interaction between platyceratid gastropods and crinoids: a cost-benefit approach: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 201, p. 199–209.
- Baumiller, T.K., and Gahn, F.J., 2002, Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid–crinoid interaction, in Kowalewski, M., and Kelley, P.H., eds., *Fossil Record of Predation: Paleontological Society Special Papers* 8, p. 195–209.
- Baumiller, T.K., and Gahn, F.J., 2018, The nature of the platyceratid–crinoid association as revealed by cross-sectional data from the Carboniferous of Alabama (USA): *Swiss Journal of Palaeontology*, v. 137, p. 177–187.
- Brett, C.E., 1978a, Systematics and paleoecology of late Silurian (Wenlockian) pelmatozoan echinoderms from western New York and Ontario [Ph.D. dissertation]: Ann Arbor, University of Michigan, 603 p.
- Brett, C.E., 1978b, Host-specific pit-forming epizoans on Silurian crinoids: *Lethaia*, v. 11, p. 217–232.
- Brett, C.E., 1978c, Attachment structures in the rhombiferan cystoid *Caryocrinites* and their paleobiological implications: *Journal of Paleontology*, v. 52, p. 717–726.
- Brett, C.E., 1981, Terminology and functional morphology of attachment structures in pelmatozoan echinoderms: *Lethaia*, v. 14, p. 343–370.
- Brett, C.E., 1984, Autecology of Silurian pelmatozoan echinoderms, in Bassett, M.G., and Lawson, J.D., eds., *Autecology of Silurian Organisms: Special Papers in Palaeontology* 32, p. 87–120.
- Brett, C.E., 1985, *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms: *Journal of Paleontology*, v. 59, p. 625–635.
- Brett, C.E., Cramer, B.D., McLaughlin, P.I., Kleffner, M.A., Showers, W.J., and Thomka, J.R., 2012, Revised Telychian–Sheinwoodian (Silurian) stratigraphy of the Laurentian mid-continent: building uniform nomenclature along the Cincinnati Arch: *Bulletin of Geosciences*, v. 87, p. 733–753.

- Brett, C.E., Thomka, J.R., and Bissett, D.L., 2018, Improving echinoderm biodiversity calculations and interpretations of paleoecology through analysis of disarticulated stem material: a Silurian example: Abstracts of the 5th International Palaeontological Congress, p. 527.
- Bromley, R.G., 1981, Concepts in ichnology illustrated by small round holes in shells: *Acta Geológica Hispánica*, v. 16, p. 55–64.
- Bromley, R.G., 2004, A stratigraphy of marine bioerosion, in McIlroy, D., ed., *The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis*: Geological Society of London Special Publication 228, p. 455–479.
- Donovan, S.K., 1991, Site selectivity of a lower Carboniferous boring organism infesting a crinoid: *Geological Journal*, v. 26, p. 1–5.
- Donovan, S.K., 2015, A prejudiced review of ancient parasites and their host echinoderms: CSI fossil record or just an excuse for speculation?: *Advances in Parasitology*, v. 90, p. 291–328.
- Donovan, S.K., 2017, A plea not to ignore ichnotaxonomy: recognizing and recording *Oichnus* Bromley: *Swiss Journal of Palaeontology*, v. 136, p. 369–372.
- Donovan, S.K., and Pickerill, R.K., 2002, Pattern versus process or informative versus uninformative ichnotaxonomy: reply to Todd and Palmer: *Ichnos*, v. 9, p. 85–87.
- Donovan, S.K., and Pickerill, R.K., 2017, The invalidity of the trace fossil *Tremichnus* Brett: *Geological Journal*, v. 52, p. 828–831.
- Donovan, S.K., Lewis, D.N., and Kabrna, P., 2006, A dense epizoobiontic infestation of a lower Carboniferous crinoid (*Amphoracrinus gilbertsoni* (Phillips)) by *Oichnus paraboloides* Bromley: *Ichnos*, v. 13, p. 43–45.
- Eckert, J.D., 1988, The ichnogenus *Tremichnus* in the lower Silurian of western New York: *Lethaia*, v. 21, p. 281–283.
- Eckert, J.D., and Brett, C.E., 2001, Early Silurian (Llandovery) crinoids from the lower Clinton Group, western New York state: *Bulletins of American Paleontology*, v. 360, 88 p.
- Foerste, A.F., 1897, A report on the middle and upper Silurian rocks of Clark, Jefferson, Ripley, Jennings, and southern Decatur counties, Indiana: Indiana Department of Geology and Natural Resources Annual Report, v. 21, p. 213–288.
- Franzén, C., 1974, Epizoans on Silurian–Devonian crinoids: *Lethaia*, v. 7, p. 287–301.
- Frest, T.J., Mikulic, D.G., and Paul, C.R.C., 1977, New information on the *Holocystites* fauna (Diploporita) of the middle Silurian of Wisconsin, Illinois, and Indiana: *Fieldiana: Geology*, v. 35, p. 83–108.
- Frest, T.J., Brett, C.E., and Witzke, B.J., 1999, Caradocian to Gedinian echinoderm associations of central and eastern North America, in Boucot, A.J., and Lawson, J.D., eds., *Paleocommunities: A Case Study from the Silurian and Lower Devonian*: Cambridge, Cambridge University Press, p. 638–783.
- Frest, T.J., Strimple, H.L., and Paul, C.R.C., 2011, The North American *Holocystites* fauna (Echinodermata, Blastozoa: Diploporita): paleobiology and systematics: *Bulletins of American Paleontology*, v. 380, 141 p.
- Kluessendorf, J., 1983, Observations on the commensalism of Silurian platyceratid gastropods and stalked echinoderms: *Transactions of the Wisconsin Academy of Science, Arts and Letters*, v. 71, p. 48–55.
- McLaughlin, P.I., Cramer, B.D., Brett, C.E., and Kleffner, M.A., 2008, Silurian high-resolution stratigraphy on the Cincinnati Arch: progress on recalibrating the layer-cake, in Maria, A.H., and Counts, R.C., eds., *From the Cincinnati Arch to the Illinois Basin: Geological Field Excursions along the Ohio River Valley*: Geological Society of America Field Guide 12, p. 119–180.
- Moodie, R.L., 1918, On the parasitism of Carboniferous crinoids: *Journal of Parasitology*, v. 4, p. 174–176.
- Müller, A.H., 1977, Zur Ichnologie der subherzynen Oberkreide (Campan): *Zeitschrift für Geologische Wissenschaften*, Berlin, v. 5, p. 881–897.
- Paul, C.R.C., 1971, Revision of the *Holocystites* fauna (Diploporita) of North America: *Fieldiana: Geology*, v. 24, 166 p.
- Pickerill, R.K., and Donovan, S.K., 1998, Ichnology of the Pliocene Bowden shell bed, southeast Jamaica: *Contributions to Tertiary and Quaternary Geology*, v. 35, p. 161–175.
- Rollins, H.B., and Brezinski, D.K., 1988, Reinterpretation of crinoid–platyceratid interaction: *Lethaia*, v. 21, p. 207–217.
- Rozhnov, S.V., 1989, New data on rhipidocystids (Eocrinoidea), in Semenova, V., ed., *Fossil and Recent Echinoderm Researches*: Tallinn, Akademiya Nauk, Estonskoi SSR, Institut Geologii, p. 38–57.
- Say, T., 1825, On two genera and several species of Crinoidea: *Journal of the Philadelphia Academy of Natural Sciences*, v. 4, p. 289–296.
- Sprinkle, J., 1973, Morphology and Evolution of Blastozoan Echinoderms: Harvard University Museum of Comparative Zoology Special Publication, 283 p.
- Sprinkle, J., 1975, The “arms” of *Caryocrinites*, a rhombiferan cystoid convergent on camerate crinoids: *Journal of Paleontology*, v. 49, p. 1062–1073.
- Thomka, J.R., and Brett, C.E., 2014a, Diploporite (Echinodermata, Blastozoa) thecal attachment structures from the Silurian of southeastern Indiana: *Journal of Paleontology*, v. 88, p. 179–186.
- Thomka, J.R., and Brett, C.E., 2014b, Taphonomy of diploporite (Echinodermata) holdfasts from a Silurian hardground, southeastern Indiana, United States: Palaeoecological and stratigraphic significance: *Geological Magazine*, v. 151, p. 649–665.
- Thomka, J.R., and Brett, C.E., 2015a, Paleoecology of pelmatozoan attachment structures from a hardground surface in the middle Silurian Massie Formation, southeastern Indiana: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 420, p. 1–12.
- Thomka, J.R., and Brett, C.E., 2015b, Palaeontological and sedimentological effects of micro-bioherms in the middle Silurian Massie Formation of southeastern Indiana, USA: *Lethaia*, v. 48, p. 172–187.
- Thomka, J.R., Brett, C.E., Bantel, T.E., Young, A.L., and Bissett, D.L., 2016, Taphonomy of ‘cystoids’ (Echinodermata: Diploporita) from the Napoleon quarry of southeastern Indiana, USA: the lower Silurian Massie Formation as an atypical Lagerstätte: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 443, p. 263–277.
- Vinn, O., Wilson, M.A., Ausich, W.I., and Toom, U., 2015, *Tremichnus* in crinoid pluricolonnals from the Silurian of western Estonia: *Carnets de Géologie*, v. 15, p. 239–243.
- von Buch, L., 1840, Über Sphaeroniten und einige andere Geschlechter, aus welchen Crinoideen entstehen: Königlich Preussische Akademie der Wissenschaften zu Berlin, Verhandlungen 1840, p. 56–60.
- Widdison, R.E., 2001, Symbiosis in crinoids from the Wenlock of Britain, in Barker, M., ed., *Echinoderms 2000*: Rotterdam, A. A. Balkema, p. 139–143.
- Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielsen, J.K., Jagt, J.W.M., Neumann, C., and Nielsen, K.S.S., 2015, In defence of an iconic ichnogenus—*Oichnus* Bromley, 1981: *Annales Societatis Geologorum Poloniae*, v. 85, p. 445–451.
- Zapalski, M.K., 2011, Is absence of proof a proof of absence? Comments on commensalism: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 302, p. 484–488.
- Zonneveld, J.-P., and Gingras, M.K., 2014, *Sedilichnus*, *Oichnus*, and *Tremichnus*: ‘small round holes in shells’ revisited: *Journal of Paleontology*, v. 88, p. 895–905.

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