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DIPLOPORITE (ECHINODERMATA, BLASTOZOA) THECAL ATTACHMENT STRUCTURES FROM THE SILURIAN OF SOUTHEASTERN INDIANA

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ABSTRACT—Taxonomic descriptions of diploporites from the middle Silurian of eastern Laurentia have focused nearly entirely on thecal plating, with minimal description or figuring of attachment structures. A recently discovered hardground surface within the Wenlock-age (Sheinwoodian) Massie Formation that is encrusted by numerous well-preserved pelmatozoan holdfasts, including structures identifiable as diploporite thecal attachments, provides an opportunity to document the morphology of these rarely described structures. Moderately thin-walled structures with a parabolic, depressed central area composed of seven distinct marginal plates with prominent pores appear to represent thecal attachments of the broad-based trematocystinid holocystitid *Paulicystis*. Thick-walled, steep-sided structures composed of five to seven fused or partially fused plates with less prominent pores, a deep stelar depression, and radiating canals appear to represent thecal attachments of undetermined, possibly holocystinid or pentacystinid holocystitids. All diploporite holdfasts are cemented to fine-grained, well-sorted skeletal substrates on elevated crests of the hardground surface, but are not found on microbioherms.

INTRODUCTION

DIPLOPORITE "CYSTOIDS" (Echinodermata, Blastozoa) are relatively rare in the Silurian of North America, where non-gomphocystitid diploporites are restricted exclusively to the Wenlock age *Holocystites* fauna of the Cincinnati Arch and upper midwestern regions (Paul, 1971; Frest et al., 1999, 2011). Consequently, the *Holocystites* fauna has attracted considerable attention, resulting in a number of detailed paleobiologic and taxonomic studies, dating back to the 1860s (e.g., Hall, 1861, 1864, 1868; Winchell and Marcy, 1865), that document the occurrence and evolution of an unexpectedly diverse and successful blastozoan fauna during the rise of camerate crinoids in Laurentia (Witzke et al., 1979; Frest et al., 1999). These studies were recently synthesized and revised in an extensive systematic treatment by Frest et al. (2011).

While the exhaustive monographic work of Frest et al. (2011) represents the culmination of over a century of research and serves as an unparalleled data source on the Silurian diploporites of Laurentia, few details on the morphology of attachment structures were included. Holdfast descriptions are restricted to brief characterizations of overall thecal shape (i.e., cylindrical thecae with narrow bases vs. globular thecae with large bases) and documentation of isolated skeletal substrates (e.g., cephalopod molds, bryozoan zoaria) to which thecae have been found attached (i.e., Frest et al., 2011, table 5); no descriptions of holdfast plating or appearance are given. It is stated that thecae as well as isolated holdfasts were discovered attached to hardground surfaces or biohermal masses, but none of these specimens were figured, described, or given museum repository numbers (Frest et al., 2011, p. 20, 24).

The absence of holdfast descriptions in this and other studies (see Gil Cid and Domínquez-Alonso, 2000 for an exception) likely reflects the nature of diploporite taxonomy, as traditional classification schemes are based nearly exclusively on oral plating and dipore morphology; isolated attachment structures can rarely be identified to low taxonomic levels because several taxa may have similar aboral morphologies and individuals of a single species may alter their aboral regions in response to different substrates (e.g., Gil Cid and García Rincón, 2012). Nevertheless, an understanding of holdfasts has the potential to provide much information on the paleoautecology and paleoenvironmental preferences of diploporites as well as the paleosynecology of benthic communities of which they are a part. Paul (1988) discussed the general lack of knowledge of the attachment habits of diploporites and other primitive echinoderms and despite research by Gil Cid and Domínguez-Alonso (2000) and Frest et al. (1999, 2011) there remains a paucity of data on these structures. In fact, criteria for identification of diploporite holdfasts in such settings are critical for paleoecological analyses of environments where intact thecae are rare or absent and, consequently, diploporites may be excluded from or underestimated in faunal lists or abundance calculations. Hence, the objective of this study is to describe isolated diploporite attachment structures attached to a hardground in the Silurian Massie Formation of Indiana, United States. It is hoped that this description will lead to discovery and recognition of similar structures in other settings and provide a clearer understanding of diploporite paleobiology and ecology.

LOCALITY AND STRATIGRAPHIC SETTING

A hardground surface within the middle Silurian (Wenlock, Sheinwoodian) Massie Formation (sensu Brett et al., 2012) is well exposed at the north end of the New Point Stone Company quarry, ~1 km east of Napoleon, Ripley County, southeastern Indiana (N39°12′31.39″, W85°18′53.74″; Figs. 1, 2). This site is renowned for producing many of the diploporite specimens used in studies of the *Holocystites* fauna (Paul, 1971) as well as the youngest eocrinoid (Frest, 2005), which have been recovered from the Lewisburg and lower Massie Formations (Fig. 2; Frest et al., 1999, 2011). The studied hardground surface has historically been recognized as the contact between the "middle carbonate" and "upper shale" members of the Osgood Formation (Foerste, 1897; Osgood Member of the Salamonie Dolomite, Pinsak and Shaver, 1964; Fig. 2); however, the lithostratigraphy of the Telychian–Sheinwoodian in this region has recently received a long-needed terminological revision (Brett et al., 2012). As currently defined, this surface represents the contact between the basal carbonate and overlying mudstone

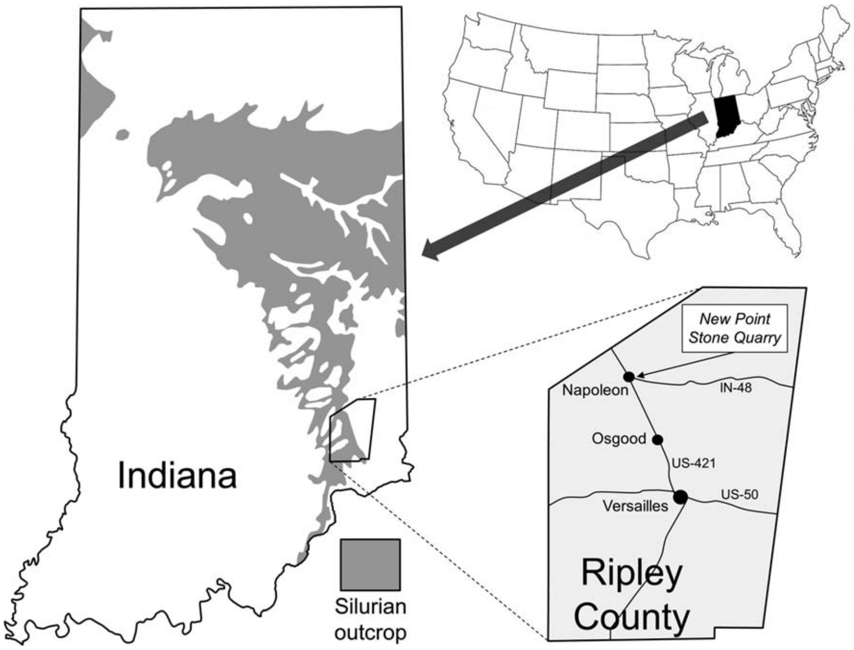

FIGURE 1—Locality of New Point Stone quarry just east of Napoleon, southeastern Indiana.

lithofacies of the Massie Formation, a lithostratigraphic term originally restricted to Ohio (Foerste, 1929, non 1931) that has been re-defined and extended into Indiana (Brett et al., 2012). The remainder of the underlying dense carbonate lithofacies (the majority of the former "middle Osgood carbonate") falls within the Lewisburg Formation (Figs. 2, 3).

Representing a major (third-order) flooding surface that is easily recognized in outcrop (Fig. 3.1), this hardground developed as a result of synsedimentary lithification during a period of rapid sea-level rise and consequent sediment starvation. This hardground was an excellent substrate for organisms that favor such stable, low turbidity conditions (see Brett, 1995), leading to the growth of bryozoan-dominated microbioherms (Archer and Feldman, 1986; Fig. 3.1) and establishment of a diverse and abundant assemblage of pelmatozoan echinoderms. The hardground surface is undulatory and irregular, seemingly reflecting enhancement of pre-omission burrows and scouring by storms (Fig. 3.2). A study focusing on the paleoecology of echinoderm attachment structures on this hardground is in progress and a more detailed discussion will be presented in a forthcoming paper. It is sufficient for the purposes of this short report simply to state that all attachment structures attributable to diploporites are directly cemented to the hardground surface and are only present on fine-grained, well-sorted, winnowed substrates associated with the slightly elevated portions of the hardground. No diploporite thecal attachments have been found on microbioherms or in the coarser, more poorly sorted lower areas of the hardground at this locality. Further, intact thecae are very rare at this horizon (though they are quite common in the lower portion of the overlying mudstone). Where present, partially articulated thecae, mostly belonging to the speciose and common genus *Holocystites* Hall, 1864, are always found in the topographic lows of the hardground and do not occur directly alongside cemented attachment structures. It is presumed that these specimens represent individuals that were displaced from their site of permanent attachment during storm events and rapidly buried in nearby lows. Alternatively or additionally, species that did not remain permanently attached as adults, such as *H. scutellatus* Hall, 1864, may have occupied the lower levels in between sites colonized by permanently attached taxa.

SYSTEMATIC PALEONTOLOGY

Higher classification of diploporites here follows Paul (1973), with superfamilial and lower classification following Frest et al. (2011). Interestingly, in these classification systems, no orders are formally recognized because each order would contain only a single superfamily (Frest et al., 2011, p. 58); hence, the diagnoses for superfamilies encompass those for orders. Although erection of ordinal rank taxonomic groups has been proposed (Broadhead, 1980), they are not commonly used in diploporite systematics and are not used here.

Figured specimens are reposited at the Cincinnati Museum Center, Cincinnati, Ohio, U.S.A. Specimens were cut out of the hardground using a handheld, diamond-tipped saw, removing the attachment structure, the immediately underlying substrate, and a few centimeters of surrounding rock. Whenever possible, however, specimens were not removed from the hardground surface in order to preserve spatial relationships valuable for future paleoecological research. Hence, descriptions are generally based on analysis of multiple specimens, but only the most exemplary were removed and reposited.

Subphylum BLASTOZOA Sprinkle, 1973
Class DIPLOPORITA Müller, 1854
Superfamily SPHAERONITIDA Neumayr, 1889
Family HOLOCYSTITIDAE Miller, 1889
Subfamily TREMATOCYSTINAE Frest and Strimple *in* Frest et al., 2011
Genus PAULICYSTIS Frest and Strimple *in* Frest et al., 2011

Type species.—*Paulicystis densus* Frest and Strimple *in* Frest et al., 2011.

Diagnosis.—A trematocystinid with a globular theca composed of numerous circlets, each comprising 20 ossicles or more if complete. Thecal plates are of one generation and are slightly

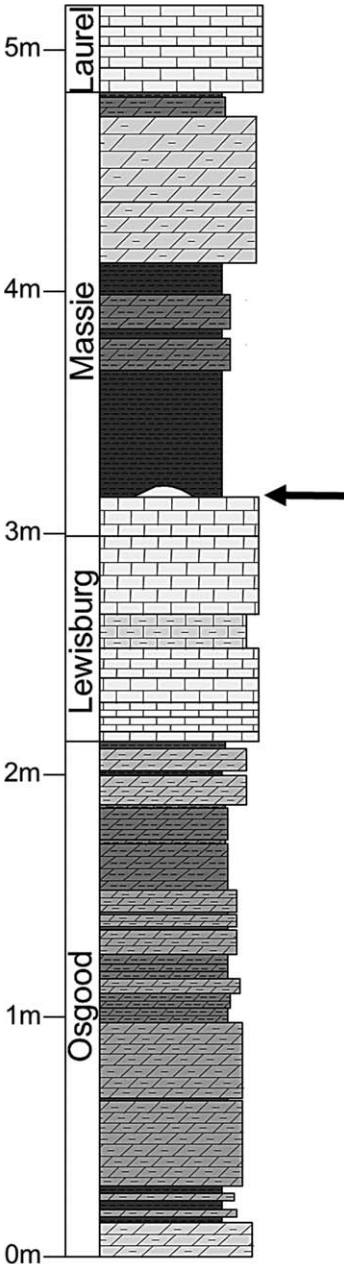

FIGURE 2—Stratigraphic column of a portion of the strata exposed at the Napoleon quarry with formation-scale units labeled and microbiohermal hardground marked by the arrow. Note that the Brassfield Formation, underlying the Osgood Formation, is not depicted, nor is the full thickness of the Laurel Formation.

swollen with impressed sutures. Brachiolar facets are large, irregularly elongate, elliptical, and extend outward onto as many as two adjacent thecal circlets. The gonopore is located in FA1. The attachment area is large, reaching three-quarters or more of the maximum thecal diameter, and is composed of fused plates (Frest et al., 2011).

Remarks.—The large attachment area of *Paulicystis* is used as a diagnostic feature of this genus; however, a detailed description of the aboral region was not provided (Frest et al., 2011, p. 83). Moreover, the specimens described were cemented to isolated skeletal substrates and not a laterally continuous hardground surface. The material described herein allows documentation of *Paulicystis* aboral thecal attachment morphology that supplements the description given by Frest et al. (2011).

PAULICYSTIS species indeterminate

Figure 4

Description.—Discoidal attachment structure, oval to very slightly lobate in outline (~2 cm × 3.5 cm), comprising an elevated marginal wall surrounding a large, central, parabolic depression. Marginal wall thin (less than one-eighth diameter of central depression), ridged, steeply sided in vertical profile. Outermost wall margin taller, sloping inwards toward interior of structure. Depressed interior composed of seven large, equally sized, regularly arranged, rectangular to trapezoidal plates. Plates somewhat wedge-like in that they are narrower in interior and expand toward margin of structure. Margin-forming plates concave-upward, strongly so near margin but becoming tangentially less steeply sloping toward interior of structure. Sharp corners and obvious plate contacts are visible in interior but become indistinct near the marginal wall, possibly indicating overgrowth of portions of the outer margin by secondary stereom. Seven marginal plates surround one large, roughly heptagonal, flat-lying to gently concave-upward central plate. All plates pierced by numerous pores, which are more prominent in the central depression and slightly less visible but nevertheless present on marginal wall. Imperfect

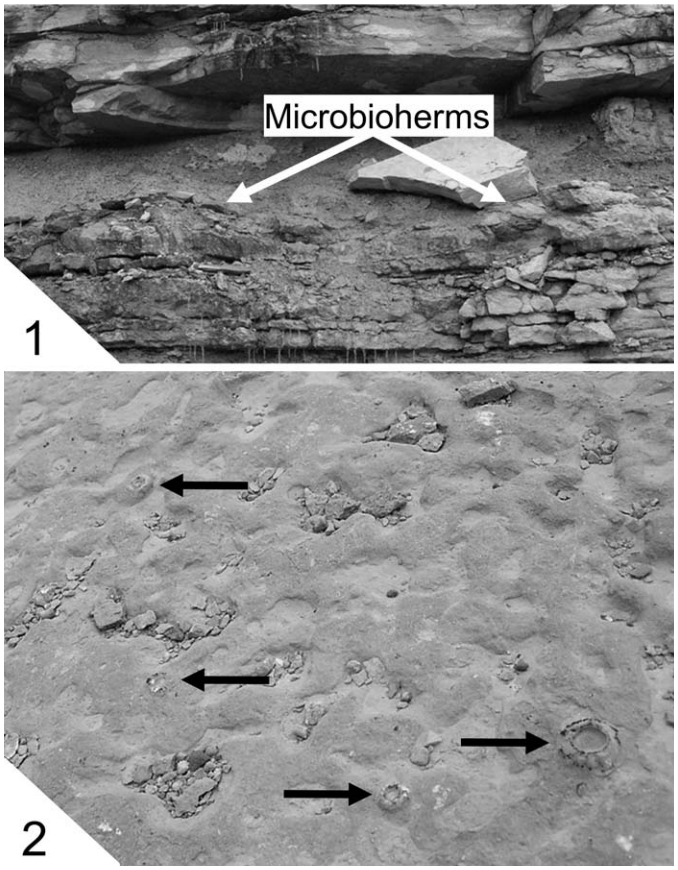

FIGURE 3—Field photographs of microbiohermal hardground. *1*, cross-sectional view of microbioherms at the contact between the basal Massie carbonate and overlying Massie mudstone facies; approximately 2.25 m of vertical section shown; *2*, field photograph of hardground surface with several in situ discoidal attachments marked by arrows; note the irregular texture formed by firmground *Thalassinoides* Ehrenberg, 1944 burrows; field of view is approximately 0.35 m wide by 0.3 m tall.

preservation inhibits examination of the microstructural details of these pore structures.

The figured specimen (CMC IP 69526) represents the most well-preserved attachment structure on the hardground and constitutes the only specimen discovered to date that clearly displays all seven marginal plates in the structure interior. Pyrite overgrowth partially obscures fine plate details on one hemisphere of the specimen (the left half of Fig. 4), though pyrite crystallization enhances visibility of plate contacts in this region. This specimen was recovered from a slightly elevated hummock crest on the moderately irregular hardground surface. The local substrate consisted of a fine-grained, well-sorted skeletal grainstone composed primarily of comminuted echinoderm material to which the thecal attachment was cemented.

Material.—CMC IP 69526, 69530, 70214–70216.

Remarks.—Although most of the diploporite holdfasts at this site display partially fused component plates and/or evidence for secondary stereomic overgrowth (see below), the large size of this structure makes it unlikely that this represents an immature individual that did not yet fully overgrow the separate plates. The fairly wide diameter of this structure limits potential cystoids to those characterized by broad thecal bases. The size and shape of aboral thecal plates and, perhaps more importantly, large holdfast size agree well with the morphology of the trematocystinid *Paulicystis* (Frest et al., 2011, pls. 10, 11), the basal areas of which were also figured. Although the specimens photographed by Frest et al. (2011) may have more than seven plates comprising their basal surface, it is difficult to tell with certainty exactly how many plates are present, and aboral thecal plating in this genus may be somewhat variable. *Paulicystis* also appears more circular in Frest et al. (2011) than the ovoid structure described here. This variation may be explained by differences in substrata: the photographed thecae in Frest et al. (2011) were found attached to isolated skeletal substrates in an overall soft mud-dominated environment rather than a laterally continuous hardground surface. Perhaps the morphologies of diploporite thecal attachment structures exhibit some plasticity that was dependent on the character of substrate.

Detailed documentation of diploporite occurrences throughout the middle Silurian of southeastern Indiana revealed that thecae of *Paulicystis* are characteristic of the clastic mudstone facies of the Massie Formation (Frest et al., 2011, figs. 8, 10) and are not common or have not yet been discovered in the basal carbonate interval of the Massie Formation. Diploporite taxa historically reported from the upper portion of the former "middle Osgood carbonate" lacked permanent attachments (Paul, 1971; Frest et al., 2011), in contrast to the permanently cemented *Paulicystis*. The established biozonation, however, is based primarily on the fauna found in the upper Lewisburg Formation and sub-hardground Massie Formation, an interval characterized by pelmatozoan grainstones that were likely characterized by shifting bioclastic sediments poorly suited for permanently attached diploporites. The hardground at the major flooding surface between the basal carbonate and mudstone of the Massie Formation, however, appears to have faunal affinities aligned more closely with the overlying highstand mudstone facies than with the underlying transgressive grainstone facies. Hence, taxa typical of the diverse diploporite assemblage found at the base of the former "upper Osgood shale," including *Paulicystis*, may have been present at the surface containing the holdfasts described here but not preserved as identifiable thecae owing to slow sedimentation, which allowed exposed thecae to undergo complete skeletal disarticulation and plate diminution.

FIGURE *4*—Broad, thin-walled attachment structure attributable to *Paulicystis* sp. indet. (CMC IP 69526) clearly showing central plate surrounded by seven bordering plates, all pierced by pores and set within inner parabolic, depressed area, ×3.

Family HOLOCYSTITIDAE Miller, 1889
Subfamily, genus, and species indeterminate
Figure 5

Description.—Discoidal attachment structures, circular to very slightly lobate in outline. Marginal wall thick, sharply set off from steeply depressed, centrally located interior cavity, which is circular in outline. The deep cavity is floored by pore-bearing skeletal material and does not extend to the substrate (Fig. 5.1), although the floor can be breached by weathering to expose underlying sediment (Fig. 5.4). No sign of a distinct central plate is present in these attachments, but the base of the platform-like central cavity does not appear massive (Fig. 5.1). Walls are moderately steep to vertical in profile, flaring outward slightly at base. Certain particularly high-walled structures display upward-tapering (Fig. 5.2). In some weathered specimens, the exterior portion of the margin is taller than the interior portion, giving the appearance of two concentric rings; this can be highlighted by pyritization of the interior ring (Fig. 5.2). Articular surface is flat, with closely spaced, radiating, branching canals similar to canaliculi previously documented in crinoid columnals (Moore et al., 1968; Franzén-Bengtson, 1983; Fig. 5.3). These canals appear to extend throughout the entirety of attachment structures rather than being surficial features. Pores are present on both the interior and exterior of attachments but are more clearly visible and possibly more numerous on interior of central cavity. Attachment structures are composed of between five and seven plates, most commonly six. Plates are roughly rectangular in vertical view, with height greater than width in all but the smallest and broadest specimens. In shorter specimens, plates are

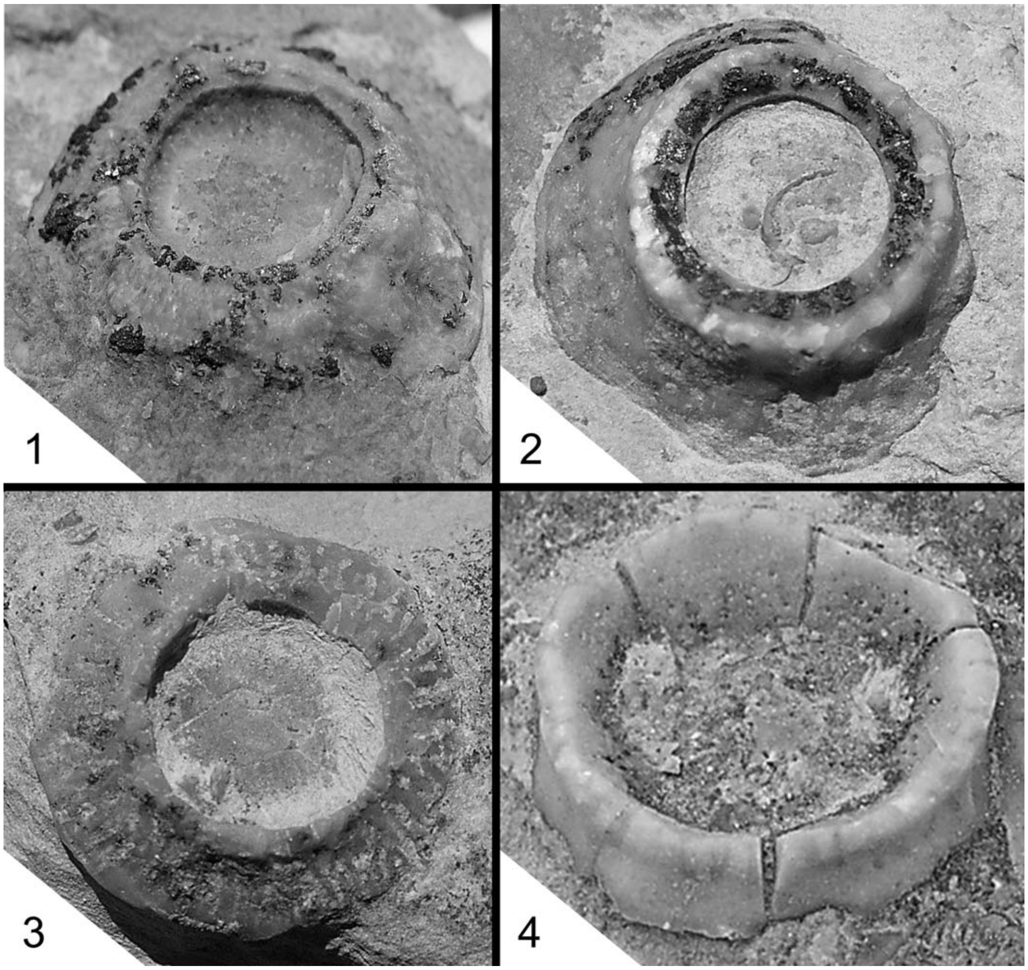

FIGURE 5—Thick-walled, partially sutured attachment structures of ambiguous holocystitid affinities. *1*, oblique view of attachment with massive, wrinkled appearance, no visible plate boundaries, a non-pyritized but depressed inner margin, and a deep, pore-bearing inter-stelar cavity (CMC IP 69527), also figured in *Figure 3.2*, lower right, ×3.5; *2*, well-preserved attachment with a massive, smooth appearance, no obvious plate boundaries or pores, a prominently pyritized inner margin, a deep but sediment-filled inter-stelar cavity, and an upward-tapering margin (CMC IP 69528), ×3.5; *3*, weathered specimen with a secondarily thinned but upward-tapering marginal wall showing moderately visible plate sutures and prominent canal structures and pores (CMC IP 70219), ×4; *4*, very weathered attachment with a smooth, high, vertical marginal wall, seven component plates, obvious plate contacts and pores, and a wide inter-stelar cavity that has been breached to expose underlying sediment (specimen uncollected), ×3.5.

tangentially concave-upward, being nearly vertical toward the margin and approaching horizontality toward interior. In taller specimens, plates are vertical to very slightly outward-flared. In all specimens, plates are U-shaped in plan view, being convex toward the exterior of structure and concave around the central cavity. Nearly all structures studied here display indistinct plate sutures indicating stereomic overgrowth; in some specimens, this undifferentiated stereom has a wrinkled appearance (Fig. 5.1). In spite of the partial fusion of component ossicles, close inspection results in recognition of at least some plate contacts. The most well-preserved specimens have the appearance of an undifferentiated, solid structure (Fig. 5.1, 5.2), but weathering increasingly reveals the radiating canal structures, plate contacts, and pores (Fig. 5.3, 5.4).

As with the previously described thecal attachment, specimens are found only on fine-grained, well-sorted skeletal grainstones on minor crests of the undulating hardground and are relatively abundant on the Napoleon hardground. Large, isolated thecal plates and rare partially articulated thecae have been recovered from this surface, but only from the poorly sorted, coarse, slightly muddier sediments of hardground troughs and never in direct association with discoidal thecal attachments. Macrocrystalline pyrite overgrowths are common on the exterior of many specimens, present as seemingly randomly distributed crusts and isolated crystals as well as preferentially pyritized interior "rings" of articular surfaces (Fig. 5.2) and plate contacts.

Material.—CMC IP 69527–69528, 70217–70229.

Remarks.—These structures appear quite similar to discoidal crinoidal or long-stemmed blastozoan holdfasts, and justification of the interpretation of these discoidal structures as diploporite thecal attachments is necessary. Narrow lumina are characteristic of nearly all simple, discoidal terminal holdfasts in Silurian crinoids and coronoids (Brett, 1981, 1984), in contrast to the wide, pore-bearing central cavities of these structures. The pore-bearing platform at base of the central cavity is also a feature that is largely absent in crinoid holdfasts, which typically are either floored by a septate basal discoid plate (as in *Cleiocrinus* Billings, 1857), floored by unplated, undifferentiated stereom with a smooth, massive appearance and more lobate margins (as in *Anomalocrinus* Meek and Worthen, 1868), or, rarely, lumina that expose the underlying substrate. Rather than being interpreted as holdfast lumina, these central cavities are best interpreted as the viscera-filled interior of a wide stele (sensu Brett, 1981) and basal theca. Many crinoid discoidal terminal holdfasts also display well developed columnal-articular surfaces high on the attachment structure, either set in a shallow depression or on the uppermost surface and not penetrating into the holdfast, and frequently are preserved with distal columnals articulated to the holdfast. The specimens described here do not display well developed columnal articulations, are never found with attached columnals, and have articular surfaces around the margins of the structure, in an arrangement suggestive of articulation to an upward-widening theca rather than a slender column.

Definitive generic identification of such thecal attachments is unlikely given the similarity of thecal attachments in nearly all basally attached diploporites; however, the difference in size and morphology between these structures and those described above strongly suggests that these represent a distinct cystoid taxon or taxa. In fact, considerable variability within this thecal attachment morphotype can be detected: some discoids are characterized by very thick walls, up to twice the thickness of the inter-stelar cavity diameter, whereas others have walls equal to or less than the thickness of the inter-stelar cavity. It is unclear whether this is an intraspecific (ontogenetic, ecophenotypic) or species- or higher-level taxonomic difference. The fact that thin- and thick-walled morphotypes are often the same size suggests that this is unlikely to be an ontogenetic variation, however. It is most likely that several diploporite genera produced thecal attachments characterized by the general morphology described in this section.

Attributing this attachment structure to one or more diploporite with certainty is further hindered by poor preservation of dipore morphology, although these certainly belong to holocystitids. The average size and number of plates in these attachments agree well with the basal aboral morphology of the pentacystinid holocystitids *Pentacystis* Paul, 1971 and *Osgoodicystis* sp. aff. *O. wykoffi* Frest and Strimple, 2011 *in* Frest et al. (2011; pls. 12, 14) as well as the trematocystinid holocystitid *Trematocystis* Miller, 1878. Alternatively, these structures may belong to a broad-based holocystinid holocystitid such as *Holocystites spangleri* Miller, 1891, though the attachment bases of *Holocystites* spp. tend to be narrower than the specimens described here. Reported occurrences of certain candidates may constrain identities further. As with the possible *Paulicystis* attachment, diploporite biostratigraphy (Frest et al., 1977, 2011) agrees with *Pentacystis* sp. and *Trematocystis magniporatus* Frest and Strimple, 2011 as potential holdfast producers if the sediment-starved upper surface of the basal Massie carbonate is treated as an ecological extension of the Massie mudstone facies. Other species of *Trematocystis* have been recovered only from the upper decimeter of the Osgood Formation, and *Osgoodicystis wykoffi* and *Holocystites spangleri* are reported only from the lower decimeter of the Lewisburg Formation (Frest et al., 2011), making them unlikely candidates. As stated above, though, it is possible, if not likely, that more than one taxon is represented by this attachment structure morphotype; further, the generic identity or identities of diploporites affiliated with these holdfasts may be yet unknown owing to the slow sedimentation and paucity of articulated thecae associated with the Massie hardground surface.

The exact function of the canaliculi-like structures is unclear. Franzén-Bengtson (1983) asserted that similar features on large crinoid columnals assisted with direct nutrient uptake, useful in supporting large-bodied crinoids. It can be postulated that canals functioning to enhance nutrient (and/or oxygen) intake would be useful in the sediment-starved setting represented by the Napoleon hardground, as currents in such an environment were likely moderate at best. However, pores occurring at only a few millimeters above the sediment-water interface would be subjected to minimal currents, making enhanced nutrient uptake unlikely. It may be more logical to interpret these canals as sensory structures, used to detect chemical or other fluctuations in bottom water. Nearly identical dendritic canal structures exist on the terminal holdfasts of *Podolithus* Sardeson, 1908, *Anomalocrinus*, and *Cleiocrinus*, as documented by Brett and Liddell (1978), as well as "holdfast type 1A" of Lewis (1982). A sensory function for such features in these Ordovician crinoids is plausible.

DISCUSSION

The occurrence of diploporite thecal attachment structures on a laterally continuous hardground surface contrasts markedly with diploporite substrates reported from the Ordovician of Spain (Chauvel, 1941; Gutiérrez-Marco and Colmenar, 2011; Gil Cid and García Rincón, 2012), Norway (Paul and Bockelie, 1983; Bockelie, 1984), and Britain (Paul, 1973; Paul and Bockelie, 1983), as well as the Devonian of Kentucky, United States (Sumrall et al., 2009). In these faunas, modes of attachment include: 1) aboral projections, such as those in *Calix* Rouault, 1851 (see Gutiérrez-Marco and Colmenar, 2011, pl. 1, figs. 2, 3), developed from modification of the lower portion of the theca and adapted for penetration into muds and other softground substrates; 2) tiny discoidal holdfasts adapted for temporary and/or loose attachment to skeletal elements, as in some *Tristomiocystis* Sumrall et al., 2009 (fig. 4.10); 3) no recognizable well-mineralized attachment structures, with the theca resting directly upon the substrate or attached epidermally, as in most *Sphaeronites* Hisinger, 1828 (Paul and Bockelie, 1984) and *Tristomiocystis* (Sumrall et al., 2009); and 4) permanent aboral cementation to discrete macrofossils, as observed in many Ordovician and Silurian diploporites (e.g., Paul, 1973; Frest et al., 1999, 2011; Gil Cid and García-Rincón, 2012). This last mode of attachment, characterized by modification of the aboral theca to encrust and overgrow isolated hard substrates, is particularly prevalent in soft or shifting substrates containing scattered skeletal material, and allowed diploporite taxa to survive in predominantly muddy environments (see Gil Cid and Domínquez-Alonso, 2000). In these cases, the aboral pole of diploporites is adapted for attachment to hard substrata, and can be modified in response to the size and shape of the specific substrate; this mode of attachment has been documented in the Massie mudstone facies overlying the encrusted hardground studied here (Frest et al., 1999, 2011)—this is where *Paulicystis* and many of the candidates for producers of the other holdfast morphotype are typically found. It is interesting to note that diploporite taxa at this site could apparently modify the morphology of their attachment structures in order to attach to both a laterally extensive carbonate hardground and isolated fossil elements in an otherwise soft, muddy environment. We suggest that this plasticity in response to substrate contributed to the success of middle Silurian diploporites, at least at this locality.

The *Holocystites* fauna is not rooted in Laurentian stock and instead represents an invasive fauna derived from Ordovician Baltican (Paul, 1971) and peri-Gondwanan (e.g., Lefebvre and Fatka, 2003) lineages. One might postulate that the availability of hard substrates played a major role in controlling migration of this fauna into Laurentia, as this variable has recently been recognized as significant in controlling the distribution of echinoderms on evolutionary timescales (Guensberg and Sprinkle, 1992; Sprinkle and Guensberg, 1995; Lefebvre and Fatka, 2003; Dornbos, 2006; Zamora et al., 2010); however, 1) because many taxa occur cemented directly to the hardground surface and also attached to fossils in overlying muddy facies, and 2) because the first invasive diploporites in eastern Laurentia occur in softground facies of the upper Osgood and lower Lewisburg Formations, it seems more likely that the occurrence of hardground substrates was not a major factor in controlling the migration of the *Holocystites* fauna. Recent work on the evolution of hard substrate occupation by pelmatozoans has shown that taxa, including diploporites, that attached to isolated skeletal substrates in softgrounds were "preadapted" for encrustation of hardgrounds (Guensberg and Sprinkle, 1992; Zamora et al., 2010); therefore, it is quite possible that this diploporite fauna, initially established on shelly but unlithified substrates, rapidly occupied and thrived on hardground substrates, leading to increased abundance, diversity, and/or morphologic variability. Hence, the occurrence of hardgrounds likely contributed to the success of the *Holocystites* fauna and associated invasive echinoderms, but did not drive their initial invasion.

Although work is ongoing, we submit that climate, rather than the occurrence of hardground substrates, was the most significant influence on the biogeographic occurrence of these diploporites. The invasion of these blastozoan elements coincides with an invasion of Old World-derived brachiopods and other taxa (e.g., Boucot, 1999; Frest et al., 1999) in the immediate aftermath of the highest global sea-level of the Silurian (Ross and Ross, 1996; Loydell, 1998, 2007; Johnson, 2006) but before a short-lived Gondwanan glaciation (Lehnert et al., 2010). Consequently, this major highstand would have opened up biogeographic pathways into Laurentia (Frest et al., 1999), and the initial stages of the subsequent glaciation established cool currents that would have allowed cold water-adapted taxa from higher latitudes to migrate northward in the brief interval before sealevel fell significantly enough to close off the corridor from peri-Gondwana to Laurentia. Further, although hardground surfaces can be traced throughout the Appalachian Foreland Basin (e.g., McLaughlin et al., 2008; Brett et al., 2012), the *Holocystites* fauna is restricted to topographic highs, suggesting that productivity and/or oxygenation also played significant roles in controlling the distribution of diploporites in the Silurian of eastern North America.

CONCLUSIONS

Thecal attachment structures attributable to holocystitid diploporites are relatively common encrusters of a hardground surface within the middle Silurian (Wenlock, Sheinwoodian) Massie Formation of southeastern Indiana, United States. Two morphologies can be recognized. A larger, oblong morphotype that is composed of seven pore-bearing plates surrounding a central heptagonal pore-bearing plate represents the trematocystinid *Paulicystis*, and a smaller, circular morphotype composed of five to seven pore-bearing plates with branching canal structures, surrounding an undifferentiated floor set in a steeply depressed central area, represent probable holocystinids or pentacystinids that cannot be identified to generic level. Pores and canal structures likely had a sensory function. These structures are directly cemented to fine-grained, well-sorted grainstones on slightly elevated hummocks. The occurrence of diploporite holdfasts on a laterally continuous carbonate surface rather than on isolated skeletal elements stands in contrast to most reports of diploporite substrates. The taxa associated with these thecal attachment structures are also reported locally from soft substrate deposits; hence, the ability to modify the aboral area in response to differing substrate conditions may be related to the success of diploporites in these units.

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