

# Taphonomy of ‘cystoids’ (Echinodermata: Diploporita) from the Napoleon quarry of southeastern Indiana, USA: The Lower Silurian Massie Formation as an atypical Lagerstätte



James R. Thomka<sup>a,\*</sup>, Carlton E. Brett<sup>b</sup>, Thomas E. Bantel<sup>c</sup>, Allison L. Young<sup>b</sup>, Donald L. Bissett<sup>c</sup>

<sup>a</sup> Department of Geosciences, University of Akron, Akron, OH 44325, USA

<sup>b</sup> Department of Geology, University of Cincinnati, Cincinnati, OH 45221, USA

<sup>c</sup> Dry Dredgers, P.O. Box 210013, Cincinnati, OH 45221, USA

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## ABSTRACT

Diploporites, like most pelmatozoan echinoderms, are characterized by complex multi-element skeletons prone to complete disarticulation if left exposed for extended periods of time. Consequently, preservation of abundant articulated diploporite thecae is rare and generally restricted to environments where rapid burial events could catastrophically entomb individuals. One such environment is represented by the lower portion of the Wenlock-age Massie Formation at the New Point Stone quarry near Napoleon, southeastern Indiana, which we recognize as a Konservat-Lagerstätte. Yet, taphonomic evidence does not support live burial. Diploporites (*Holocystites* spp.) are dominantly preserved as intact thecae without any portions of brachioles and with damage (plate shifting and plate loss/plate jumbling) on one side. Post-mortem encrustation is common, but epibionts are typically present on the well-preserved sides of thecae. Geopetal sediment-fill of thecae shows that the well-preserved side commonly faced upward following burial. This taphonomic state is paradoxical, as burial of live diploporites would have resulted in preservation of complete individuals with no encrusters and only compaction-induced damage; rapid burial of diploporites following a short interval of exposure would have resulted in preservation similar to observed patterns, but with encrusters and geopetal infills indicating that the poorly preserved side faced up; and burial after extended exposure would have resulted in thorough disarticulation of thecae. Rather, a variable and, in some cases, complex taphonomic history is suggested for diploporites from the Napoleon quarry, with at least some individuals having experienced one or more brief episodes of exhumation prior to final burial. Early diagenetic cementation of initial theca-filling sediment is the most likely mechanism for keeping thecae intact during subsequent exposure.

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## 1. Introduction

In recent reviews of echinoderm taphonomy, both Ausich (2001) and Nebelsick (2004) identify taphonomic investigation of extinct echinoderm classes as a subject worthy of major future work. Indeed, an evaluation of echinoderm-taphonomic literature confirms that the vast majority of research to date has focused on extant clades, particularly crinoids and echinoids (see bibliography in Ausich, 2001). The potential reasons for this disparity in research focus are various, but likely center around 1) the use of echinoderm remains as predictive tools for recent environmental trends (e.g., McClintock et al., 2011; Walker et al., 2013) and ecological crises (e.g., Moran et al., 1986; Greenstein, 1989; Walbran et al., 1989; Greenstein et al., 1995; Gischler, 2010), for which extinct clades are ill-suited; 2) the value of actualistic taphonomic research on modern echinoderms as comparative

tools for understanding the taphonomy and paleoecology of ancient representatives (e.g., Allison, 1990; Gorzelak and Salamon, 2013, among many others); and 3) the relatively poor record of many pre-Cenozoic echinoderm groups, which often precludes collection of large numbers of specimens. This last point strongly affects the number of detailed taphonomic studies that can be conducted on echinoderm clades known only from the Paleozoic fossil record. Consequently, deposits yielding abundant remains of rare, extinct echinoderms are very important sources of data and worthy of focused taphonomic study.

Interesting and significant research has been performed on the preservation of helicoplacoids (Dornbos and Bottjer, 2001), edrioasteroids (Meyer, 1990; Cornell et al., 2003; Shroat-Lewis et al., 2011), and stylophorans (Lefebvre, 2007; Martin et al., 2015), but little taphonomic research has focused on blastozoans. With the exception of a few recent studies on eocrinoids (Lin et al., 2008; Zamora et al., 2013; Allaire et al., 2015), taphonomic research on representatives of this subphylum has largely been limited to inclusion of blastoids (Meyer et al., 1989; see also Sprinkle and Gutschick, 1967) and rhombiferans

\* Corresponding author. Tel.: +1 630 935 2983.

E-mail address: [jthomka@uakron.edu](mailto:jthomka@uakron.edu) (J.R. Thomka).

(Taylor and Brett, 1996; Brower, 2011, 2013) in taphonomic grade studies of entire assemblages. Despite comprising a significant portion of Paleozoic echinoderm diversity (Sprinkle, 1973, 1980; Sprinkle and Guensburg, 2004; Lefebvre et al., 2013), blastozoans can currently provide taphonomic and paleoenvironmental insights that are much more generalized (Brett et al., 1997; Gil Cid et al., 2003) than the refined interpretations that can be obtained by careful analysis of crinoid preservation (e.g., Thomka et al., 2011).

Within Blastozoa, diploporite “cystoids” represent a clade for which taphonomic patterns and processes are largely unknown, as very few studies have addressed diploporite taphonomy directly; exceptions include Bockelie (1981, p. 191), Gil Cid et al. (2004), Vidal et al. (2011), Thomka and Brett (2014b), and Sheffield and Sumrall (2015). The much larger body of literature on diploporite systematics is dominated by papers that contain only short descriptions of the mode of occurrence of studied material (e.g., Mergl and Prokop, 2006), or no details of specimen preservation at all. Hence, the primary goals of this study are 1) to document the taphonomic state of the diploporite *Holocystites* from the Silurian Massie Formation at the Napoleon quarry of southeastern Indiana, where articulated specimens are locally abundant; 2) to interpret preservational patterns and infer biostratigraphic and diagenetic processes that affected this assemblage; 3) to determine whether the taphonomic state indicates simple rapid burial or a more complex taphonomic history; and 4) to describe and categorize the diploporite-bearing interval at the Napoleon quarry as a Lagerstätte deposit.

## 2. Diploporite occurrences

Despite having a constructional morphology suggestive of a preservation potential similar to that of crinoids (Brett et al., 1997), diploporites have a fossil record dominated by incomplete specimens and, more commonly, isolated ossicles (Sprinkle, 1973). Deposits containing articulated diploporite thecae in abundance are few and typically occur in the Middle–Upper Ordovician of Baltica, Avalonia, and northern peri-Gondwana (e.g., Chauvel, 1941; Paul, 1973; Paul and Bockelie, 1983; Bockelie, 1984; Parsley, 1990; Lefebvre et al., 2005; Mergl and Prokop, 2006; Gutiérrez-Marco and Colmenar, 2011; Vidal et al., 2011; Eriksson et al., 2012; Gil Cid and García-Rincón, 2012; Nardin et al., 2014). This reflects the evolutionary origin of diploporites in the Old World and the relatively endemic distribution of blastozoans in the Ordovician (Paul, 1976, 1977, 1979, 1988; Lefebvre et al., 2013).

The Laurentian record of Ordovician pelmatozoans is dominated by crinoids (Sprinkle, 1980; Lefebvre and Fatka, 2003; Deline et al., 2012) and diploporites are comparatively rare (Sprinkle, 1973; exceptions include *Echinospaerites* in the Chambersburg Limestone of the Appalachian Basin—Raymond, 1916, pp. 238–243, and Kimmswick Limestone of the Mississippi Valley—Foerste, 1920; *Eumorphocystis* in the Bromide Formation of Oklahoma—Parsley, 1982). However, an interesting pattern of diploporite dispersal emerges in the Silurian: whereas diploporites become relatively scarce in Silurian Old World faunas, they suddenly become common in Wenlock faunas of eastern-midcontinental United States, specifically southeastern Indiana, southwestern Ohio, northeastern Illinois, and southeastern Wisconsin (Foerste, 1917, 1920, 1931; Paul, 1971; Frest et al., 1977, 1999, 2011). These taxa belong to the distinctive *Holocystites* Fauna (sensu Frest et al., 2011, after Paul, 1971), comprising all non-gomphocystitid diploporites known from the Silurian of North America. This rapid increase in diploporite abundance and diversity is related to an influx of blastozoans during the late Telychian (latest Llandovery) and early Sheinwoodian (earliest Wenlock), which saw the first coronoids, hemicosmitid rhombiferans, and holocystitid, aristocystitid, and sphaerontid diploporites invade the Laurentian interior (Witzke, 1976; Frest et al., 1999, 2011; Thomka and Brett, 2014a). After this brief interval of abundance in North America, diploporites dramatically decreased in diversity and relative ecological significance worldwide

until dwindling and eventually succumbing to extinction in the Devonian (Sprinkle, 1973; Witzke et al., 1979; Clement and Broadhead, 1994; but see Foerste, 1917, 1920; Busch, 1943; Brett, 1985; Sumrall et al., 2009; Jell, 2011 for some later Silurian and Devonian diploporite occurrences).

During the Middle Ordovician–middle Silurian apex of diploporite abundance, specimens are commonly preserved as internal molds (e.g., Paul, 1973; Frest et al., 1977) and original skeletal material is relatively rare. Argillaceous carbonate strata in the Silurian of southeastern Indiana, United States, however, preserve diploporites, as well as associated echinoderms, as largely unaltered skeletons with delicate ornamentation and microstructure (see select plates in Frest et al., 2011). This material, though apparently unique to this region, provides an unparalleled opportunity to document taphonomic patterns among Diploporita.

## 3. Stratigraphic setting

The studied material was recovered from the clastic mudstone facies of the middle Silurian (Wenlock: Sheinwoodian) Massie Formation. The mudstone lithofacies of the Massie Formation can be traced throughout the Cincinnati Arch region, where it forms a distinctive marker unit that stands out sharply from the shallow-water carbonates that dominate the western margin of the Appalachian Foreland Basin (McLaughlin et al., 2008b; Brett et al., 2012; Etensohn et al., 2013). In spite of its persistence, the Massie Formation is largely devoid of fossils beyond southeastern Indiana owing both to late diagenetic dolomitization and what is likely a true signal of ecological patchiness, based on comparison with similar unevenly fossiliferous units such as the Rochester Shale of western New York and Ontario (Brett, 1983, 1999) and Waldron Shale of Indiana and Kentucky (e.g., Feldman, 1989). Fossiliferous exposures of the Massie Formation are increasingly rare as a result of the unit's poor resistance to weathering and lack of economic value, and fossil-bearing outcrops represent exceptional glimpses into the paleoecology of a unit that, although remarkably persistent, is largely incapable of producing a macrofauna (but see Foerste, 1935).

One such unusually fossiliferous locality is the New Point Stone quarry at Napoleon, Ripley County, southeastern Indiana (N39°12'31.39", W85°18'53.74"; Fig. 1). This site is famous for its echinoderm fauna, and has produced many of the specimens used to define and classify the *Holocystites* Fauna (Paul, 1971; Frest et al., 2011; Thomka and Brett, 2014a). All diploporite material studied here was recovered from the lower decimeter of the Massie mudstone lithofacies at this locality (Fig. 2). This stratigraphic interval in Ripley County has historically been known as the ‘upper shale’ of the Osgood Formation as originally defined by Foerste (1897), but recent lithostratigraphic revisions have restricted the term Osgood Formation to a lower interval and extended the term Massie Formation into Indiana as the proper name for this unit (Brett et al., 2012). At the Napoleon quarry, this unit contains the greatest abundance of diploporite material, though diploporites also occur in the underlying carbonate lithofacies of the Massie Formation and Lewisburg Formation (Frest et al., 2011; Fig. 2A). Even within the Massie Formation mudstone, diploporites are notoriously patchily distributed (Paul, 1971; Frest et al., 2011). For example, at the northern end of the quarry, where attachment structures and microbioherms are abundant (Thomka and Brett, 2014b, 2015a,b), almost no diploporite thecae can be found, whereas exposures and spoil piles at the south-central area of the quarry (Fig. 2B–C) have been fruitful for more than three decades. This spatial patchiness likely reflects a true biological signature rather than an effect of taphonomic processes, as comparatively barren areas are sedimentologically and faunally identical (echinoderm content notwithstanding) to diploporite-rich areas.

The contact between the middle mudstone interval of the Massie Formation and the underlying basal carbonate bed (Fig. 2) is sharp and represents a hardground surface that is densely encrusted by the attachment structures of a diverse suite of pelmatozoan

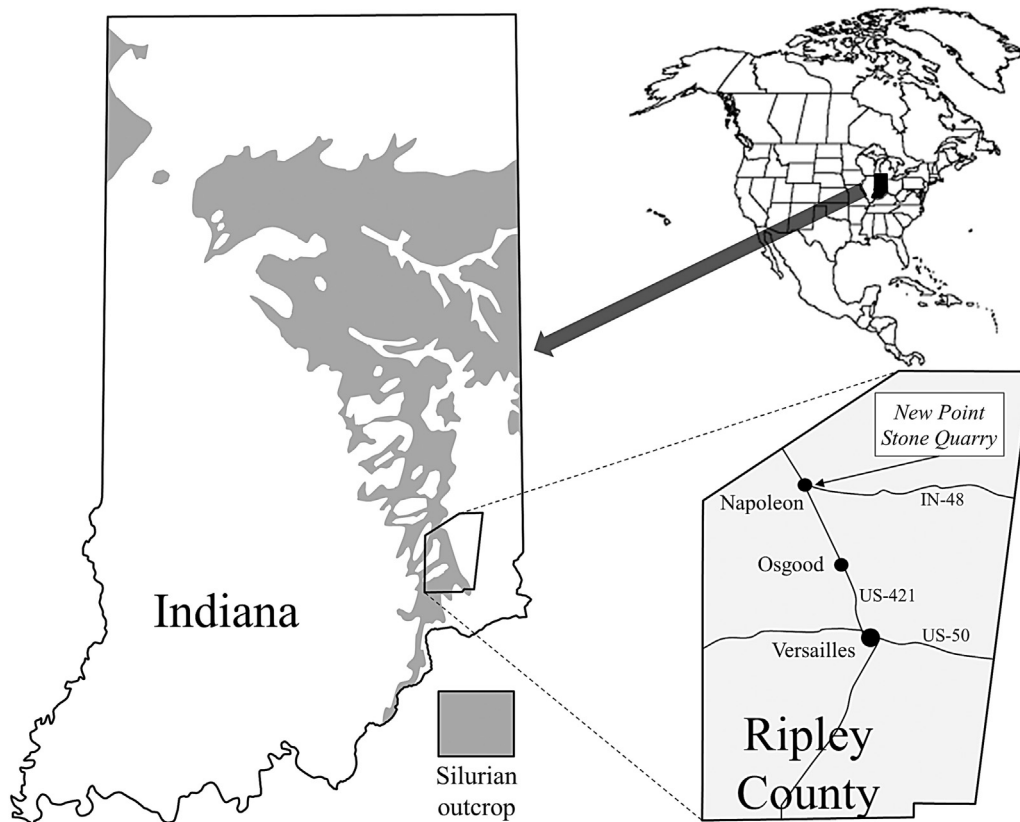


Fig. 1. Location of the New Point Stone quarry, east of Napoleon, Ripley County, Indiana. From Thomka and Brett (2015a).

echinoderms (Thomka and Brett, 2015a). This hardground resulted from supersaturation of interstitial calcium carbonate, reflecting static redox boundaries during a period of sediment starvation. Development of this geochemical state is related to rapid sea-level rise, and this hardground contact is widely traceable throughout the Appalachian Basin (Brett et al., 1990, 2012; Brett and Ray, 2005; McLaughlin et al., 2008b; Thomka and Brett, 2015b). The immediately overlying sediments are medium gray, siliciclastic clay-dominated muds representing initial siliciclastic influx during late transgressive to early highstand conditions. Hence, the transition from the basal carbonate bed of the Massie Formation to the overlying mudstone interval represents a major flooding surface (a third-order surface of maximum starvation; McLaughlin et al., 2008a) below which sediment starvation permitted establishment of a turbidity-intolerant, suspension feeder-dominated fauna adapted to hard substrata (Thomka and Brett, 2014b, 2015a,b), and above which elevated sedimentation restricted the fauna to forms more tolerant of siliciclastic influx (see Brett, 1995), reflecting initially slow background sedimentation but with episodes of rapid deposition. The Massie mudstone interval is densely fossiliferous at its base and becomes increasingly sparse upward, with the upper decimeter nearly barren, which we interpret as representing increased sedimentation during middle to late highstand conditions.

#### 4. Materials and methods

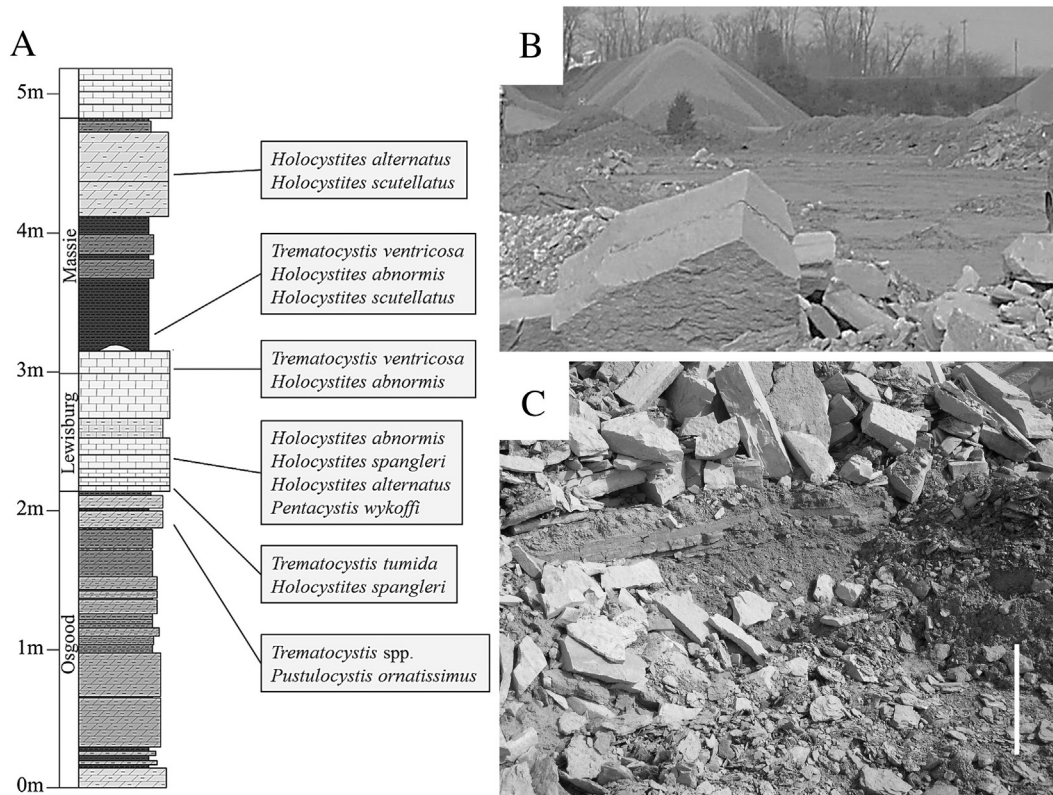
##### 4.1. Diploporite thecae: sources and general preservation

The Napoleon quarry diploporite fauna is famous not only for elevated diversity and abundance, but also for exceptional preservation (Fig. 3). Diploporites are commonly preserved as articulated thecae with intact plate ornamentation and diploporite morphology. However, even relatively well-preserved specimens in the lower Massie mudstone are rarely preserved in living position (Thomka and Brett, 2014a; see also Gil Cid

and Domínguez-Alonso, 2000). It is estimated that over 10,000 thecae have been recovered from the study interval over the last thirty years (DLB, unpublished data). While it is impossible to assemble and study a sample of that size, available specimens provided a representation accurate enough to document preservational patterns and infer taphonomic processes that acted upon diploporites.

Specimens assigned to the genus *Holocystites* were selected for taphonomic analysis. This genus was chosen because it is the most abundant echinoderm taxon at the Napoleon quarry and is readily recovered from the lower Massie mudstone. Further, many of the partial thecae could only be reliably identified to genus, and selecting a single species of *Holocystites* would likely have imparted a taphonomic bias toward more intact specimens or robust taxa. Finally, cursory taphonomic observations reveal that specimens belonging to this genus and recovered from the lower Massie mudstone, regardless of specific designation, are preserved non-uniformly and grossly similar to other, rarer diploporite taxa from the same interval. A representative sample of 284 specimens was studied, most attributable to *Holocystites scutellatus*, with subordinate *Holocystites alternatus* and *Holocystites clavus*.

Diploporite thecae studied here were derived from three sources. These are 1) specimens deposited at the Cincinnati Museum Center, Cincinnati, Ohio (specimen numbers beginning with CMC IP are given in appropriate figure captions); 2) articulated or partially articulated specimens in private collections; and 3) specimens obtained through bulk sampling at the Napoleon quarry. This third data source was critical, as it prevented bias toward study of exceptionally well-preserved, large, or inflated specimens that would be readily collected over smaller, damaged, strongly compacted, or less complete specimens. To further ensure that no biases exist within the dataset, approximately one square meter of Massie mudstone was collected in its entirety from a portion of the Napoleon quarry where diploporite remains are common. All diploporite material more complete than isolated thecal ossicles was



**Fig. 2.** Stratigraphy of a portion of strata exposed at the Napoleon quarry. A) Stratigraphic column of the study interval and associated units (modified from Thomka and Brett, 2014a). Note that only a portion of the Laurel Formation is shown and the Brassfield Formation, underlying the Osgood Formation, is not shown. Zonation of common diploporites (from Frest et al., 2011) is shown. Lithostratigraphic terminology follows Brett et al. (2012). B) Field photograph of an exposure in the central portion of the quarry from which many of the specimens were recovered. Diploporites are abundant in an approximately 5–10 cm zone of very argillaceous wackestone and overlying siliciclastic mudstone that forms the floor of the benched-off area shown. C) Field photograph of a small, hand-dug trench excavated into the area shown in B. The diploporite-bearing interval is shown in the rough position of the scale bar, with overlying siliciclastic muds increasingly sparsely fossiliferous upwards. This zone yields diploporites of the “*Trematocystis ventricosa*, *Holocystites abnormis*, *Holocystites scutellatus*” zone of A. Scale bar = 0.5 m.

inspected, and data from this unbiased sample did not differ from those derived from other sources, lending credence to the reliability of results presented here.

#### 4.2. Diploporite thecae: taphonomic assessment

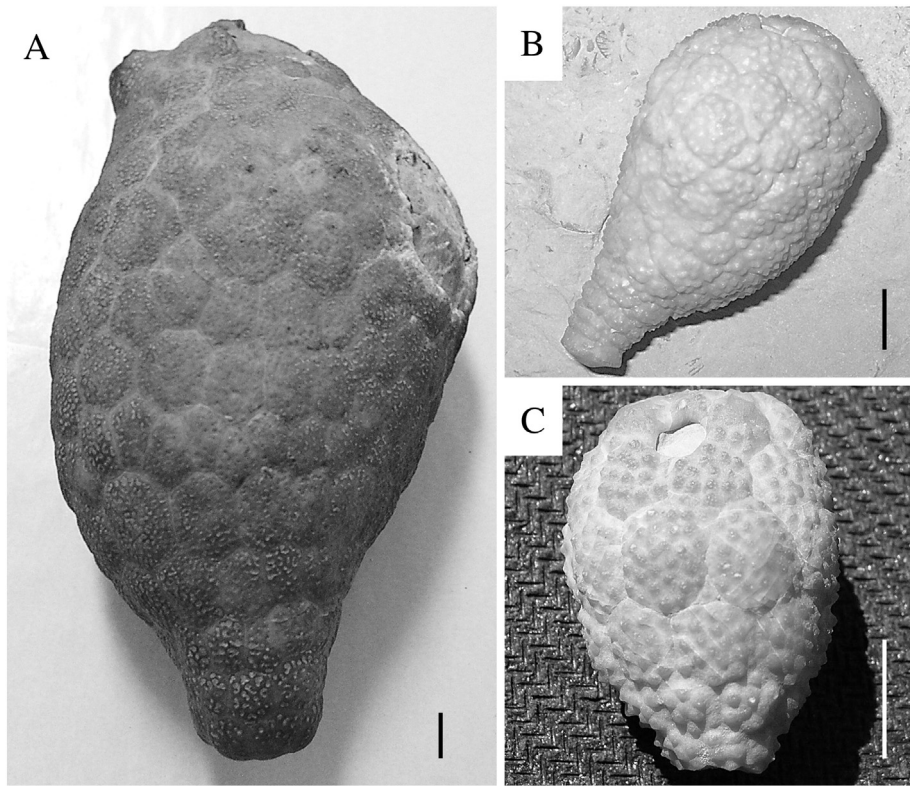
All specimens were assessed based on five independently documented taphonomic criteria: 1) state of completeness, 2) style of thecal disruptions, 3) locations of encrusting organisms, 4) degree of compression, and 5) nature of thecal-filling sediment. Specimens repositated at the Cincinnati Museum Center could not be cut open for analysis of sediment infill, nor could specimens not donated for such a purpose by private collectors. Consequently, the number of specimens for which the first four criteria could be assessed is greater than that for which all five criteria are known. A total of 202 thecae were cut open to provide data on sediment infill.

For assessment of completeness, each specimen was classified as 1) a complete individual, characterized by an intact theca articulated to a stele and relatively complete feeding appendages; 2) an intact theca articulated to feeding appendages (or at least some brachiolar plates) but lacking a stele; 3) an intact theca articulated to a stele but lacking any portion of feeding appendages; 4) an intact theca; or 5) a partial theca. Note that the term stele is used in the loosest sense (cf. Brett, 1984) when characterizing these specimens, encompassing both the regularly plated “aboral processes” of *H. scutellatus* (Frest et al., 2011) and the more irregularly plated, viscera-filled true steles of other, elongate *Holocystites* species. Selected examples of these states of completeness are shown in Fig. 4.

The character of disruptions to diploporite thecae was documented in order to record the relative frequency of skeletal damage reflecting

specific taphonomic processes. Two primary types of plate disruption pattern were noted. “Plate shifting” is characterized by thecal plates that are in their proper position relative to adjacent plates within the same circler (or surrounding plates in mosaically plated taxa) but shifted out of a parallel plane (Fig. 5A–B). This reflects post-burial damage as plates were pushed into the interior of the theca by compaction; based on observations of diploporite specimens collected *in situ* and analysis of crinoids from other Paleozoic mudrocks (JRT, unpublished data), this form of disruption is found exclusively on the underside of skeletal modules (see also Nebelsick, 1999). In contrast, the pattern herein termed “plate loss/plate jumbling” is characterized by thecal ossicles that have been removed entirely (Fig. 5C) and/or ossicles that have been rotated, overturned, or otherwise moved out of their proper position on the theca (Fig. 5D). This pattern reflects physical, biostratinomic disruption of the upper sides of thecae that were completely or partially exposed at the sediment–water interface (e.g., Meyer and Milsom, 2001; Thomka et al., 2011). All specimens were classified as 1) undisrupted; 2) showing plate shifting on one side; 3) showing plate shifting on both sides; 4) showing plate loss/plate jumbling on one side; and 5) showing plate loss/plate jumbling on both sides.

The presence and location of encrusting organisms on diploporite thecae was documented. Given the exothecal respiration of diploporites (Paul, 1971) and the tendency of holocystitids to respond to biotic interactions by producing swellings and galls (e.g., Frest et al., 2011), *syn vivo* encrustation is far less likely than post-mortem encrustation. Hence, all of the encrustation patterns described represent occupation of dead, exposed diploporite material. The vast majority of encrusters were thin, laminar bryozoans, mainly fistuliporoids (Fig. 6B), which could occasionally form relatively thick, prominent overgrowths

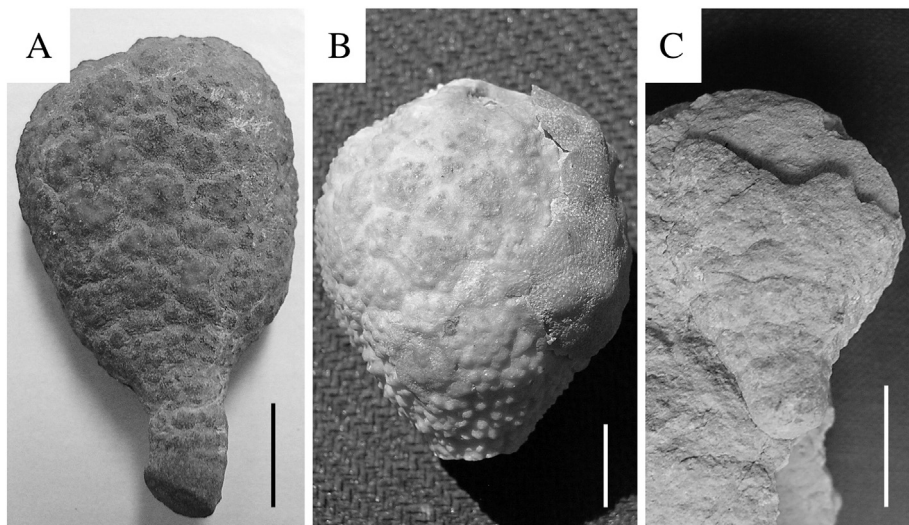


**Fig. 3.** Examples of exceptionally preserved diploporites from the lower mudstone of the Massie Formation at the Napoleon quarry. Note that some of these specimens represent taxa that are not described in this study, but nevertheless illustrate the preservational quality of diploporites from the studied interval. A) Large, inflated, intact *Triamara cutleri* (CMC 62655) theca displaying ossicle ornamentation, a complete stele, and well-preserved ambulacral tracts (not visible in photograph). Note that this genus was not included in this study, but nevertheless illustrates the preservational quality of diploporites from the studied interval. B) Moderately large, inflated *Holocystites scutellatus* theca (CMC 69277) with intact stele and well-preserved plate ornamentation. C) Relatively small *Holocystites* sp. cf. *alternatus* (in private collection) displaying complete, regular plate circlets composed of plates with ornamentation and a large anal opening lacking cover plates. All scale bars = 1 cm.

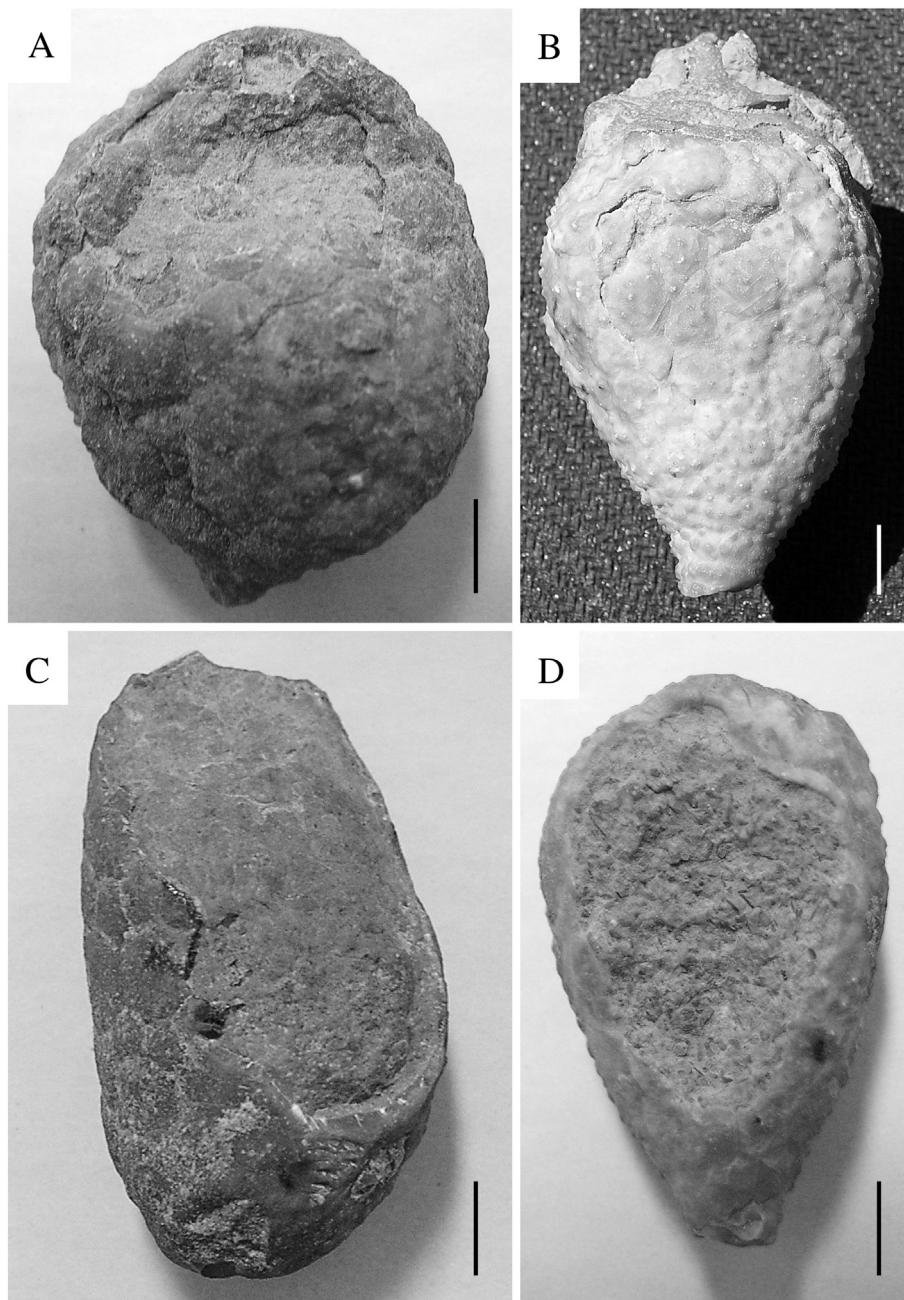
(Fig. 6A). Small ramose bryozoans (Fig. 6C), solitary rugose corals (*Enterolasma* sp.), and small pelmatozoan echinoderm holdfasts (Fig. 6D) were also observed. An important aspect of this taphonomic attribute was the location of encrusters relative to the plate disruption patterns described above (see Fig. 5). Hence, each specimen was categorized as 1) un-encrusted; 2) encrusted on one side of an undamaged theca; 3) encrusted only on the damaged side of a damaged theca;

4) encrusted only on the undamaged side of a damaged theca; 5) encrusted on both the damaged and undamaged sides of a damaged theca; or 6) encrusted on both sides of an undamaged theca.

The degree of compression was documented for each specimen in order to contribute data on the relationships between theca-filling material and taphonomic damage to the theca as a whole. Specimens were classified as 1) inflated, characterized by no distortion to the



**Fig. 4.** Examples of states of specimen completeness used to describe diploporites in this study. All specimens represent *Holocystites scutellatus*. A) Articulated theca with an intact stele and no feeding appendages (CMC 59335). For other examples, see Figs. 3B, 5A–B. B) Articulated theca lacking feeding appendages and stele (in private collection). For other examples, see Figs. 3C, 5C–D. C) Partial theca, missing the oral portion (in private collection). Scale bars = 1 cm.



**Fig. 5.** Examples of plate disruption patterns on diploporite thecae. Plate shifting occurs on the downward-facing side of thecae, whereas plate loss/plate jumbling occurs on the upward-facing side of thecae. All figured specimens represent *Holocystites scutellatus*. A–B) Articulated thecae (CMC 59338 and specimen in private collection, respectively) displaying plate shifting. Note that plates are in their correct position but have been slightly pushed into the interior of the theca by compaction. C–D) Articulated thecae (CMC 62653 and specimen in private collection, respectively) displaying plate loss/plate jumbling. Note that thecal plates are missing entirely or are moved out of their proper position. Scale bars = 1 cm.

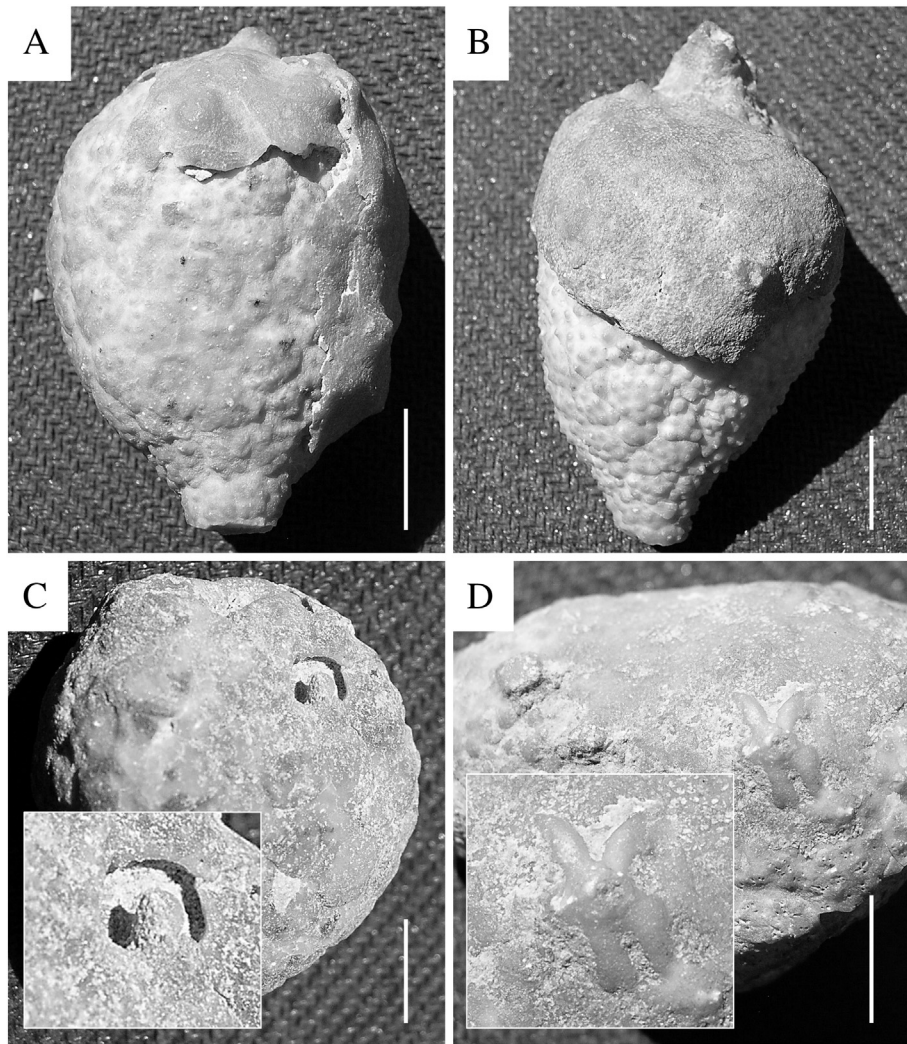
roundness of thecae; 2) slightly compressed, characterized by minor flattening of one or more sides of thecae; 3) strongly compressed, characterized by significant reduction in the thickness of thecae; or 4) crushed, characterized by near-flattening of thecae into a single plane. Examples of these states of preservation are shown in Fig. 7.

A proportion of specimens was cut open and polished to reveal the nature of thecal infilling material. Particular emphasis was placed on recognizing geopetal indicators, including graded sedimentary fill (Fig. 8A–B) and sediment–sparry calcite relationships (Fig. 8B). As with encrusters, data on infill were analyzed in the context of the location of damage to thecae. Hence, each specimen was categorized as 1) displaying ambiguous fill, where no indicator of orientation during burial could be recognized (Fig. 8C); 2) displaying a geopetal fill within a specimen that is undamaged on both sides or, far less commonly,

damaged on both sides; 3) displaying a geopetal fill indicating that one well-preserved side faced upward and the opposite, damaged side faced downward; or 4) displaying a geopetal fill indicating that one well-preserved side faced downward and the opposite, damaged side faced upward.

## 5. Results and taphonomic interpretations

Data on the relative distribution of states of completeness, nature of thecal disruptions, occurrences and locations of encrustation, severity of compression, and geopetal implications of thecal-infilling sediment are presented in Table 1 and Fig. 9. No completely intact specimens (category 1) nor any specimens that retained feeding appendages while lacking a stele (category 2) were found (Fig. 9A). This research



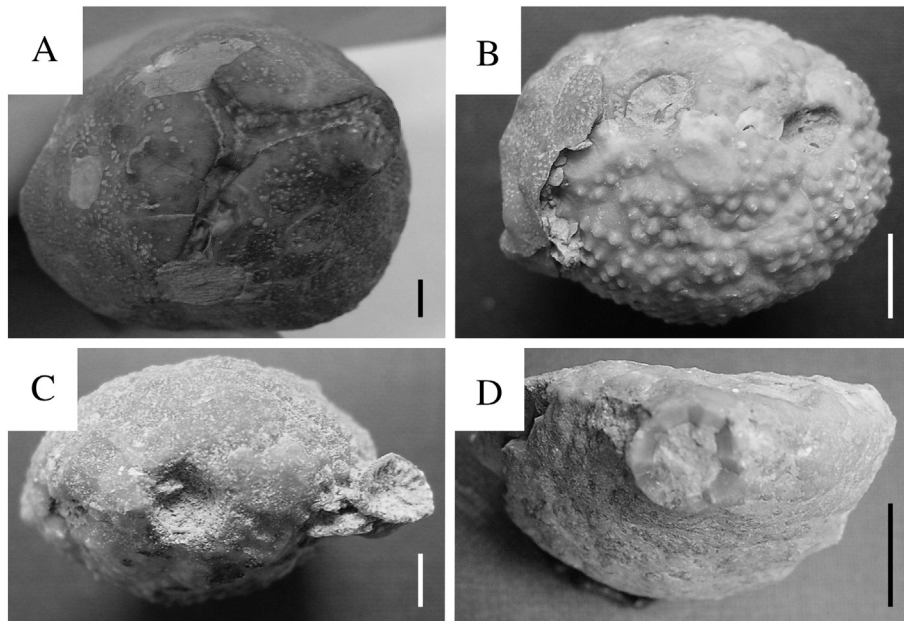
**Fig. 6.** Examples of encrustation on diploporite material. All figured specimens represent *Holocystites scutellatus* and are in a private collection. A) Articulated theca encrusted by multiple generations of thin, laminar bryozoans. An older zoarium has overgrown the oral pole of the theca, and this is, in turn, overgrown by a younger zoarium on the right side of the theca. B) Intact theca (same specimen as in Fig. 5B) encrusted by large, multi-laminar bryozoan colony. C) Inflated theca with a small ramose bryozoan colony encrusting the anal opening (enlarged in inset image). Note that disarticulation and loss of anal cover plates must have occurred prior to colonization and growth of bryozoan colony. D) Relatively large theca encrusted by a small dendritic radicular attachment structure (enlarged in inset image) attributable to a juvenile crinoid, likely *Eucalyptocrinites* (cf. Thomka and Brett, 2015a,b). Note that the crinoid holdfast is encrusting a thin bryozoan layer that overgrew the surface of the diploporite theca. Scale bars = 1 cm.

confirms the relative volatility of holocystitid diploporite brachioles: review of the numerous specimen descriptions in Paul (1971) and Frest et al. (2011) reveals that only a handful of specimens (no more than six, depending on interpretation of plating) are preserved with any brachiolar plates at all, and those with putative partial brachioles retain only one or two plates on each of one or two appendages. This has been interpreted as indicating that such appendages, though associated with relatively wide articular facets, were evidently unskeletonized or very lightly skeletonized, with particle capture occurring primarily via mucous (Paul, 1971, 1973, 1977). This pattern may be alternatively interpreted as representing the presence of appendages bearing a small amount of inter-brachiolar connective tissue and/or relatively labile connective tissues, resulting in very rapid post-mortem disarticulation. However, the tendency of feeding appendages to undergo disarticulation faster than other skeletal modules probably does not indicate the presence of muscular articulations within brachioles of these diploporites, as it may for crinoids (Ausich and Baumiller, 1993).

The majority of specimens (58%) are preserved as intact thecae (category 4), and there are approximately equal numbers of diploporites preserved as thecae attached to steles (category 3) and partial thecae (category 5; 21% each). This indicates that separation of the stele from

the theca occurred relatively late in the disarticulation sequence, just prior to or coincident with disarticulation of the theca itself. This stands in contrast to the preservation of diploporite remains from the hardground underlying the Massie mudstone lithofacies, where separation between thecae and permanently cemented aboral thecal attachments occurred early in the taphonomic history (Thomka and Brett, 2014b). Seemingly, the attachment strategy employed by diploporites that occupied the softground mud lithofacies—direct encrustation and overgrowth of small skeletal debris by the aboral region (Gil Cid and Domínguez-Alonso, 2000; Frest et al., 2011)—resulted in less skeletal differentiation between the main body of the theca and the aboral pole, thereby causing these regions to have similar responses to biostratinomic processes.

As a whole, data on specimen completeness indicate that this assemblage of diploporites is well-preserved, with nearly 80% of the sample consisting of articulated thecae with or without steles (Table 1; Fig. 9A). This reflects rapid burial by fine-grained siliciclastic sediment, likely in the form of episodic distal storm events (Thomka and Brett, 2015b). Yet, specimens are not preserved uniformly and the total absence of feeding appendages indicates some degree of decay prior to burial. Evidence for slight decay preceding rapid burial is commonly



**Fig. 7.** Examples of compression documented for diploporite specimens. A) Oral view of *Triamara* theca that is fully inflated, showing no compaction-related damage. Note that this diploporite genus was not included in the dataset described herein, but nevertheless best illustrates inflation. Same specimen as in Fig. 3A. Scale bar = 1 cm. B) Oral view of *Holocystites scutellatus* theca displaying slight compression, with minor flattening of the two wide sides of the theca. Same specimen as in Fig. 4B. Scale bar = 0.5 cm. C) Oral view of *H. scutellatus* theca (specimen in private collection) displaying strong compression, with major modification of the cross-sectional shape of the theca. Note the encrusting solitary rugose coral. Scale bar = 0.5 cm. D) Aboral view of *H. scutellatus* theca (specimen in private collection) displaying a crushed state. This specimen is flattened along the wider sides of the theca. Scale bar = 1 cm.

observed in similar distal, muddy, storm-influenced environments (e.g., Taylor and Brett, 1996; Brett and Taylor, 1997; Brett et al., 1997; Ausich, 2001; Thomka et al., 2011).

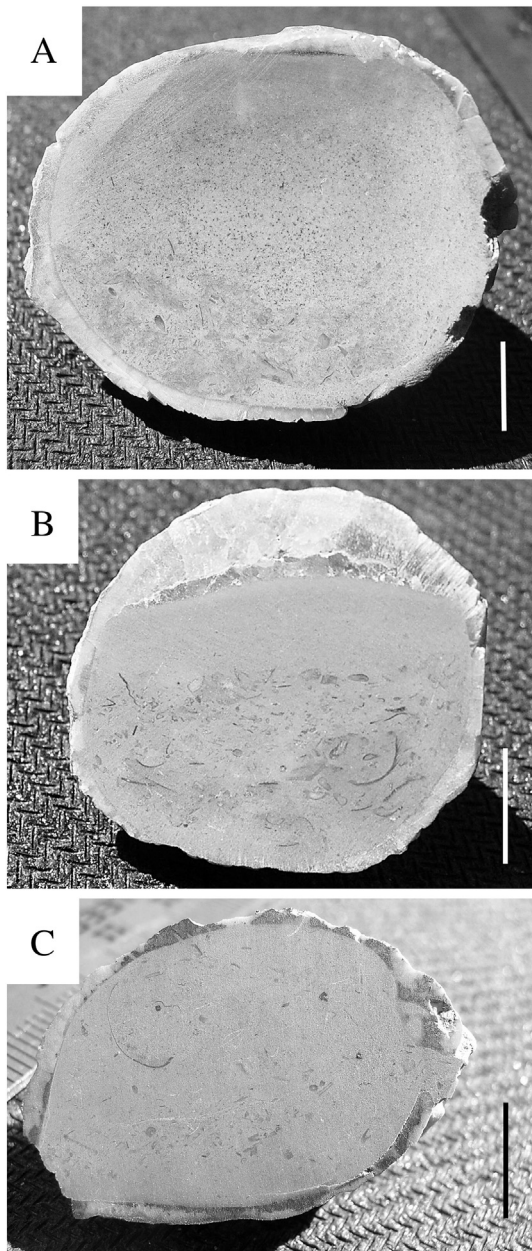
The vast majority of specimens show some form of disruption to the theca, with only 18% of specimens preserved undamaged (Fig. 9B). Over 73% of specimens display plate disruptions on one side of the theca; less than 9% display damage to both sides (Table 1). Plate loss/plate jumbling on one side of the theca is the most common form of thecal disruption, being observed in more than half of studied specimens; this is slightly greater than twice the number of specimens displaying plate shifting to one side of the theca (Fig. 9B).

In total, 40.5% of diploporites are either undamaged or display only plate shifting on one side (Table 1; Fig. 9B). These specimens seemingly represent individuals that were subjected to relatively simple taphonomic histories. 4.5% of specimens display plate shifting on both sides, indicating at least one cycle of burial, compression, exhumation, reorientation, and re-burial, but without recognizable damage resulting from exposure at the sediment–water interface. In contrast, 55% of the sample displays plate loss/plate jumbling, reflecting biostratigraphic modification during partial surficial exposure. In some instances, plate loss/plate jumbling is seemingly the product of a simple taphonomic history; however, other specimens show evidence of a more complicated history, particularly when relationships between plate loss/plate jumbling and encrustation patterns are considered (see below). The 4% of specimens that display plate loss/plate jumbling on both sides of the theca likely represent some of the most taphonomically complex diploporite remains, as at least two episodes of physical disruption during surficial exposure are recorded.

Approximately 42% of specimens were encrusted to some degree (Fig. 9C). The high frequency of encrustation indicates that diploporite remains served as important “islands” of hard substrata in a muddy environment and, given their predominantly articulated state, were likely colonized rapidly after death and/or exhumation and exposure following shallow, temporary burial. Encrustation of echinoderm tests and thecae is a common and ecologically significant process in post-Paleozoic softgrounds (e.g., Nebelsick et al., 1997; Taylor and Wilson, 2003; Zamora et al., 2008) and similar patterns certainly occurred

in the Massie Formation (see also Liddell and Brett, 1982). Of the encrusted specimens, most (27%) preserve encrusting organisms on the well-preserved side of damaged thecae. This provides strong evidence for overturning at some point during the post-mortem history of certain thecae, as encrustation had to occur on the upward-facing side of exposed thecae, but many of the specimens displaying this encrustation pattern also show plate loss/plate jumbling (also an indicator of the upward-facing side) on the un-encrusted side. Very few specimens (less than 5%) are encrusted only on the disrupted sides of damaged thecae, and some of these display plate shifting, which is an indicator for the downward-facing side (an additional line of evidence for reorientation). Further, nearly 20% of specimens are encrusted on both sides of the theca (Fig. 9C), including numerous individuals that are differentially preserved on opposite sides. As a whole, data from encrustation patterns indicate 1) that diploporites played an important role in providing habitable space for hard substrate-occupying organisms; and 2) that diploporite thecae were commonly subjected to post-mortem overturning, possibly more than once in some cases, before final burial. The precise timing of encrustation and overturning relative to shallow burial, exhumation, partial burial, and/or plate disruption is difficult (or impossible) to determine in many cases.

Most diploporites were affected by compression to some degree, as only 16% of specimens are fully inflated (Fig. 9D). Nevertheless, the inflated proportion, along with the larger component represented by slightly compressed thecae (27%; Fig. 9D), contains nearly all of the spectacularly preserved, largely complete specimens (e.g., Figs. 3, 5). The slightly compressed specimens commonly display plate shifting to one side. These specimens seemingly represent individuals with relatively simple taphonomic histories consisting primarily of decay-induced loss of feeding appendages and other delicate structures, burial, and potentially early diagenetic cementation of sediment within thecae. Strong compression is the most common mode of preservation with nearly half of the sample (45%) represented. Given that all specimens lack feeding appendages and many lack steles, this predominance by strongly compacted thecae likely indicates greater exposure time, and therefore increased decay, prior to burial (cf. e.g., Brett et al., 1997;



**Fig. 8.** Examples of infill relationships within diploporite thecae. A) Graded sediment fill composed of coarse bioclastic particles overlain by finer pelleted? material and, eventually, dark mud. This represents a geopetal indicator. B) Geopetal fill comprising bioclastic mud overlain by sparry calcite. Note that the sediment is graded. C) Ambiguous sediment that is not useful as a geopetal indicator. Scale bars = 1 cm.

Ausich, 2001; Thomka et al., 2011). This interpretation is further supported by the observation that most specimens that are crushed are partial thecae, some of which are heavily encrusted. Diploporites that experienced greater decay at the sediment–water interface prior to burial had weakened sutures between thecal plates due to degradation of connective tissues, probably lost much of their thecal volume as viscera decayed, and would have been less likely to be infilled with sediment (Zamora et al., 2008); all of these factors would have made thecae more susceptible to severe compression. There are no other consistent relationships between magnitude of compression and taphonomic attributes; seemingly post-burial compaction was not a major control on the taphonomy of this echinoderm assemblage, in contrast to similar Paleozoic deposits in which compression shaped

**Table 1**

Summary of taphonomic data for sample of Napoleon quarry diploporites studied here. Note that all specimens represent *Holocystites*, but no species-level designations were employed.

<i>Specimen completeness</i>		
Theca with brachioles and stele	0	0%
Theca with brachioles	0	0%
Theca with stele	61	21%
Theca	164	58%
Partial theca	59	21%
<i>Thecal disruption patterns</i>		
No damage	51	18%
Plate shifting on one side	64	22.5%
Plate shifting on both sides	13	4.5%
Plate loss/plate jumbling on one side	144	51%
Plate loss/plate jumbling on both sides	12	4%
<i>Encrustation patterns</i>		
No encrusters	164	58%
Encrusters on one side of undamaged theca	14	5%
Encrusters on undamaged side only	76	27%
Encrusters on damaged side only	12	4%
Encrusters on both sides of undamaged theca	7	2%
Encrusters on damaged and undamaged sides of theca	11	4%
<i>Compression</i>		
Inflated	46	16%
Slightly compressed	76	27%
Strongly compressed	129	45%
Crushed	33	12%
<i>Infill patterns</i>		
Ambiguous	127	63%
Geopetal fill in undamaged theca	10	5%
Geopetal fill: undamaged side-up	29	14%
Geopetal fill: damaged side-up	36	18%

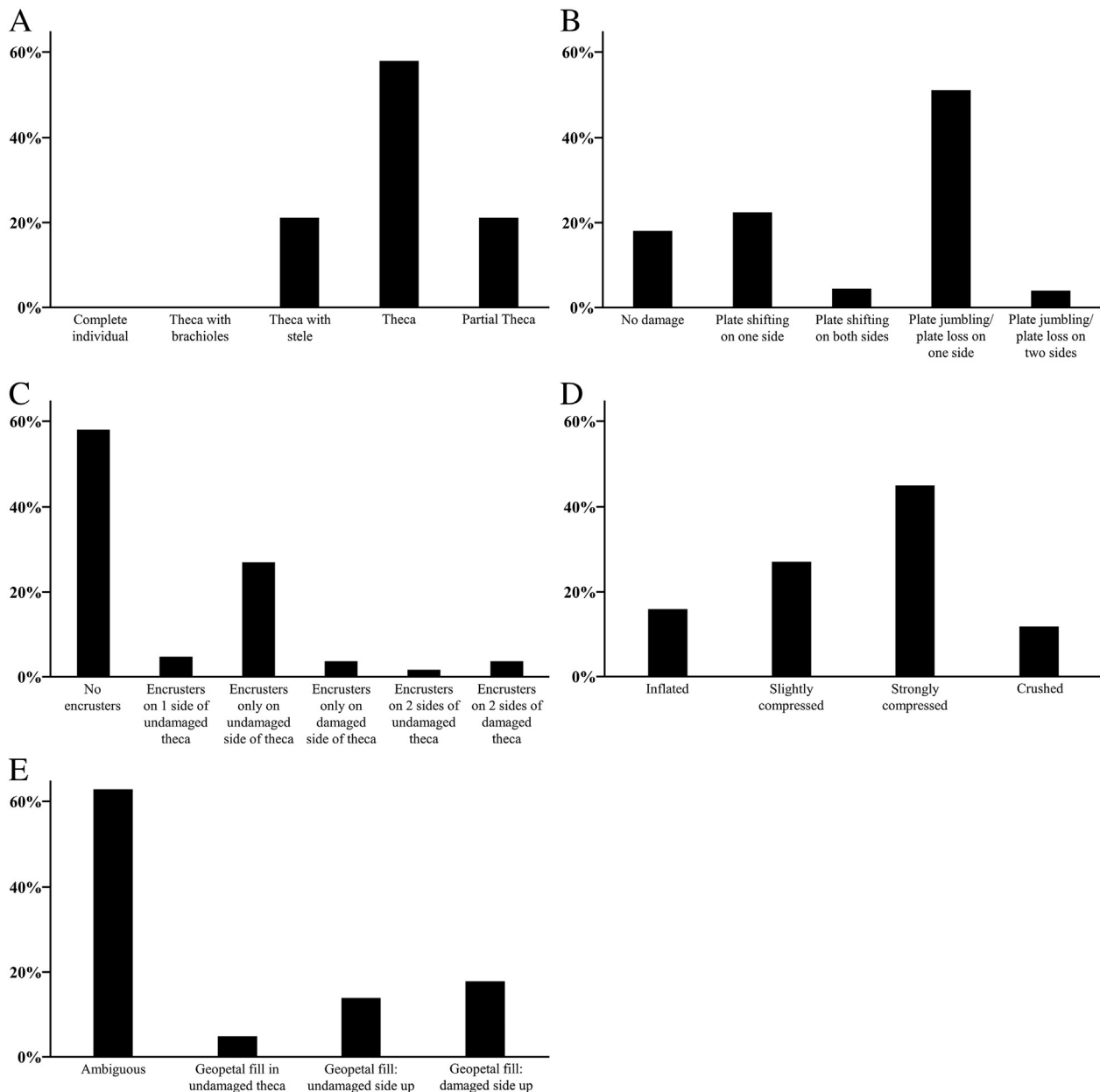
preservational patterns to a more significant degree (e.g., Thomka et al., 2011).

Of the 202 specimens that could be cut open to expose infills, 63% were filled with sediment that did not permit recognition of orientation during burial (Fig. 9E). Of the 37% of thecae with geopetal infills, most are damaged on one side; there are nearly equal numbers of specimens characterized by a damaged side that faced upwards (18%) and downwards (14%; Fig. 9E). This is important information, as it provides direct evidence for overturning of thecae before or after infilling with sediment (and potentially early diagenetic cementation of infill). Specimens that display plate shifting on one side and geopetal infills indicating that the shifted side faced upward represent individuals that were overturned at some point, as do specimens that display plate loss/plate jumbling on one side and geopetal fills indicating that the disrupted side faced upward. However, encrustation patterns may provide separate evidence for overturning during the biostratigraphic history of the specimen.

## 6. Discussion

### 6.1. Implications for genetic history of the assemblage

The preservation of diploporites at the Napoleon quarry as thecae that are damaged on one side and undamaged on the other has long been recognized and has historically been interpreted as the effect of partial burial (e.g., Frest et al., 1977; see also Meyer and Milsom, 2001). This carries the important implication that the prolific diploporite assemblage recovered from the basal Massie mudstone represents a single exceptionally diverse and abundant echinoderm fauna (Frest et al., 2011). However, taphonomic data presented herein



**Fig. 9.** Summary of taphonomic data on sample of diploporites from the Napoleon quarry (N = 284 for all features except for infill, for which N = 202). A) Data on states of specimen completeness. Note that no specimens are preserved with any portions of brachioles articulated to thecae. B) Data on plate disruption patterns observed on diploporite thecae. See text for clarification of the nature of specific disruptions. C) Data on location of encrusting organisms on diploporite thecae. Note that certain modes of occurrence are directly tied to differential preservation of opposite sides of the theca, with a damaged and an undamaged side; for this graph, no distinction is made between plate shifting and plate jumbling/plate loss. D) Data on compression of diploporite specimens. See text for descriptions of each compression category. E) Data on infill of diploporite thecae that were cut open. Note that geopetal fills include both graded sediment and sediment/calcite spar relationships, and that certain descriptive categories are directly tied to differential preservation of opposite sides of thecae.

indicate a more complicated history for the diploporite assemblage: a scenario of simple rapid burial of a single diverse and crowded community, occasionally preceded by brief periods of partial exposure, is not supported by available evidence.

The taphonomic complexity documented herein suggests an extended biostratinomic history for some diploporite thecae in the lower Massie mudstone from the Napoleon quarry. Since infilling of thecae with sediment could only have occurred after death of individuals, and encrustation is quite unlikely to have begun during the life of the organism given the epithelial nature of respiration (Paul, 1971; Brett, 1984), strong evidence for a complex taphonomic history comes from the frequency of contradictory orientation indicators observed on specimens (i.e., plate disruption patterns and/or encrusting fauna independently denoting contrasting “up directions”) and the inferred

timing of encrustation of partially disarticulated diploporite individuals (i.e., laminar bryozoans encrusting the oral area of thecae only after loss of feeding appendages must have occurred). Collectively, these patterns indicate that numerous thecae remained in stable positions long enough to serve as substrata for encrusting organisms, which in many instances include sizeable colonies or display overgrowth by later generations of encrusting taxa before and/or after being overturned. This is further made apparent once geopetal infills are considered, as a sizeable number of thecae must have been partially or completely filled with sediment, and later, sparry calcite, while in an orientation dramatically different from that indicated by external features.

These conclusions have important implications for genetic interpretation of this fauna. It is clear that many specimens were subjected to multiple episodes of reorientation and some appear to have been

partially or completely buried prior to exhumation, re-exposure, and thecal plate loss/plate jumbling. An important issue is why the relatively delicate multi-element diploporite thecae did not undergo complete disarticulation as a result of prolonged residence within the taphonomically active zone, as would be expected based on experimental observations of other morphologically similar echinoderms (e.g., crinoids: Meyer, 1971, 1997; Liddell, 1975; Meyer and Meyer, 1986; Brett et al., 1997; Ausich, 2001; Baumiller, 2003; Gorzelak and Salamon, 2013). This is particularly intriguing given the propensity for multi-element skeletons to rapidly disarticulate after exhumation and exposure following preliminary burial (e.g., Allison, 1986; Plotnick, 1986; Kidwell and Baumiller, 1990; Gorzelak and Salamon, 2013). In fact, certain thecae, such as the specimen in Fig. 10A, are highly corroded and severely physically degraded, clearly indicating an extended residence time in a taphonomically active environment—yet, the theca did not disarticulate into isolated ossicles.

The most logical explanation for the increased tendency for thecae to remain articulated in spite of increased exposure time and/or exhumation and re-exposure is very early cementation of material within the theca (see Zamora et al., 2008 for a similar scenario in Cretaceous echinoids). This would result in thecae essentially becoming cemented together and serving as single, solid masses that were more taphonomically robust than the otherwise delicate multi-element skeletal modules. Many of the most degraded diploporite thecae are infilled primarily or exclusively with crystalline material (Fig. 10B), which would have strongly held together thecal plates during exposure and physical reworking rather than subjecting thecae to total disarticulation. Importantly, this would also have allowed articulated thecae that

became exposed following cementation of infill to remain intact, accounting for at least some of the specimens with geopetal infills that contradict encrustation and/or plate disruption patterns (Fig. 9). The example shown in Fig. 10 is a somewhat extreme example, but the ability of diploporite thecae to resist disarticulation, even for a relatively short period following partial or total exhumation and re-orientation, is likely sufficient to account for the taphonomic patterns documented here.

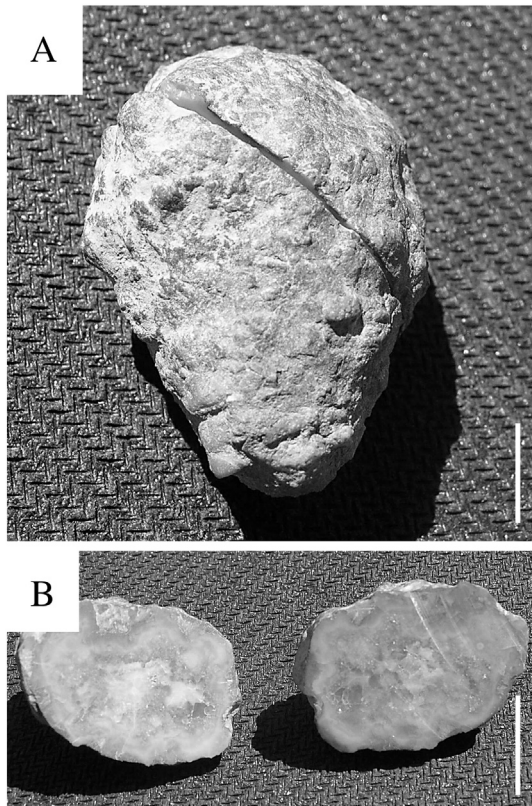
This interpretation carries important implications for the nature of diploporite diversity and abundance at the study site. Because thecae were seemingly able to resist total disarticulation during exhumation, partial exposure, and/or reworking, in contrast to most comparable settings, this diploporite fauna represents a time-averaged assemblage reflecting stratigraphic condensation during a latest transgressive to early highstand interval. Thus, the prolific diploporite fauna characteristic of the Napoleon quarry is likely due, at least in part, to temporal mixing of numerous, individually less diverse and abundant coenoses. The preservation of diploporites predominantly as articulated thecae does not reflect a single rapid burial event, smothering a single community, but rather reflects repeated rapid burial events and subsequent biostratigraphic processing, ultimately resulting in concentration and amalgamation of event-buried individuals.

## 6.2. Taphonomic variability and taphonomic pathways

Documentation of taphonomic variability within assemblages of closely related taxa from the same deposit is capable of producing significant insights into commonly overlooked taphonomic processes and strengthening interpretations by providing a baseline for the degree of intrinsic variability experienced by an assemblage (Thomka et al., 2011, 2012). The material studied herein represents a single genus from a single, thin bed, making this assemblage an ideal subject for determining a variety of major and refined factors that controlled diploporite taphonomy.

It is clear that variable and, in some cases, complex taphonomic pathways were followed by *Holocystites* thecae from the Napoleon quarry. In one sense, this is demonstrated merely by the non-uniform preservation of specimens; however, this is a bit too simplistic, as differing degrees of exposure prior to final burial can account for taphonomic variability of such a scale. Instead, the complex suite of co-occurring taphonomic properties observed in Napoleon diploporites—including locations of damage to thecae, styles of disruption of thecae, locations of encrusting organisms, and nature of thecal-filling materials—collectively indicate differential sequences of events that operated on specimens displaying different states. A more exhaustive analysis of potential biostratigraphic pathways and resultant taphonomic states will be presented in a forthcoming paper; however, a few significant, generalized pathways are worth highlighting.

Specimens analyzed, described, and figured most commonly in systematic studies of diploporites from the Napoleon quarry (e.g., Paul, 1971; Frest et al., 2011) are characterized by no encrusters or a few, small encrusters; no disruptions to thecal plating or only subtle plate shifting on one side; and complete thecae with little surficial degradation. An example of such a specimen is shown in Fig. 3C. Interestingly, specimens preserved in such a state are capable of providing much morphological and anatomical data, but offer few taphonomic insights compared to more poorly preserved specimens. In fact, the historical emphasis on systematic studies, largely focusing on similarly well-preserved specimens, may have contributed to the classical interpretation of a simple taphonomic history for diploporites from the Napoleon quarry. The taphonomic pathway that led to this mode of preservation is relatively simple: the individual died, likely underwent a brief interval of decay (enough to result in loss of brachioles, oral/anal cover plates, and, in some cases, the stele), and then were rapidly buried by fine-grained sediment and not exhumed. Many specimens display plate shifting on one side reflecting post-burial compression.



**Fig. 10.** An example of a very poorly preserved diploporite specimen from the study area. A) *Holocystites scutallatus* theca (specimen in private collection) that is strongly degraded, showing heavy corrosion and/or abrasion, loss of surface features, and showing evidence for considerable residence time within the taphonomically active zone. However, the theca remained intact rather than undergoing complete disarticulation into isolated ossicles. B) Infill of the same specimen showing that the interior theca is completely filled with crystalline calcite. Early cementation of thecae by calcite spar would have held together thecal plates during prolonged exposure and physical reworking following exhumation and secondary exposure. Scale bars = 1 cm.

In contrast, diploporite specimens that are not as well preserved, and have not been featured as frequently in previous publications, provide the most taphonomic data. Diploporites from the Napoleon quarry preserved as articulated thecae displaying plate jumbling/plate loss on one side, abundant and often large encrusters on the opposite side, and geopetal sedimentary infill indicating that the well-preserved side faced upward during burial, an example of which is shown in Fig. 5C, reflect a considerably more complex taphonomic pathway than that described for the previously described specimen. In this case, the diploporite must have died and experienced decay to the point of disarticulation of brachioles, loss of oral/anal cover plates, and detachment of the stele. At this point, one of two potential sequences of events could have occurred. In the first scenario, the slightly disarticulated theca was encrusted on the upward-facing side and then buried, resulting in the geopetal sediment fill. Later, this encrusted theca was exhumed and exposed at the sediment–water interface, then overturned, leading to plate jumbling/plate loss on the un-encrusted side of the theca. The theca was then buried for the final time. In the second scenario, the slightly disarticulated theca was partially buried and experienced plate jumbling/plate loss on the exposed side before being completely buried. After some period of time, this theca was exhumed and overturned, allowing the well-preserved side to be encrusted during a brief interval of exposure before final burial. Once buried, the theca was filled with sediment, leading to geopetal infill. It is likely that both taphonomic pathways are represented by specimens preserved in such a state; however, the first scenario is likely represented by specimens that are relatively inflated, since the theca would have been infilled with cemented material prior to exhumation, and the second scenario is likely represented by specimens that are relatively strongly compressed, as, in this case, infill occurred after two episodes of exposure and loss of viscera within thecae.

A final mode of preservation commonly encountered in this assemblage is partial thecae that are strongly compressed to crushed and encrusted on one side. An example of such a specimen is shown in Fig. 4C. These represent individuals that either were exposed at the sediment–water interface in a stable orientation for an extended period of time, leading to more thorough disarticulation and encrustation, and thecal collapse as viscera was lost to decay. Alternatively or additionally, these may represent individuals that were initially buried rapidly but not filled with sediment or calcite spar and then exhumed, leading to severe degradation of thecae. Like the relatively pristine thecae described above, these specimens represent an easily understood, simple taphonomic pathway.

### 6.3. Silurian Lagerstätten

The Silurian Period is generally perceived to contain few Lagerstätte deposits, particularly when compared to the Ordovician and Devonian Periods (Kluessendorf, 1994). Well-known Silurian Konservat-Lagerstätten yielding articulated multi-element skeletons of marine organisms include the Telychian-age North Esk Inlier “starfish beds” of Scotland (Donovan et al., 2011); the early Sheinwoodian-age Napoleon Lagerstätte described herein and the roughly coeval Rochester Shale *Homocrinus* Lagerstätten of western New York (Brett and Eckert, 1982; Taylor and Brett, 1996; Brett and Taylor, 1997, 1999); the Wenlock-age Herefordshire Lagerstätte of England (e.g., Siveter et al., 2004, 2007); the lower Sheinwoodian through Gorstian strata of Gotland, Sweden (Franzén, 1983; Hess, 1999); and the Homeric-age Waldron Shale of southeastern Indiana (Feldman, 1989) and Much Wenlock Limestone of West Midlands, Britain (Watkins and Hurst, 1977; Ray and Thomas, 2007).

Although the lower Massie Formation contains diploporite thecae that lack such delicate features as brachioles, the degree of articulation (i.e., the number of completely intact thecae) and the preservation of intricate surface features on ossicles qualifies this interval as a Konservat-Lagerstätte, given the tendency of diploporites to be preserved as isolated

ossicles, incomplete thecae, and molds. The Napoleon Konservat-Lagerstätte is unique among the Silurian deposits listed above because of the numerical dominance of articulated blastozoans over crinoids. Although blastozoans are present in an articulated state in nearly all of the multi-element skeleton-bearing Lagerstätten, these deposits are largely renowned for their crinoid faunas and contain blastozoans as a clearly subordinate fauna. Even in settings where blastozoans are particularly abundant, such as certain calcareous mudstone lithofacies of the Rochester Shale where the hemicosmitid rhombiferan *Caryocrinites* can be the most common echinoderm taxon (Brett, 1983, 1999; Frest et al., 1999), associated faunas are of low diversity, and it seems likely that such deposits represent rare environments where many otherwise common taxa were excluded by paleoenvironmental parameters (e.g., lowered benthic oxygenation, unstable substrates).

In many ways, the Napoleon Konservat-Lagerstätte is more similar to Middle Ordovician “cystoid beds” described from Baltica and peri-Gondwana (Bockelie, 1981, 1984; Paul and Bockelie, 1983; Lefebvre et al., 2005; Eriksson et al., 2012; Nardin et al., 2014) than it is to lithologically equivalent mudstone-hosted Lagerstätten in the Silurian of eastern Laurentia. The sheer abundance of individuals, the dominance by blastozoans, and the non-uniform and occasionally complex taphonomic histories of many specimens (often involving re-working, reorientation, partial burial, and encrustation) are all elements that are observed in “cystoid bed” intervals (Bockelie, 1981; Paul and Bockelie, 1983). This is a function of the low rate of sedimentation characteristic of such stratigraphic intervals at the Napoleon quarry (Brett et al., 2012; Thomka and Brett, 2014b, 2015b) and at other “cystoid bed” localities (e.g., Eriksson et al., 2012). This, perhaps coupled with an intrinsic elevated resistance to skeletal disarticulation, allowed multiple generations of individuals to be condensed into single, thin intervals, essentially producing Konzentrat-Lagerstätten. Middle Ordovician “cystoid beds” represent carbonate environments where sedimentation was minimal and cessation of thecal disarticulation was due largely to very early diagenetic mineralization within thecae (Bockelie, 1981; Donovan and Portell, 2000; Donovan et al., 2005), resulting in articulation of thecae during subsequent exposure. Diploporites from the Napoleon Konservat-Lagerstätte appear to have been affected to some degree by a similar process (Fig. 10); however, because of the mud-dominated lithology and the episodic obrution events responsible for mortality and (at least initial) burial of individuals by fine-grained sediment, preservational quality of specimens was also improved significantly (e.g., Thomka and Brett, 2015b). Hence, many diploporites are preserved nearly intact and with pristine surface features (Figs. 3, 6), in contrast to preservation in other, more physically processed “cystoid beds”.

The effects of overall low sedimentation conditions, episodically punctuated by “mud smothering” events and commonly followed by early diagenesis of thecal infills, led to development of an assemblage with a high proportion of articulated and generally well-preserved specimens, but specimens that otherwise paradoxically show evidence for extended biostratigraphic histories. Moreover, this unique taphonomic setting, associated with stratigraphic condensation, led to a mass accumulation of diploporite thecae reflecting within-habitat time-averaging of reworked and/or shallowly buried individuals. Thus, the Napoleon assemblage is endowed with properties characteristic of both echinoderm Konservat-Lagerstätten and Konzentrat-Lagerstätten (Seilacher et al., 1985; Brett and Seilacher, 1991; Brett et al., 1997). Ongoing and future work is likely to increase the number of recognized atypical Lagerstätten generated by such processes.

### 6.4. Comparative taphonomy of diploporites

Diploporites are generally viewed as being prone to rapid post-mortem disarticulation in the absence of rapid burial (Brett et al., 1997; Ausich, 2001). However, abundant diploporite thecae are present in settings where co-occurring crinoids and presumably taphonomically

comparable echinoderms are preserved as isolated ossicles. Although the Lagerstätte described herein is the result of the combined effects of rapid burial by fine-grained sediment and early cementation of sedimentary fill, other Paleozoic deposits are also characterized by diploporite thecae that serve as the primary articulated skeletal module while other organisms experienced total disarticulation. For example, in addition to the Napoleon Lagerstätte and the Ordovician Baltican “cystoid beds” (e.g., Eriksson et al., 2012; Nardin et al., 2014) directly discussed above, deposits containing abundant articulated diploporite thecae within relatively coarse, cross-bedded skeletal grainstone facies occur within the Middle Ordovician Kimmswick Limestone of the greater Mississippi Valley region (Bassler, 1915), the middle Silurian Gasport Formation of New York (Brett, 1985), and the Middle Devonian Boyle Formation of central Kentucky (Sumrall et al., 2009). These occurrences represent high-energy environments where disarticulation and physical degradation would have been rapid; co-occurring crinoids are represented by separate ossicles or by articulated calyxes of particularly robust taxa (e.g., *Eucalyptocrinites*).

This pattern may suggest that diploporite thecae were more resistant to disarticulation than previously recognized. Perhaps a slightly elevated resistance to disarticulation was sufficient to foster early mineralization relative to other echinoderms; alternatively, the sac-like, ligamentary-bound diploporite theca may have been capable of remaining articulated in agitated environments due to physical factors. Additional work is necessary to test this hypothesis, but diploporite thecae, at least those attributable to certain taxa, may be better considered as taphonomically comparable to echinoderm skeletal modules such as *Eucalyptocrinites* and *Periechocrinus* calyxes, microcrinoid cups, and *Caryocrinites* thecae. The tendency of diploporite thecae to remain articulated or partially articulated may account for the complex biostratigraphic histories of “cystoid beds” and genetically related diploporite-bearing deposits.

## 7. Conclusions

Diploporites are exceptionally abundant and well preserved in the lower few centimeters of the middle Silurian Massie Formation mudstone at the Napoleon quarry of southeastern Indiana. Specimens are preserved as articulated thecae, in contrast to the typical taphonomic state of diploporites, which are typically found as isolated ossicles or molds. Consequently, this stratigraphic interval and locality are herein designated as the Napoleon Konservat-Lagerstätte. This Lagerstätte is significant in that it represents one of the only post-Ordovician deposits from which numerous articulated non-blastoid blastozoan thecae can be obtained in greater numbers than those of crinoids.

In spite of the articulated state of diploporite remains, specimens are not pristine and do not suggest catastrophic final burial of live individuals. The majority of specimens are preserved as articulated thecae, though many are lacking the stele. No brachiolar plates are articulated to thecae and, with very few exceptions, neither are oral and anal cover plates. The loss of these delicate structures indicates some degree of degradation prior to final burial. Most specimens are imperfect on one side of the theca; damage includes shifting of plates relative to adjacent plates in the same circler and jumbling and loss of plates. Many thecae were encrusted post-mortem by laminar bryozoans and, less commonly, pelmatozoan attachment structures.

Taphonomic evidence does not support the long-held interpretation that differential preservation of opposite sides of thecae always represents damage to exposed portions of the skeleton during partial burial. Encrusting organisms are most commonly found on the well-preserved side of *Holocystites* specimens, and sediment infill of thecae demonstrates that the damaged side often represented the downward-facing side and was pushed inward after burial. A complex and variable biostratigraphic sequence is proposed for *Holocystites* thecae recovered from the Napoleon Lagerstätte, with some individuals having experienced brief pre-burial decay, burial and subsequent exhumation,

and rapid cementation of thecal-filling mud prior to exposure and encrustation.

The most well-preserved thecae appear to have only experienced minor decay-induced disarticulation prior to final burial and display only compaction-induced damage (plate shifting) on their lower surfaces. Specimens characterized by intermediate preservation show evidence for one or more episodes of exposure and re-positioning following initial shallow burial; very rapid cementation of sediment within thecae served to keep these modules intact. For specimens in this taphonomic state, plate jumbling may in fact denote the upward-facing surface of the theca during partial burial. Incomplete specimens represent individuals that were exposed for longer durations prior to initial burial and/or individuals that did not experience early cementation of thecal-filling sediment prior to secondary exposure.

This research highlights the sensitivity of diploporite blastozoans to biostratigraphic processes and the significant role of rapid burial and early cementation in preservation of articulated skeletons in siliciclastic mudrocks. Further, this study demonstrates the capacity of blastozoan thecae to record evidence for subtle and complex taphonomic changes that are important to proper interpretation of sedimentary and biotic patterns.

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