Taphonomy of diploporite (Echinodermata) holdfasts from a Silurian hardground, southeastern Indiana, United States: palaeoecologic and stratigraphic significance

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Abstract – A microbioherm-bearing hardground within the middle Silurian (Wenlock) Massie Formation near Napoleon, southeastern Indiana, United States is encrusted by the attachment structures of numerous pelmatozoan echinoderms. Among the most common of these holdfasts are multi-plated discoidal structures representing the thecal attachments of diploporite 'cystoids'. This large population of holdfasts permits the first detailed taphonomic and palaeoecologic study of hardground diploporite attachments, allowing for increased morphological understanding of these rarely studied structures and facilitating identification of holdfasts in deposits where they might have been overlooked or misidentified. The biostratinomic sequence commences with detachment of thecae, followed by weathering of isolated discoidal holdfasts to bring out radiating canal structures and plate sutures, eventually leading to removal of the interior floor to expose the underlying substrate. Continued exposure can result in separation of component holdfast plates, though cementation to the substrate prevents scattering of plates. Diagenetic precipitation of pyrite occurred after burial; the large size of crystals suggests late diagenesis, perhaps seeded by early diagenetic pyrite crystallites produced by decay of ligamentary tissue. Extrinsic taphonomic factors include overgrowth of holdfasts by laminar stenolaemate bryozoans and other echinoderm attachment structures. Diploporite holdfasts are not bored and are absent on microbioherms. Taphonomic data indicate the time-averaged nature of this hardground and its diploporite assemblage and permit prediction of similar occurrences at major flooding surfaces.

Keywords: Diploporita, attachment structures, encrustation, Wenlock, *Holocystites* fauna.

1. Introduction

Diploporite 'cystoids' are a clade of early to middle Palaeozoic (Ordovician–Devonian) blastozoan echinoderms characterized by dipore-based respiratory structures, globular thecae commonly with irregular plating, and a passive suspension-feeding sessile mode of life (Broadhead, 1980). Although many diploporites were free-living as adults, lying directly but loosely on the seafloor, others remained permanently affixed to hard substrates throughout life (e.g. Paul, 1971, 1973; Frest, Mikulic & Paul, 1977; Frest, Strimple & Paul, 2011). Consequently, attachment structures representing direct cementation to isolated skeletal substrates (e.g. shells), isolated lithified substrates (e.g. cobbles, exhumed concretions) and hardground surfaces have the potential to provide much insight into diploporite palaeobiology and palaeoecology, particularly in settings where articulated thecae are rare or absent (Thomka & Brett, in press). Indeed, given the propensity for rapid post-mortem disarticulation of diploporite thecae (Brett, Moffat & Taylor, 1997) and the relative robustness of many echinoderm attachment structures (Lewis, 1982), research focused on holdfasts may yield important ecological insights.

Hard substrates are commonly densely encrusted by pelmatozoan holdfasts (see Brett, 1988, 1991; Wilson & Palmer, 1992; Taylor & Wilson, 2003; McLaughlin, Brett & Wilson, 2008 among many others); however, multiple generations of encrusters can be preserved attached to a single surface. Although this time-averaging (Walker & Bambach, 1971) complicates ecological interpretations derived from direct observations, taphonomic data can be used to successfully differentiate attachment structures that were subjected to varying degrees of physical or biological alteration prior to burial (Brett & Liddell, 1978; Paul & Bockelie, 1983; Brett, Deline & McLaughlin, 2008). Hence, assessment of diploporite holdfast preservation can be critical for understanding short-term trends in substrate preferences, biotic interactions and time resolution in select Palaeozoic hard substrate environments.

A recently discovered carbonate hardground in the middle Silurian of southeastern Indiana, United States was encrusted by numerous attachment structures representing a variety of crinozoan and blastozoan echinoderms, including abundant diploporite thecal attachments (Thomka & Brett, in press). This surface presents a rare opportunity not only to document spatial and substrate relationships among diploporites, an area of research in which few studies have been published (see Gil Cid & Domínguez-Alonso, 2000 for an important exception), but also to record the signature
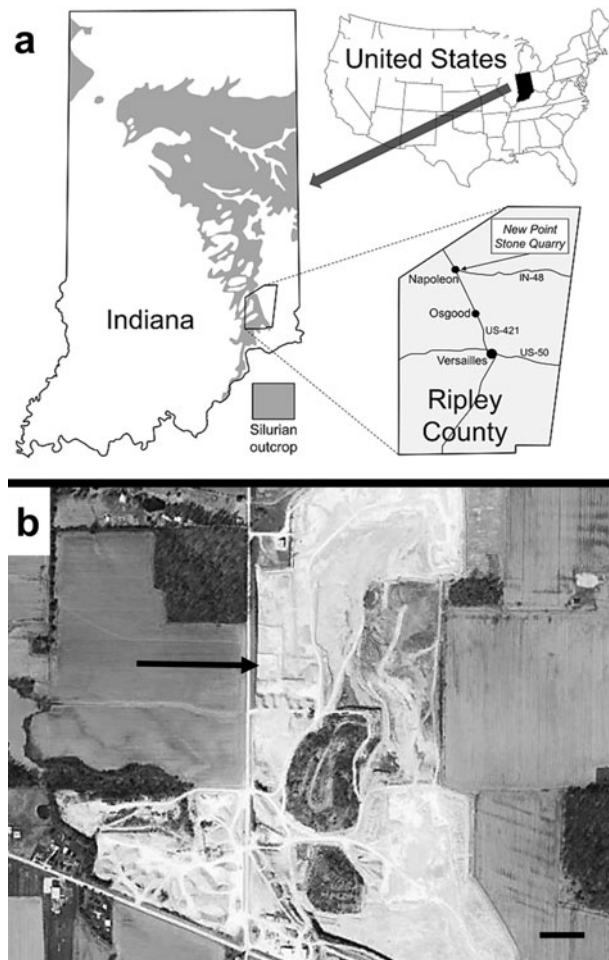
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Figure 1. Study site. (a) Location of study area approximately 1 km east of Napoleon in northern Ripley County, southeastern Indiana, east-central United States. Modified from Thomka & Brett (in press). (b) Aerial photograph of quarry, with holdfast-bearing hardground marked by the arrow. Scale bar is approximately 100 m.

of taphonomic processes on skeletal modules that have the highest chance of preservation and recognition in a group with an overall poor fossil record. In addition, reconstructing the taphonomic history of diploporite holdfasts has led to documentation of several biotic interactions between diploporites and associated biota that have significance for Silurian benthic palaeosynecology.

2. Locality and stratigraphic setting

The encrusted hardground serving as the basis of this study is exposed at the northern end of the New Point Stone Company quarry located approximately 1 km east of Napoleon in northern Ripley County, southeastern Indiana, east-central United States (Fig. 1). This is not an active portion of the quarry and has not historically been visited by fossil collectors or geological field trips. The surface was cleared of overburden, presumably by a bulldozer, and has served as a benched-off potential dump pile site. Fortunately, scrapes cre-

ated by quarrying machinery are readily recognizable and are easily distinguished from taphonomic features produced prior to sediment burial. Further, no evidence for skeletal disarticulation or significant dissolution occur from exposure of the surface to modern weathering.

Historically, much of the stratigraphy exposed at the Napoleon quarry was considered part of a single unit, the Osgood Formation (Foerste, 1897) or Osgood Member of the Salamonie Dolomite (Pinsak & Shaver, 1964). The horizon under study is identified in older literature as that separating the 'middle Osgood carbonate' from the 'upper Osgood shale' (e.g. Frest, Strimple & Paul, 2011; Fig. 2). In light of recent regional lithostratigraphic revisions (Kleffner et al. 2012; Brett et al. 2012), this surface is located at what is now considered the contact between the basal carbonate and overlying mudstone lithofacies of the Massie Formation (Silurian: Wenlock, Sheinwoodian; Fig. 2).

This contact represents a major flooding surface developed during an episode of rapid sea-level rise (McLaughlin et al. 2008; Brett et al. 2012). The net effects were a shut-off of clastic sedimentation and stasis of redox boundaries in the shallow subsurface, allowing cementation of the seafloor (e.g. Brett, 1995). Such flooding surfaces are consistent and predictable throughout the Northern Appalachian Basin (Brett, Goodman & LoDuca, 1990; Brett & Ray, 2005; McLaughlin, Brett & Wilson, 2008), and this specific surface is widely traceable and easily recognizable throughout the Cincinnati Arch region and Northern Appalachian Basin, where it is typically associated with small, biogenically produced build-ups (Brett, Goodman & LoDuca, 1990; McLaughlin et al. 2008; Brett et al. 2012). These microbioherms (sensu Archer & Feldman, 1986) are present at the Napoleon quarry and are encrusted, along with the planar hardground surface from which the microbioherms themselves emanate, by pelmatozoan attachment structures (Fig. 2). Although diploporite encrustation of microbioherms at this horizon has been reported by Frest, Strimple & Paul (2011), no diploporite thecal attachments have been discovered attached to microbioherm masses at the locality in this study (see Section 5.c below).

Lithologically, the encrusted surface is a skeletal packstone to grainstone composed primarily of comminuted echinoderm ossicles. This surface is immediately overlain by, and stands in stark contrast to, medium grey mudstones representing deposition during a sea-level highstand (Brett et al. 2012). The hardground is slightly undulatory owing to storm scouring prior to cementation (see also Palmer & Palmer, 1977). Slightly elevated crests are characterized by smaller and better sorted bioclastic particles and a total absence of clastic mud, whereas slightly depressed troughs are coarser, moderately to poorly sorted, and contain a minor proportion of mud. Diploporite attachments are cemented only to the crests of the hardground (Thomka & Brett, in press).
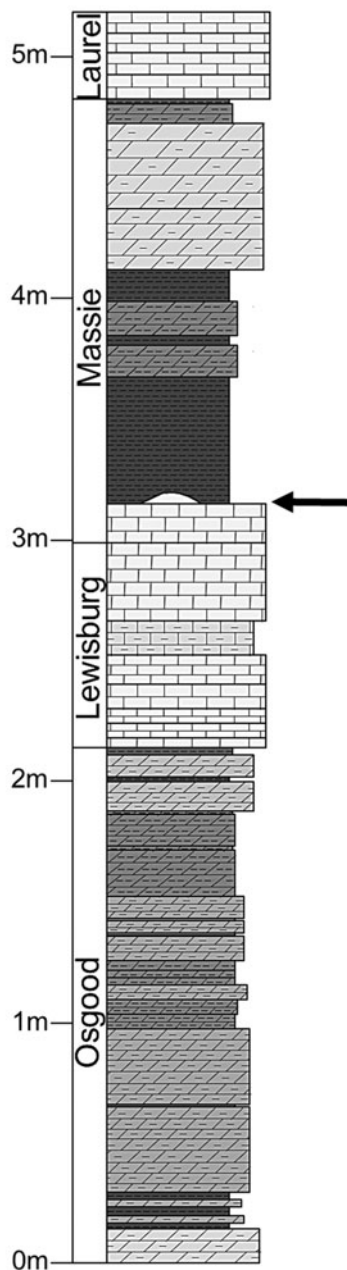
Figure 2. Stratigraphic column of a portion of strata exposed at the Napoleon quarry with formation-scale lithostratigraphic units labelled. The encrusted hardground is marked by the arrow. Note that the Brassfield Formation, underlying the Osgood Formation, is not depicted, nor is the full thickness of the Laurel Formation. Stratigraphic terminology follows Brett *et al.* (2012). From Thomka & Brett (in press).

3. Methods and materials

Attachment structures were studied in the field for state of completeness, nature and location of mineral overgrowths, relationships to other biogenic or physical structures, and presence and clarity of internal features. Critical specimens were removed from the hardground with a hand-held diamond-tipped saw and reposited at the Cincinnati Museum Center in Cincinnati, Ohio (repository numbers beginning with CMC are listed in appropriate figure captions). Many holdfasts, how-

ever, were left in place on the hardground to permit future studies. Holdfasts left in place were nevertheless inspected for taphonomic properties. Nearly all specimens displayed features well enough that they did not require extensive laboratory preparation or cleaning.

Work by Thomka & Brett (in press) showed that diploporite attachment structures from the Napoleon hardground are of two morphologies. Large, ovoid, relatively thin-walled structures composed of seven to eight pore-bearing plates surrounding a central heptagonal plate (Fig. 3a) have been attributed to the wide-based trematocystinid holocystitid *Paulicystis*. Smaller, circular, thick-walled structures composed of five to seven plates bearing pores and branching canals (Fig. 3b) were attributed to an undetermined diploporite, likely a pentacystinid or holocystinid holocystitid. Although *Paulicystis* holdfasts are less common than the smaller discoidal structures, sufficient numbers of specimens were discovered (over 60) to permit documentation of taphonomic patterns for both morphotypes.

4. Results

4.a. General considerations

Documentation of taphonomic features allowed recognition of a spectrum of preservational states that is demonstrably not the result of ontogenetic or ecophenotypic variation. Ecophenotypic variation can largely be excluded because all studied structures are present on the same local substrate conditions on a single hardground surface. Thus, although local substrate-controlled variability has been documented within other co-occurring pelmatozoan holdfasts, these differences reflected morphological responses to local conditions associated with hardground crests, hardground troughs and microbioherms, respectively (Thomka & Brett, 2013). In contrast, diploporite attachment structures were exclusively on hardground crests (Thomka & Brett, in press). Ontogenetic variability can also be excluded because specimens with the same taphonomic characteristics span a considerable size range and, conversely, specimens of the same size occur in a variety of taphonomic states. Secondary overgrowth of plate sutures in the smaller, ovoid holdfasts is not an ontogenetic signature of mature individuals: clarity of plate contacts is a taphonomic feature and not indicative of an immature individual that did not yet generate secondary stereom to overgrow plate boundaries (Thomka & Brett, in press).

Taphonomic patterns are detailed below for both of the diploporite attachment structure morphotypes. Taphonomic processes are divided into two categories: biostratinomic processes refer to the physical, biological and chemical events that occurred during the interval in between the death of the organisms and final burial (in contrast to the more restricted definition of this term originally established by Seilacher, 1973); diagenetic processes refer to all events that occurred in
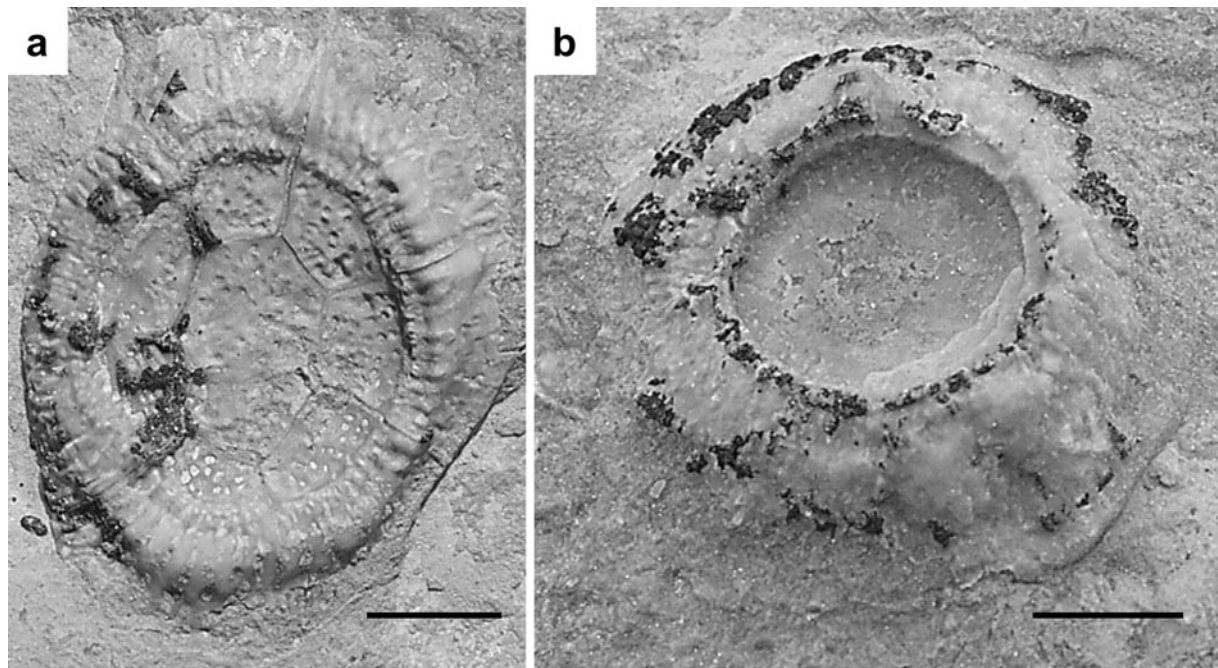
Figure 3. Well-preserved examples of the two diploporite attachment structure morphotypes present on the Napoleon hardground. (a) Thin-walled holdfast composed of seven marginal wall plates surrounding a central heptagonal plate, all pore-bearing (CMC IP 69526). This structure has been attributed to *Paulicystis*. (b) Thick-walled, multi-plated holdfast with radiating canals, pores and stereomic overgrowth of plate contacts (CMC IP 69527). The generic identity of these structures is currently unknown. Scale bars are 0.5 cm.

between the final burial of an organism and its discovery as a fossil.

4.b. Biostratinomic disarticulation and degradation

None of the holdfasts on the hardground surface are attached to partial or complete thecae. This indicates that soon after death, the theca underwent rapid disarticulation and became detached from the aboral attachment structure, which was firmly cemented to the substrate. Rare partially articulated thecae were discovered on the hardground, but only in hardground troughs and never on the hardground crests where holdfasts are found; further, most identifiable thecae are attributable to *Holocystites scutellatus*, which lacked a permanent attachment (Fig. 4). While the theca, composed of numerous small ossicles, underwent rapid and complete skeletal disarticulation, associated attachment structures, despite also comprising multiple ossicles, remained more intact, owing to their cementation to the substrate. Hence, following the rapid detachment of thecae, holdfasts were subjected to *in situ* degradation.

For *Paulicystis* attachment structures, well-preserved specimens, representing individuals that underwent detachment of the thecae followed shortly by final burial, are characterized by the presence of clearly visible plates in the depressed central area of the holdfast, as shown in Figure 3a. The majority of specimens have evidence of continued degradation during exposure such that only the marginal wall remains identifiable but the interior is indistinct or eroded away completely (Fig. 5). Evidently the thinness of the depressed interior of these attachment structures (i.e. the interior of the
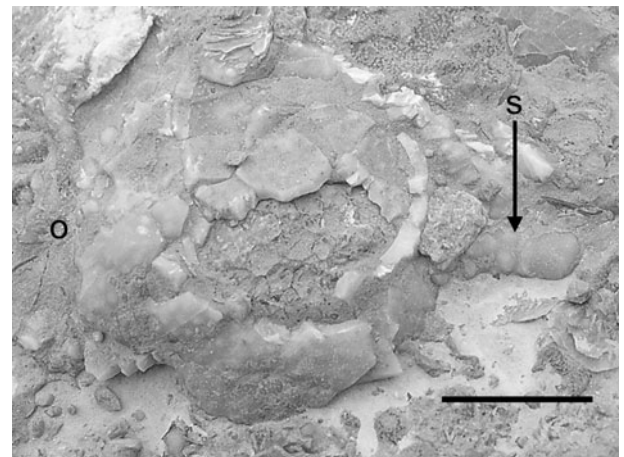

Figure 4. Partially articulated theca of *Holocystites scutellatus* in a hardground trough (specimen uncollected, currently on hardground). These diploporites lack permanent attachments and are not affiliated with the holdfasts analysed in this study. The stubby stele is marked by the 's' and the oral area is marked by the 'o'. Scale bar is 1 cm.

stele *sensu* Brett, 1981, 1984) made this portion particularly prone to destruction relative to the thicker and more strongly sutured holdfast margin.

Among the *Paulicystis* attachment structures that experienced sufficient weathering to remove or obscure holdfast interiors, a spectrum of preservational states can be recognized. Holdfasts subjected to minor weathering are characterized by a well-developed margin with visible plate contacts (Fig. 5a). The plates of holdfasts in this taphonomic state are always in close contact with each other. The thin, pore-bearing,
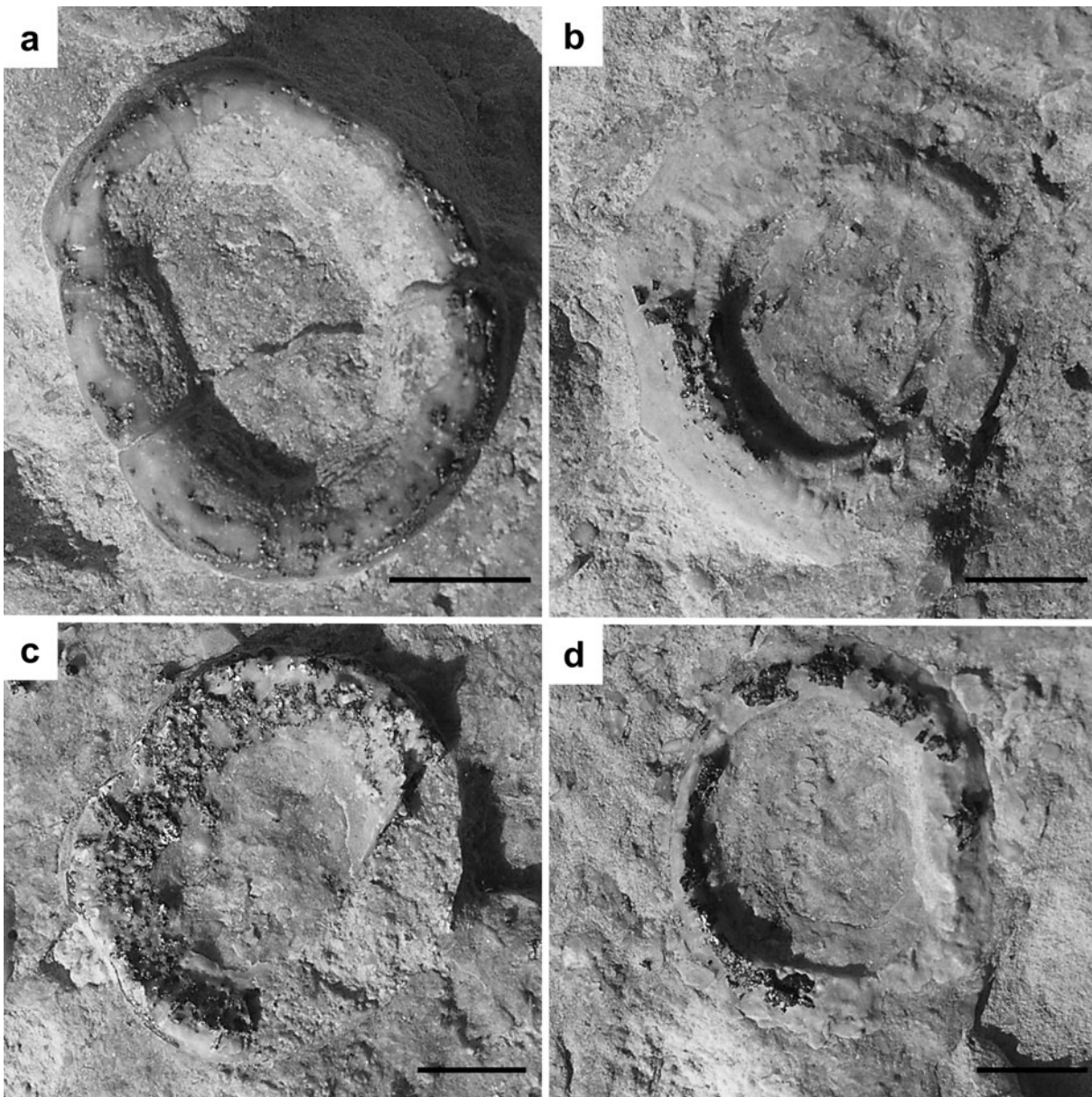
Figure 5. Thecal attachment structures of *Paulicystis* that experienced differing amounts of weathering prior to final burial. (a) Holdfast (CMC IP 69530) with eight clearly recognizable component plates comprising the margin, but a central cavity obscured by weathering; this represents a holdfast subjected to exposure intermediate between the specimens in Figure 3a and (b). (b) Moderately weathered holdfast (CMC IP 70214) with faint plate contacts, partially eroded margin, particularly on one side, and obscured and partially eroded central cavity; this represents a holdfast subjected to exposure intermediate between the specimens in (a) and (c). (c) Moderately weathered holdfast (CMC IP 70215) with faint plate contacts, strongly eroded margin with a simple ovoid outline and reduced height, and central cavity that was breached to expose the underlying substrate. (d) Severely weathered holdfast (CMC IP 70216) with faint plate contacts, preservation of only the tallest and thickest portions of the margin, and a central cavity that was breached to expose the underlying substrate. All scale bars are 1 cm.

parabolically depressed central area was almost immediately destroyed, being present only on a single specimen (Fig. 3a). In addition, the thin, slightly lobate, substrate-parallel outermost margin may be eroded away, giving the holdfast a simple ovoid outline, as shown in Figure 5a; however, some structures have been discovered that retain at least a partial thin margin and also display enhanced weathering of the central cavity and a thick, vertical marginal wall (Fig. 5b). Continued exposure results in obscured plate boundaries, giving attachment structures a massive appearance;

progressive erosion of the elevated marginal wall, decreasing the vertical relief of structures; and erosion of the thin, lobate margins, giving specimens simple, narrower outlines (Fig. 5c). It is possible that erosion of the elevated margin occurs before the lobate margins, but most specimens have erosion at both sites. Specimens with evidence of having been subjected to physical weathering for the greatest duration are characterized by high marginal walls that were altered to produce lobate margins (Fig. 5d), although these reflect degradation of what was previously the highest

and thickest portions of holdfasts; the lobate margins of well-preserved holdfasts are composed of thin, delicate skeletal material, whereas the lobate margins of poorly preserved holdfasts are remnants of robust portions of the organism. Interior cavities are always completely eroded away, and the height of marginal walls is decreased (Fig. 5d). In fact, attachment structures in this taphonomic state are only recognizable as low, oblong rings representing the remnants of what were formerly the highest parts of the marginal wall (Fig. 5d).

For specimens attributable to the unknown holocystitids (Fig. 3b), a similar biostratinomic progression can be established. The most well-preserved holdfasts are characterized by plate sutures that are not obvious, pores that are only clearly visible in the interior of depressed central cavities, and radiating canal structures that are not visible. Further, the thin outermost margin, in contact with the substrate, is intact and has a slightly lobate shape (Fig. 3b). Continued exposure results in erosion of the thin outermost margin, creating a slightly ragged or irregular margin that ends sharply at the thick, elevated marginal wall (Fig. 6b, c) and erosion of the thin, pore-bearing material at the bottom of the interior cavity, exposing the underlying substrate (Fig. 6a, b). Many specimens in this taphonomic state also display increased visibility of pores, particularly on the exteriors of holdfasts (Fig. 6a, c). A few specimens maintain a portion of the outermost margin around part of the holdfast, but it is typically dramatically thinned or absent in other portions of the holdfast (Fig. 6c). Moderately weathered holdfasts are characterized by complete erosion of the outermost margin, giving the structure a circular outline (Fig. 6d, f). Plate boundaries may be visible, reflecting degradation of secondary stereom overgrowths (Fig. 6d, e). Pores can become readily visible on the exterior of the structure as well as the interior, if any portion of the bottom of the interior cavity remains (Fig. 6e). The most prominent feature of moderately weathered diploporite attachment structures is the enhancement of branching, radiating canal structures (Fig. 6d, e), interpreted by Thomka & Brett (in press) as serving a sensory function. These structures, which resemble canaliculi (Moore, Jeffords & Miller, 1968; see also Franzén-Bengtson, 1983), can become the dominant macroscopic feature of holdfasts in this taphonomic state (Fig. 6d). Continued degradation obscures all structural details except for occasional pores on the exterior of holdfasts. Attachment structures subjected to this degree of weathering are relatively thick, circular structures with indistinct plate contacts and few surface features (Fig. 6f).

Holdfasts that were very strongly weathered prior to burial are difficult to identify as diploporite thecal attachment structures without comparison to more complete specimens. Examples are shown in Figure 7. Some attachment structures have minor separation between the upper portions of component plates. However, the cementation of the basal portions of these structures to the hardground surface was strong enough to prevent complete removal of plates; consequently, holdfasts remained in place even as plates slightly shifted away from each other at sutures (Fig. 7a). Some holdfasts are so worn that they are little more than calcareous 'pads' resembling isolated crinoid columnals (Fig. 7b). Others are characterized by greater vertical relief but display radiating canal structures so prominently that other features are obscured (Fig. 7c). Attachment structures in this state resemble the septate basal discs of *Cleiocrinus* described by Brett & Liddell (1978). Severely degraded diploporite holdfasts on the Napoleon hardground rarely permit distinction between the two holdfast morphotypes; however, the more circular shape of the majority of structures in this taphonomic state suggests that the producers were primarily undetermined holocystitids associated with the holdfast type depicted in Figure 3b. It is possible that the thinness of *Paulicystis* attachment structures relative to the other morphotype resulted in complete destruction of these holdfasts, whereas the thicker, presumably more robust, morphotype could experience greater degradation without obliteration.

4.c. Overgrowth relationships

Research on modern environments indicates that available space is a critical limiting factor in hard substrate communities (Dayton, 1971; Jackson *et al.* 1971; Jackson, 1977, 1979). Increasingly, evidence for competitive biotic interactions on Palaeozoic hardgrounds and encrusted skeletal elements has been documented, supporting the ecological paradigm established for the Recent. The Napoleon hardground provided several examples of biostratinomic processes involving overgrowth of diploporite attachment structures by other organisms and spatial relationships between diploporite attachment structures.

Laminar stenolaemate bryozoans overgrew diploporite holdfasts (Fig. 8a, b). The term 'overgrew' is used here in favour of 'encrusted' because bryozoan zoaria clearly began astogeny on the hardground crests and expanded onto the outer surface of holdfasts that were cemented to the same surface, rather than passively beginning growth on the holdfasts themselves. It is interesting to note that bryozoan colonies never overgrew the articular area of diploporite attachments and many appear truncated or broken, suggesting that the lower part of the theca remained articulated to the attachment structure and was likely overgrown itself, but subsequently detached through decay-induced thecal disarticulation. In all instances, bryozoans overgrew diploporite holdfasts, and no evidence for biotic response to overgrowth by diploporites has been detected. The consistent overgrowth of solitary organisms by colonial organisms supports relationships documented in Recent (e.g. Jackson, 1977) and Palaeozoic (Sprinkle & Rodgers, 2010) environments, wherein an adaptive advantage is bestowed on colonial taxa presumably because they have a faster growth rate.
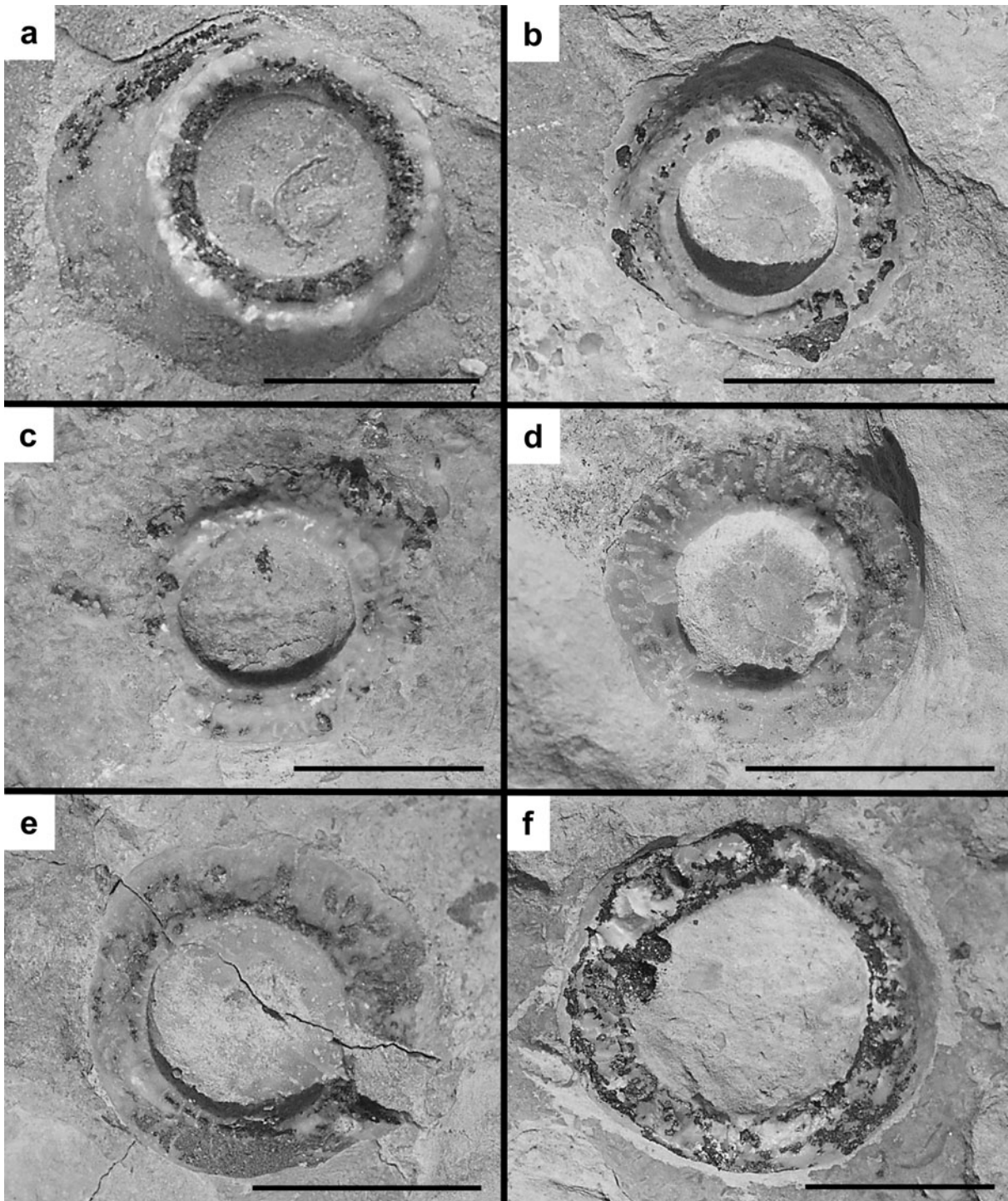
Figure 6. Thecal attachment structures of undetermined holocystitid diploporites that experienced differing amounts of weathering prior to final burial. (a) Relatively well preserved, upward-tapering holdfast (CMC IP 69528) with a circular outline (reflecting removal of slightly lobate marginal material), moderately visible pores, faint plate contacts and canal structures, and a pyritized inner ring, and a deep, sediment-filled central cavity; this represents a holdfast subjected to exposure intermediate between the specimens in Figure 3b and (b). (b) Relatively well-preserved holdfast (CMC IP 70217) with poorly visible pores, faint plate contacts, a visible but un-pyritized inner ring and a formerly circular marginal outline that been slightly degraded; this represents a holdfast subjected to exposure intermediate between the specimens in (a), (c) and (d). (c) Moderately preserved holdfast (CMC IP 70218) with remnants of the lobate margin (heavily degraded and thinned on one side) and interior platform, but poorly visible pores and moderately visible plate contacts and canal structures; this represents a holdfast subjected to exposure intermediate between the specimens in (a) and (d). (d) Moderately to poorly preserved holdfast (CMC IP 70219) with a weathered margin and interior resulting in thinned, circular outlines to both, and prominent canal structures and moderately visible plate contacts and pores; this represents a holdfast subjected to exposure intermediate between the specimens in (b), (c) and (e). (e) Moderately to poorly preserved holdfast (CMC IP 70220) with a circular margin beginning to weather irregularly, no trace of an interior ring, and prominent canal structures, pores and plate contacts; this represents a holdfast subjected to exposure intermediate between the specimens in (d) and (f). (f) Poorly preserved holdfast (CMC IP 70221) with perfectly circular outline, no inner ring, faint canal structures, pores and plate contacts; this represents a holdfast subjected to exposure intermediate between the specimens in (e) and Figure 7a. All scale bars are 1 cm.
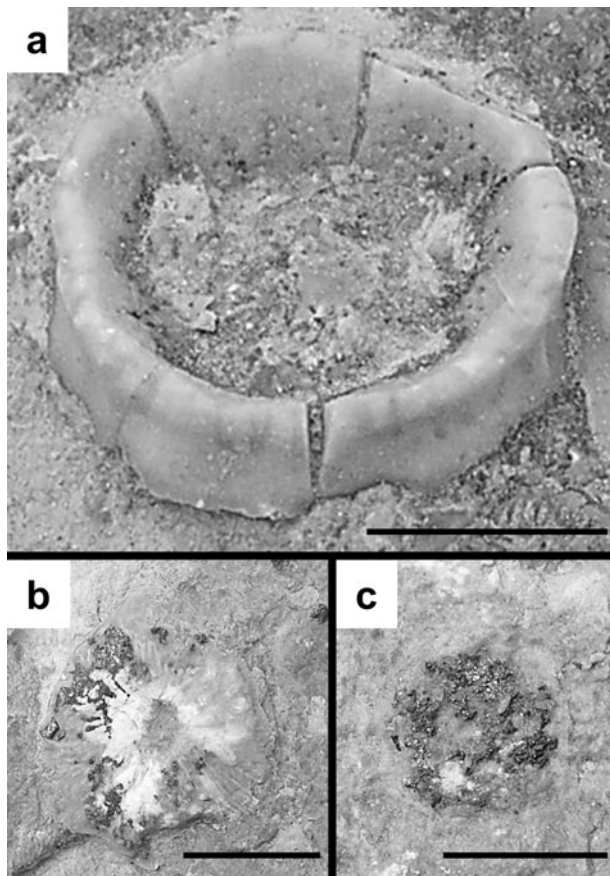
Figure 7. Diploporite attachment structures that were strongly weathered prior to final burial. (a) Multi-plated holdfast (specimen uncollected) showing prominent pores; wide, interior cavity breached to expose underlying substrate; and separation between component plates. Scale bar is 1 cm. (b) Holdfast (CMC IP 70222) that is reduced to a low, calcareous pad with prominent canal structures and moderately visible plate contacts. Scale bar is 0.5 cm. (c) Barely recognizable holdfast (CMC IP 70223) preserved as a heavily pyritized disc. Scale bar is 0.5 cm.

Diploporite holdfasts on hardground crests are also rarely overgrown by attachment structures of the rhombiferan *Caryocrinites* (Fig. 8c, d). The overgrowing holdfasts can be identified as those of *Caryocrinites* because of the presence of a distinctively large, trilobate lumen (Brett, 1978*b*). In all instances, the encrusted diploporite attachment structures represent the morphotype attributable to the undetermined holocystitids. Further, diploporite attachments encrusted by rhombiferan holdfasts are always quite poorly preserved. The encrusted holdfast in Figure 8c is little more than a septate pad (comparable to the taphonomic state of the specimen in Fig. 7b), and that in Figure 8d is a topographically irregular disc with an appearance dominated by canal structures. Interestingly, dendritic radices belonging to *Caryocrinites* as well as crinoid taxa with similar holdfast morphologies are otherwise absent on the hardground crests occupied by diploporites; evidently, *Caryocrinites* did not directly encrust the crests of the Napoleon hardground itself but, instead, preferentially overgrew select diploporite holdfasts (Thomka & Brett, 2013). Why this relationship

existed, and why only degraded diploporite attachments that were exposed and weathered for a relatively long time were utilized as substrates remains enigmatic. One potential explanation is that some poorly preserved diploporite attachment structures served as emergent 'islands' of hard substrata protruding above a thin veneer of sediment deposited during the initial phases of burial of the hardground.

One specimen (CMC IP 70226) has encrustation of a fairly well-preserved diploporite attachment structure by a small holdfast of unknown affinities (Fig. 8e). The overgrowing structure is circular, contains a minute, centrally located, circular lumen, and does not display obvious radicles. This may represent overgrowth by a juvenile crinoid, possibly a small cladid or disparid, or a coronoid (Brett *et al.* 1983). Another slab (CMC IP 70227) recovered from the Napoleon hardground contains two diploporite attachment structures in direct contact with each other (Fig. 8f). This pair of holdfasts is significant because it may preserve evidence for spatial competition: the typically circular outlines of attachment structures were modified to more polygonal shapes along the hemisphere where the specimens meet. Such outline modifications have been documented in edrioasteroids (Meyer, 1990; Sumrall, Sprinkle & Bonem, 2006) and holdfasts of the crinoid *Anomalocrinus* (Brett, Deline & McLaughlin, 2008) that grew in crowded conditions. This is a common phenomenon among sessile non-colonial invertebrates. It is interesting to note that one of the specimens is better preserved than the other and that the better preserved holdfast displays the most pronounced outline flattening (Fig. 8f, specimen on left). It is also possible that, rather than reflecting competition, the more degraded specimen may actually represent the isolated holdfast of a dead diploporite that affected the growth of a living individual, represented by the less degraded specimen. Further support for this scenario comes from the slightly lobate margins of the less degraded specimen, which overgrow the more degraded holdfast to a minor extent (Fig. 8f). This relationship might represent a form of gregarious behaviour similar to that proposed for clustered crinoid attachment structures described by Donovan, Harper & Håkansson (2007) and Donovan & Harper (2010).

Although several types of overgrowth interactions can be documented on the Napoleon hardground and its diploporite attachment structure population, it is not possible to construct a competitive hierarchy of encrusters, as is common in modern ecological studies (e.g. Jackson & Buss, 1975; Connell, 1976; Jackson, 1979; see also McKinney, 1995). This is owing to the low number of observed interactions and the paucity of observations on overgrowth relationships between the various organisms that encrusted diploporite holdfasts. It does appear, however, that diploporite attachment structures formed the bottom of any competitive network, as they did not overgrow other organisms and might not have even been able to completely overgrow isolated holdfasts representing dead individuals.
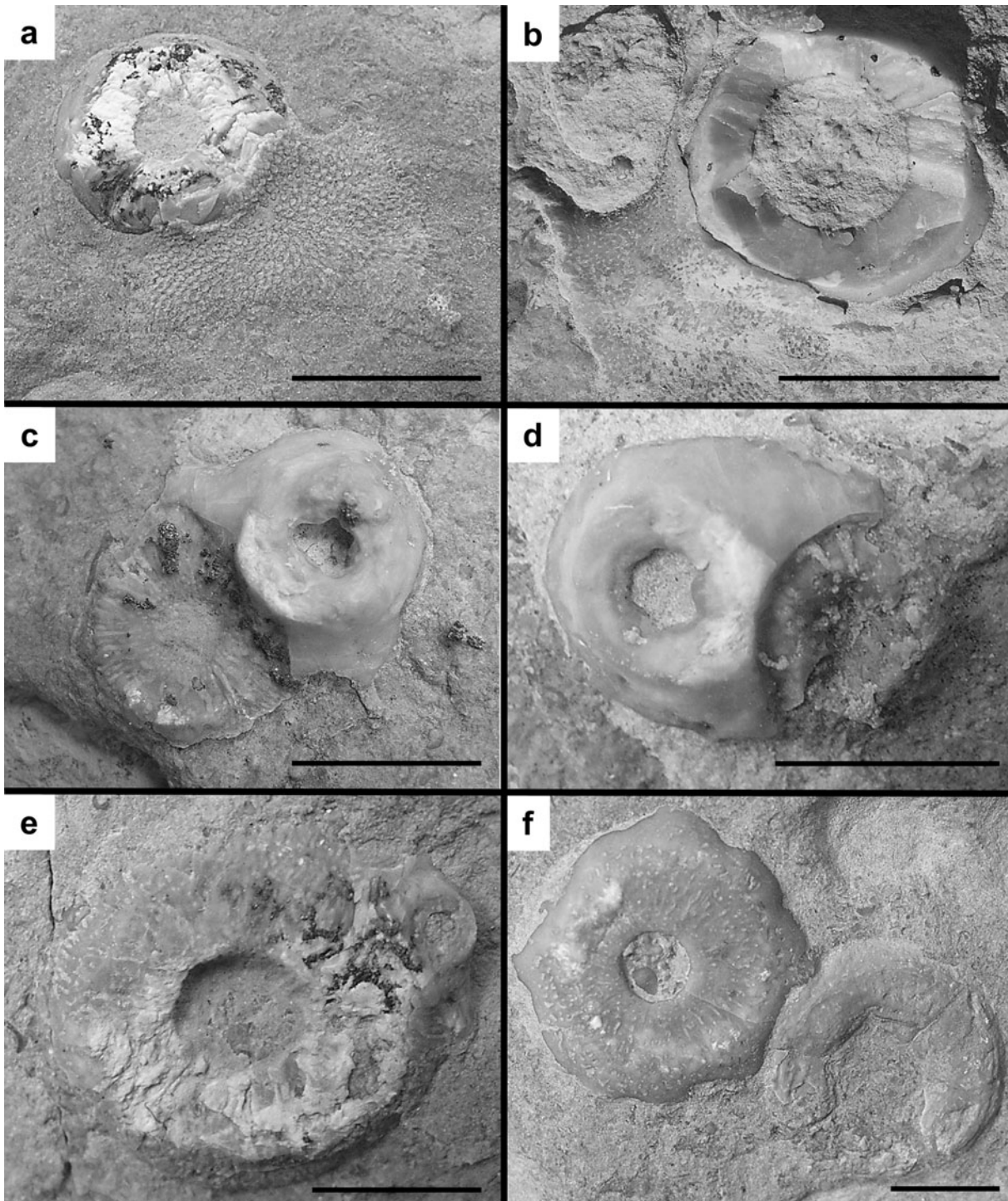
Figure 8. Relationships between diploporite attachment structures and other encrusters on the Napoleon hardground. (a, b) Overgrowth of holdfasts by laminar stenolaemate bryozoan colonies (CMC IP 70224 and CMC IP 70225, respectively). (c, d) Diploporite holdfast overgrown by attachment structure of *Caryocrinites* (Rhombifera). Note that these *Caryocrinites* attachment structures are more conical and morphologically simple than the branching dendritic radices common to this genus, and that diploporite attachments are poorly preserved, comparable to the specimen in Figure 7b (CMC IP 70228 and CMC IP 70229, respectively). (e) Attachment structure encrusted by a small (juvenile crinoid?) holdfast with a round lumen (CMC IP 70226; at the approximate '3 o'clock' position). (f) Two diploporite attachment structures in direct contact with each other. Note that the specimen on the left is better preserved than that on the right, and that the interaction between these two resulted in modification of the shape of both specimens from a strongly circular outline to a more polygonal outline (CMC IP 70227). All scale bars are 1 cm.

4.d. Diagenetic processes

Nearly all specimens have pyrite crystals on the external surface of the holdfast margin. Pyrite mineralization is a common feature throughout the Ap-palachian Foreland Basin during this interval, in contrast to slightly older deposits, which tend to preserve iron in different phases (McLaughlin, Emsbo & Brett, 2012). In some cases, pyrite is amorphous, lacking obvious crystal habit; in others, the pyrite is

macrocrystalline, in a cubic form. Morphologic variability in diagenetic pyrite is common in deposits containing abundant pyrite, and the distribution of pyrite crystal morphologies has been documented in detail by several case studies (e.g. Hudson, 1982; Canfield & Raiswell, 1991).

Pyrite can be distributed seemingly randomly over holdfasts, but certain specimens have preferential pyritization of the slightly depressed innermost marginal wall (Fig. 6a) to form an 'interior ring' of pyrite (Thomka & Brett, in press). The restriction of pyrite to interior rings suggests early diagenetic processes associated with a chemically reactive microenvironment (*sensu lato*; see McNamara *et al.* 2009) generated by decay of soft tissues. This assertion is supported by pyritization of canal structures in radicles of the dendritic radicular attachment structures attributable to co-occurring rhombiferans and crinoids.

Interestingly, the large size of many pyrite crystals suggests a late diagenetic origin that, at first glance, appears to contradict the evidence for early diagenesis discussed above. This most likely reflects late diagenetic pyrite growth that was seeded by early diagenetic crystallites, which developed in decay-induced microenvironments (see also Canfield & Raiswell, 1991; Thomka & Lewis, in press). Because much diagenetic mineralization is surface reaction-controlled, pyrite that formed very rapidly after death, even if amorphous or microcrystalline, can serve as a locus for later mineral growth as local redox reactions liberated ions that were rapidly incorporated into minerals that then nucleated on the antecedent crystallites. Hence, even though macrocrystalline pyrite reflects late diagenetic processes, its distribution provides insight into sites of early diagenesis which, in turn, likely indicate locations of reducing microenvironments.

A large body of literature exists on early diagenetic minerals and their relationship to preservation of unmineralized tissues (e.g. Allison, 1988; Allison & Briggs, 1991; Briggs, 2003), and it is beyond the scope of this study to provide an extensive review of this subject. Nevertheless, it is well documented that decay of connective tissues can lead to mineralization, essentially preserving a guide to the distribution of material that was lost relatively early in the taphonomic history of specimens. Preservation of soft tissues in Palaeozoic echinoderms has been previously documented by Glass & Blake (2004), Glass (2006), Kammer & Ausich (2007) and Ausich, Bartels & Kammer (2013), among others. To be clear, we do not suggest that soft tissues are preserved on the Napoleon hardground fauna, but the non-random distribution of pyrite on the diploporite holdfasts studied here matches the location of where connective tissue would be expected, and the decay of these presumed tissues could easily have led to mineral growth. It is unclear at this point as to whether these connective tissues were ligamentary or muscular in composition, but it seems more likely that ligaments were used to simply connect plates in the aboral portion of the theca to plates comprising holdfasts.

5. Discussion: palaeoecologic implications

5.a. Taphonomy of attachment structures

Although much published data are available on echinoderm taphonomy (see summaries by Lewis, 1980; Donovan, 1991; Brett, Moffat & Taylor, 1997; Ausich, 2001; Nebelsick, 2004), few studies to date have addressed, much less focused on, taphonomic patterns among pelmatozoan attachment structures. Notable exceptions include studies of Ordovician holdfasts by Brett & Liddell (1978) and Brett, Deline & McLaughlin (2008). Both of these studies documented morphologic features that became visible as a result of weathering, in strong agreement with the results of the current study. A network of radiating, branching canals nearly identical to those in diploporite holdfasts from the Napoleon hardground was brought out by weathering in the terminal holdfasts of the Ordovician crinoids *Anomalocrinus* (Brett, Deline & McLaughlin, 2008) and ?*Carabocrinus* (Lewis, 1982). In addition, weathering brings out pore structures in the holdfast of the Ordovician crinoid *Cleiocrinus* (Brett & Liddell, 1978) and the holdfast morphogenus *Podolithus* (Conkin, 2003), as well as unidentified discoidal attachments from the Silurian of Gotland, Sweden (Franzén, 1977). The multi-plated nature of the integument of *Cleiocrinus* was also revealed through weathering (Brett & Liddell, 1978).

Whereas it may be somewhat counterintuitive that pristine, unweathered specimens are often less capable of clearly showing morphologic features than are imperfectly preserved specimens, it is logical when considering pelmatozoan echinoderm attachment structures. The final configuration of attachment structures is dictated by three factors: (1) relationship to column or stele (i.e. is the attachment simply a modified portion of the pelma or is it a specialized, unique terminal ossicle or multi-plated structure?); (2) capacity to overgrow primary skeletal structures with secondary stereom (i.e. does the ultimate attachment closely correspond to distal skeletal morphology or is it concealed by amorphous skeletal overgrowth?); and (3) substrate consistency (i.e. is the substrate stable, permitting direct attachment by a simple structure or is it unstable, requiring increased surface area for greater purchase?). More detailed considerations of the relationships between pelmatozoans and substrate are discussed by Brett (1984, 1991) and Seilacher & MacClintock (2005); but in the context of this discussion, it is apparent that certain palaeoenvironmental conditions can trigger minor to substantial modification via secondary stereom secretion. Hence, originally multi-plated or otherwise skeletally complex structures may appear simple or undifferentiated while the organism was alive or shortly after death. Nevertheless, minor differences in density between stereomic overgrowths, underlying solid primary skeletal structures, and underlying multi-plated primary skeletal structures are highlighted by weathering during exposure. Future research into pelmatozoan autecology is likely to benefit

significantly from detailed analysis of attachment structures in various states of completeness and displaying various extents of degradation. Pristine specimens may prove most useful for initial taxonomic identification, but taphonomic evaluation will highlight palaeoecologically significant structural frameworks and skeletal modifications.

The variation in taphonomic states within this assemblage of attachment structures reflects within-habitat time-averaging (Kidwell, 1993), as expected given the inferred slow sedimentation rate. The consequent 'time-richness' of this fauna makes such assemblages ideal for providing insights into intrinsic factors that influence the taphonomy of a given taxon, as an entire preservational spectrum can be documented from a single surface with few interpretive complications arising from preservation in different taphofacies (see Brett & Baird, 1986). Documentation of taphonomic properties of specimens at low taxonomic levels among an assemblage recovered from the same general taphofacies is critical to understanding the magnitude of taphonomic variability that can potentially be expressed by echinoderm skeletal modules (e.g. holdfasts, thecae, columns; Allison, 1990; Thomka *et al.* 2011, 2012). Such knowledge is important in recognition and identification of specimens in settings where ideal or complete preservation is uncommon.

5.b. Significance of diagenetic fossil colour

A number of recent publications have documented colour variation among fossil echinoderms, resulting in recognition of original, biologically meaningful organic molecules (Wolkenstein *et al.* 2006, 2008; O'Malley, Ausich & Chin, 2008, 2013; Niedźwiedzki, Salamon & Wolkenstein, 2011). Preservation of biomarkers in ancient organisms requires exceptional preservation, and isolated attachment structures showing evidence of varying extents of exposure and degradation are unlikely to record primary organic signatures. The holdfasts studied here display colour variations, but rather than reflecting the presence of taxon-specific organic molecules, this phenomenon represents diagenetic colouration. Recently, Kolbe *et al.* (2011) studied Palaeozoic brachiopod shells and documented consistent relationships between diagenetic fossil colour and taphonomic state. Macrofossils on the Napoleon hardground do not display the variety of colouration evident within the brachiopod dataset of Kolbe *et al.* (2011), but consistent relationships, corroborated by other taphonomic criteria, can be recognized in the holdfast population studied here.

Well-preserved attachment structures are nearly always whitish to light grey, and poorly preserved specimens become increasingly dark (e.g. Fig. 6a–e). This relationship is consistently true for diploporites, but is also well illustrated by the colour difference between the well-preserved *Caryocrinites* holdfasts that encrusted remnants of diploporite attachment structures in Figures 8c, d. Interestingly, the correlation between increasing darkness and degradation persists only when considering moderately preserved specimens: holdfasts that are particularly incomplete display relatively light colours (Figs 5d, 8f).

Results on diploporite holdfast colouration, although preliminary and not subjected to quantitative analysis, agree with the results of Kolbe *et al.* (2011), who found a similar darkening of brachiopod shells in association with evidence for prolonged exposure. This pattern was interpreted as being related to increased sulfide mineralization, an explanation that also seems appropriate for the attachment structures studied here. Although documentation of colour variation was not the primary objective of this study, colour nevertheless provided an additional line of evidence for assessing degree of degradation. The fact that darkening is consistent with physical signs of increased exposure corroborates interpretations made in Section 4.b. Finally, it is hoped that inclusion of data on diagenetic fossil colour here, although only in the form of relatively simple observations, will encourage incorporation of diagenetic colour data along with other taphonomic indicators in future analyses of ancient deposits.

5.c. Encrustation of microbioherms

Although diploporite holdfasts are common on the Napoleon microbiohermal hardground, the fistuliporoid bryozoan-dominated microbioherms themselves are not encrusted by diploporites. Instead, microbioherms served as substrates for long-stemmed pelmatozoans: attachment structures attributable to the monobathrid camerate crinoid *Eucalyptocrinites* and the hemicosmitid rhombiferan *Caryocrinites* are quite abundant (Thomka & Brett, 2013). Interestingly, these same taxa, as well as other long-stemmed crinoids such as *Periechocrinus* and *Dimerocrinites* (Brett, 1984), occur in hardground troughs. The occurrence of pelmatozoans with the longest columns, and therefore the greatest capability to elevate thecae well above the substrate, on top of microbioherms is counterintuitive, as these taxa could easily access higher currents while occupying relatively low areas (such as the hardground troughs where they are also common). Diploporites lack a true column and are incapable of elevating themselves more than a few centimetres above the substrate: one would logically expect the positive topographic relief of microbioherms to be the ideal substrate for diploporite encrustation. Instead, they are restricted only to hardground crests, which are elevated relative to hardground troughs, but are nevertheless considerably lower than microbioherms.

The reason for this segregation of attachment structures is currently unclear, but Thomka & Brett (2013) discussed some potential explanations. It is possible that diploporites have particularly poor larval dispersal abilities and, consequently, that larvae simply could not become established atop microbioherms. This seems unlikely, however, as diploporite thecal attachment structures are occasionally present on
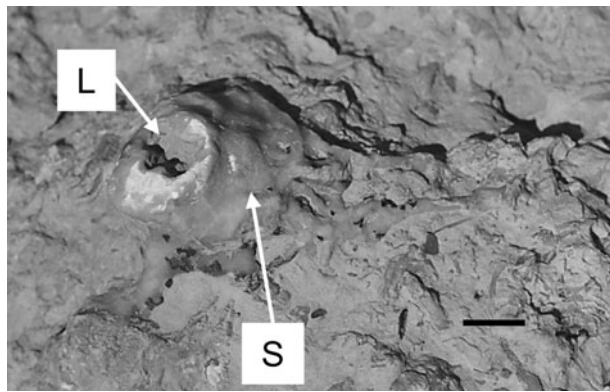
Figure 9. Holdfast of *Eucalyptocrinites* (Crinoidea) on microbioherm, displaying extreme swelling by growth of secondary stereom. L – distorted lumen; S – secondary stereomic overgrowth. The exact reasons for this skeletal modification, which is also observed on the attachment structures of the rhombiferan *Caryocrinites*, are unknown. Scale bar is 1 cm

hardground crests immediately adjacent to microbioherms. Another unlikely explanation for the absence of diploporites on Napoleon microbioherms and the extreme secondary thickening of other holdfasts (Fig. 9) is protection against anoxic, corrosive or otherwise toxic pore waters, as described by Seilacher & MacClintock (2005). The diverse benthic fauna and lack of evidence for increased organic matter concentration at the microbiohermal surface supports the interpretation of an oxygenated hardground.

A potential cause that is more plausible, but hard to test, involves antagonistic interactions between encrusting pelmatozoans and components (microbes?) of the microbioherm. Because diploporites are thecally attached (Brett, 1984), their steles, filled with viscera, would have been close to the substrate, and any adverse effects resulting from interactions with microbioherm biota or sediment would have been potentially dangerous to diploporites. In contrast, crinoid and rhombiferan holdfasts were far removed from thecae, and the narrow axial canals of distal columns belonging to encrusting taxa would have contained only a minimal amount of viscera. Further, radicles of *Caryocrinites* are composed of solid, undifferentiated stereom (Brett, 1978*b*); and those of *Eucalyptocrinites*, although composed of true cirral ossicles, are overgrown and thickened by rigid secondary stereom. This would have been quite effective in protecting viscera within columns or dististelar radicles from underlying or surrounding sediment.

An additional potential explanation for the absence of diploporites on microbioherms is that encrustation of the outer surfaces of microbioherms by long-stemmed pelmatozoans occurred after the hardground surface was buried by a thin layer of clastic sediment. If true, then the diploporites surrounding the topographically positive microbioherms would have been adapted for soft substrata, lacking a permanent attachment structure. In this scenario, diploporite encrustation would have occurred earlier in the growth history of microbi-

oherms. Therefore, future work will focus on searching for diploporite attachment structures on interior laminae of cut microbioherms from the Napoleon hardground.

5.d. Bioerosion and embedment structures

Borings preserved in hard substrates have a long geologic record, and the Ordovician–Devonian is considered an interval of intensified bioerosion, both in terms of diversity of bioeroding organisms and variety of bored substrates (Warme, 1975; Radtke, Hofmann & Golubic, 1997; Taylor & Wilson, 2003). Therefore, it is interesting to note the complete absence of borings into the Napoleon hardground. The undulating hardground is not bored, but is instead characterized by abundant firmground *Thalassinoides* burrows (see Bromley, 1975) presumably produced by trilobites (Cherns, Wheeley & Caris, 2006). These firmground burrows pre-date encrustation by diploporites, as evidenced by attachment structures that conform to burrow microtopography as well as an absence of *Thalassinoides* that cross-cut holdfasts. Hence, the surface must have been cemented enough to allow encrustation and oxygenated enough to support a diverse epibenthic fauna, but somehow it lacked organisms that bored into the hardground to produce domiciles.

One might suggest that the Napoleon surface lacked borings because it was never fully cemented, making it a firmground. Encrustation of firmgrounds by discoidal echinoderm holdfasts is known (Zamora *et al.* 2010), but the surface studied here is densely encrusted – not only by pelmatozoans, but by laminar bryozoans and corals as well – and is heavily mineralized. These are characteristics of hardgrounds – commonly with borings – in the lower Palaeozoic of the Appalachian Foreland Basin and are not typical in firmgrounds (McLaughlin, Brett & Wilson, 2008). It is far more likely that the surface under study here is a true hardground. Alternatively, it might be suggested that a veneer of some sort, possibly a microbial mat, might have developed on top of the hardground surface, preventing borings (e.g. Cornell, Brett & Sumrall, 2003). This also seems unlikely given the microbioherms that encrust the same horizon, the absence of diagenetic evidence for organic coatings on the hardground (i.e. pyritic or carbonaceous films), and the local substrate exposed beneath diploporite holdfasts subjected to weathering, which is identical to the surrounding, exposed hardground surface. The absence of borings into hardground troughs is likely owing to thin burial of these topographic lows by sediment washed off hardground crests and microbioherms. Ongoing research may reveal why much of the Napoleon hardground was not a suitable substrate for domichnial borings, but it may simply be a peculiarity without a detectable cause.

In contrast to the hardground surface, bioerosion structures are present on skeletal material associated with the hardground and microbioherms. The embedment structure *Tremichnus* (*sensu* Brett, 1985; but see
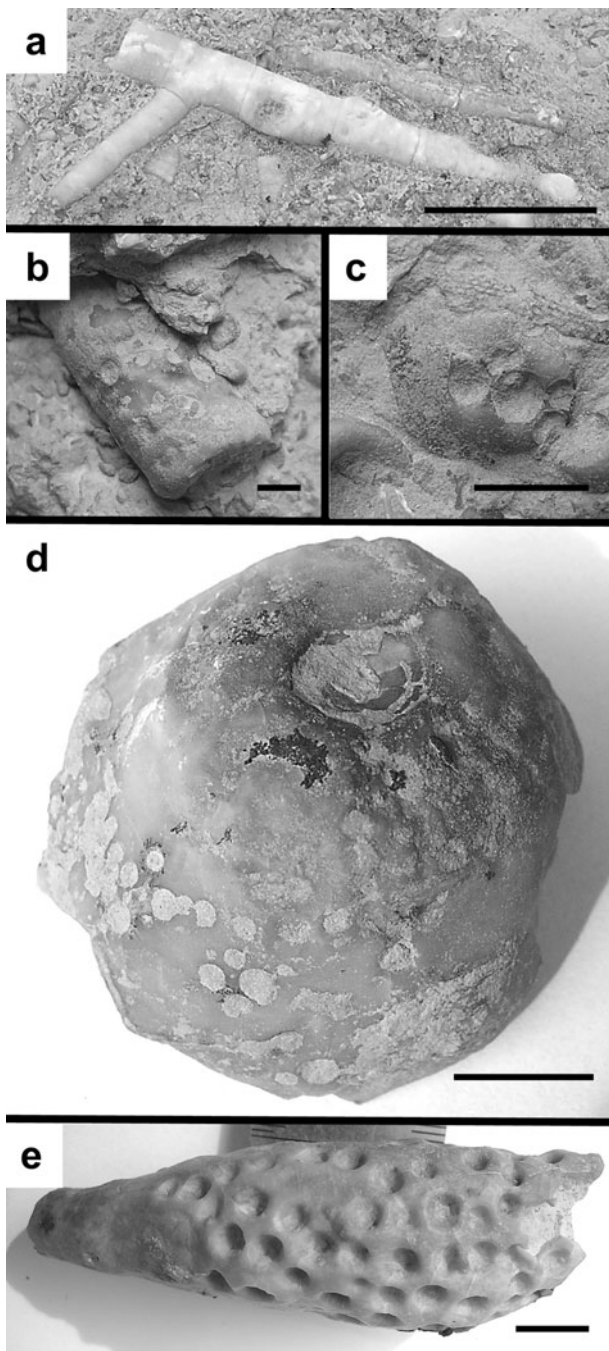
Figure 10. Bioerosion and embedment structures on skeletal material from the Napoleon site. (a) Cirriferous crinoid column, slightly swollen in response to the embedment structure *Tremichnus*. Scale bar is 1 cm. (b) Large pluricolumnal (*Periechocrinus*?) with numerous small, unswollen *Trypanites* borings. Scale bar is 0.25 cm. (c) Small, vertically oriented column with several very small, unswollen *Trypanites* borings. Scale bar is 0.25 cm. (d) Calyx of *Eucalyptocrinites* displaying numerous *Trypanites* borings. Scale bar is 1 cm. (e) Articulated diploporite theca (*Holocystites* sp. cf. *H. clavus*) with numerous examples of the swollen embedment structure *Tremichnus cystoidiphilus*. Scale bar is 1 cm. Specimens in (d) and (e) are in the University of Cincinnati Geology Department Teaching Collection.

Pickerill & Donovan, 1998; Donovan & Pickerill, 2002) is common on crinoids and diploporites from this locality (Fig. 10a, e), and often associated with severe

swelling (Fig. 10e), indicating that the structures were produced while the echinoderm host was still alive. Interestingly, no holdfasts have been discovered with swollen borings, suggesting that attachment structures were not sites of parasitism, whereas thecae were infested. The palaeoecology of these infestations is relatively well-studied and their occurrence is known to be host-specific (Frest, Mikulic & Paul, 1977; Brett, 1978*a*, 1985; Eckert, 1988; Widdison, 2001; Donovan & Lewis, 2010; Frest, Strimple & Paul, 2011); therefore, it is possible that the diploporites affiliated with these attachment structures were not hosts.

The simple boring *Trypanites* is moderately common, occurring almost exclusively on crinoid columns (Fig. 10b, c) and, less commonly, calyxes (Fig. 10d). No *Trypanites* have been discovered in isolated diploporite thecal plates, partially articulated thecae or attachment structures. The preferential excavation of domichnial borings in crinoidal material over diploporite material does not have an obvious explanation; perhaps the somewhat thinner, porous cystoid plates were unsuitable, whereas the thick, less porous and particularly abundant crinoid columns were substrates capable of being bored. In studies of Palaeozoic borings produced by acrothoracic barnacles, Rodda & Fisher (1962) and Ettensohn (1978) documented that borings were preferentially, if not exclusively, present in the thickest skeletal material available, logically concluding that boring organisms favour thick skeletal substrates for production of domichnial bioerosion structures. Although the producer of *Trypanites* is most likely a sipunculid worm and certainly not a barnacle, the ecological relationship inferred above is not taxon-specific. Biostratinomic evidence described in Section 4.b above demonstrated that at least some attachment structures remained exposed on the hardground for extended periods of time; this would have made such thick, calcareous masses ideal substrates for boring even if the hardground surface itself was an unsuitable substrate for some reason. Holdfasts were overgrown in some cases by bryozoans and other pelmatozoans (Fig. 8), indicating that these structures were suitable substrates for some organisms, but apparently not the producers of *Trypanites*.

6. Discussion: stratigraphic implications

Hardground surfaces are distributed non-randomly throughout the stratigraphic record (Brett, 1988, 1995; Wilson & Palmer, 1992; for more specific examples from the Appalachian Basin see McLaughlin, Brett & Wilson, 2008; McLaughlin *et al.* 2008). A number of independent lines of evidence contribute to the conclusion that the encrusted hardground studied here is genetically linked to a rapid change in base level that led to ecologic, environmental and geochemical conditions favouring incipient sea-floor cementation in low turbidity bottom water (see discussion in Section 2 above). This unique combination of physical parameters made possible the development of a distinctive

biofacies and taphofacies reflecting sediment starvation. Because of the distinctive sedimentary conditions established during colonization of the Napoleon hardground, this surface can be used as an important stratigraphic marker for regional correlation (Brett, Goodman & LoDuca, 1990; Brett & Ray, 2005; Brett *et al*. 2012) and, more importantly, the occurrence of similar surfaces and biotas can be predicted at analogous positions within other third-order (and potentially smaller scale) sequences in the Silurian of North America and elsewhere.

The potential for prediction of comparable faunas at major flooding/starvation surfaces may lead to significant new discoveries of middle Silurian diploporite taxa, although preservation as articulated thecae is unlikely given inferred palaeoenvironmental parameters (e.g. Brett & Baird, 1986; Brett, Moffat & Taylor, 1997). Holocystitid diploporites are known from coeval facies in the Romeo Member of the Joliet Formation in northeastern Illinois and southeastern Wisconsin (Frest, Mikulic & Paul, 1977; Frest, Brett & Witzke, 1999; Frest, Strimple & Paul, 2011; D. G. Mikulic, pers. comm. 2012), considerably upramp from the deposits studied here and quite disparate lithologically. In such settings, diploporites and associated pelmatozoans are typically abundant only in direct association with microbiohermal build-ups (e.g. Frest, Brett & Witzke, 1999). Correlations between strata of the Cincinnati Arch region and the rim of the Michigan Basin (i.e. Illinois and Wisconsin) have historically been complicated, but the occurrence of diploporites and their encrusting attachment structures on hard substrata appears to have at least regional biostratigraphic significance (see also Frest, Mikulic & Paul, 1977; Frest, Brett & Witzke, 1999; Frest, Strimple & Paul, 2011).

Microbioherms and a relatively diverse pelmatozoan fauna are also well documented at the contact between the Laurel Limestone and Waldron Shale (Wenlock: Homerian) in the Cincinnati Arch region (Foerste, 1898; Kindle & Barnett, 1909; Halleck, 1973; Frest, 1975; Ausich, 1975; Archer & Feldman, 1986; Frest, Brett & Witzke, 1999), a surface that is known to represent a hardground in nearly all localities where it is exposed (Halleck, 1973; McLaughlin *et al*. 2008). The consistent presence of microbioherms at a major flooding/starvation surface that is slightly younger than, but at an exactly analogous position to, the hardground in the lower Massie Formation lends credence to the stratigraphic interpretation of the Napoleon quarry and the conditions responsible for genesis of hardgrounds in both sequences. In both the Sheinwoodian and the Homerian, rapid base level rise resulted in sediment starvation and the dramatic transition from carbonate to mudrock lithologies, separated by a hardground that serves as a substrate for a unique assemblage of encrusting and build-up-producing taxa. This contact, in spite of obfuscation of surface details by dolomitization (e.g. McLaughlin *et al*. 2008), represents an excellent prospect for future discoveries of rare Silurian echinoderms, including diploporites, which become significantly rarer faunal elements above the Massie Formation. By late Sheinwoodian–Homerian time, holocystitid diploporites are thought to be restricted in distribution to shallow-water deposits in western Ohio and around the southern rim of the Michigan Basin (Frest, Mikulic & Paul, 1977; Frest, Strimple & Paul, 2011); concentrated collection at the Laurel–Waldron contact, however, may very well reveal their persistence in deeper settings in the Cincinnati Arch region.

7. Conclusions

Thecal attachment structures attributable to diploporite echinoderms are fairly common on a hardground, representing sediment starvation during a major sea-level highstand, within the Silurian (Wenlock) Massie Formation in Ripley County, southeastern Indiana, United States. Observation reveals that these attachment structures do not display uniform preservation with regard to visibility of plate contacts and internal morphologic features, sites of early diagenetic mineralization and relationships to encrusting organisms.

Well-preserved specimens appear solid, with poorly visible plate contacts, pores and canals, as well as a pore-bearing platform flooring the depressed interior of the structure. Pre-burial weathering resulted in the enhancement of pores, canals and plate contacts; increased weathering resulted in removal of the platform floor to expose underlying sediment. Particularly poorly preserved specimens display separation of component plates, though plates remain in association and cemented to the hardground.

Few attachment structures are encrusted by other organisms, but laminar bryozoans occasionally overgrew the upper surface of holdfasts following detachment of the thecae. Degraded holdfasts were encrusted by the attachments of *Caryocrinites*. No diploporite holdfasts are bored; the exact reasons for this are unclear.

Nearly all specimens have macrocrystalline pyrite on their upper and lateral surfaces. Some specimens have preferentially pyritized 'inner rings', and co-occurring dendritic attachment structures contain pyritized lumens. Although the large size of pyrite crystals suggests a late diagenetic origin, the distribution of pyrite may indicate late diagenetic growth of pyrite on early diagenetic precursor crystallites that formed through decay of ligamentary tissue.

In a larger sense, taphonomic analysis of pelmatozoan attachment structures has great potential for providing insights into sedimentary dynamics, palaeoautecology and biotic interactions and simultaneously serving as a tool for comparative taphonomic analysis and stratigraphic correlation. The occurrence of time-averaged holdfast populations on major flooding/starvation surfaces can be predicted using an approach that integrates sequence stratigraphy and taphofacies analysis. Such surfaces can be prospected for rare taxa and faunal occurrences that are palaeoecologically and stratigraphically significant.

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