Palaeontological and sedimentological effects of micro-bioherms in the Middle Silurian Massie Formation of southeastern Indiana, USA

JAMES R. THOMKA AND CARLTON E. BRETT

LETHAIA

Small build-ups composed primarily of micrite and benthic skeletal remains, termed 'micro-bioherms', have been recognized within Silurian strata of eastern and midcontinental United States for well over 75 years; however, previous research has focused nearly entirely on such structures within the upper Wenlock (Homerian) Waldron Shale. An undolomitized section of the lower Wenlock (Sheinwoodian) Massie Formation in Ripley County, southeastern Indiana, was studied to assess the influence of micro-bioherms on palaeoecological, taphonomical and sedimentological patterns. Increased baffling of fine-grained material by organisms composing and/or encrusting build-ups is evidenced by muddy sediment containing pascichnial traces surrounding micro-bioherms. Pelmatozoan attachment structures densely encrust micro-bioherms, but are swollen by secondary stereomic overgrowths reflecting some form of antagonistic interaction or investment in strong affixation to elevated substrates. Clusters of bumastine trilobite material occur in 'pockets' related to cavities within build-ups, and otherwise rare spathacalymenid trilobites, often exceptionally preserved, are found in muds in the vicinity of partially buried micro-bioherms. Coeval sections nearby are nearly unfossiliferous as result of dolomitization, but contain recognizable skeletal material in greatest abundance in micro-bioherm flank beds. The occurrence of these bodies within the Massie Formation is genetically linked to a major transgressive episode, but also reflects a mid-Silurian climatic/palaeoceanographic change.

DOI 10.1111/let.12097 © 2014 Lethaia Foundation. Published by John Wiley & Sons Ltd
True micro-bioherms developed in intermediate settings of Middle Silurian (Wenlock) age, specifically in mid- to outer-ramp settings in the Cincinnati Arch region and the adjacent Wabash Platform (Brett et al. 2012a; Ettensohn et al. 2013), as well as coeval sections in western New York (Brett et al. 1990). These settings, which are dominated by argillaceous carbonates and thin mudrock intervals, represent depositional environments that were too deep and/or turbid, at least intermittently, to support growth of true reefs or large mounds during the Wenlock. Micro-bioherm-bearing deposits are most readily studied in the southeastern Indiana-southwestern Ohio-northern Kentucky tristate region, where these bodies display sub-metre relief and diameters and are not laterally continuous with each other (Fig. 1).

Unfortunately, late diagenetic dolomitization has strongly influenced preservation of the Middle Silurian succession of the Cincinnati Arch region, resulting in altered sedimentary fabrics and sparsely fossiliferous sections in units known to represent normal marine environments (McLaughlin et al. 2008; Ettensohn et al. 2013). Dolomitized micro-bioherms can easily be recognized due to their irregular shape and clumpy, massive texture (Fig. 1A–C), as well as the effects of anisotropic compaction of overlying sediments around the solid carbonate masses (Fig. 1D). In spite of their prominence in tristate area strata, micro-bioherms cannot provide detailed data on microstructure, lithology, faunal composition and internal fabric after extensive dolomitization. Likewise, unique encrusting faunas or palaeoecological patterns cannot be documented after alteration via dolomitization.

A few undolomitized micro-bioherm-bearing sections have been documented in the Middle Silurian of southeastern Indiana, but previous research has focused entirely on build-ups within the Homerian (upper Wenlock) Waldron Shale and at the contact between the Waldron and underlying Laurel Lime- stone (Foerste 1898; Kindle & Barnett 1909; Halleck 1973; Ausich 1975; Archer & Feldman 1986; Feldman 1989). Micro-bioherms have recently been recognized in the Sheinwoodian (lower Wenlock) Massie Formation in this region (McLaughlin et al. 2008; Brett et al. 2012a; Thomka & Brett 2014a,b), but have not previously been studied with regard to their influences on the palaeontology and sedimentology of the unit containing them.

Thus, the goals of this study are as follows: (1) to present the stratigraphical setting of micro-bioherms in the Massie Formation of southeastern Indiana and interpret the factors controlling their

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**Fig. 1.** Micro-bioherms in the lower Massie Formation at several localities in northern Kentucky. The approximate core of micro-bioherms is marked by the ‘m’. All micro-bioherms shown here are strongly dolomitized and represent the typical state of such structures in the Cincinnati Arch region. Scale bars = 30 cm. A, typical domal micro-bioherm at roadcut on I-265 exit 19, Jeffersontown, Kentucky (N38°08′05.81″, W85°32′33.05″). B, massive, amorphous micro-bioherm in roadcut on KY-329, Crestwood, Kentucky (N38°08′52.81″, W85°28′26.06″). The head of the hammer is resting on the hardground surface upon which the micro-bioherm grew. C, large, massive micro-bioherm underlain by thin interval of mudstone. Note that the top of the micro-bioherm is truncated by the erosive base of the upper calcarenitic facies of the Massie Formation. Same locality as in 1B. D, narrow, indistinct micro-bioherm in roadcut on I-71S, Oldham County, Kentucky (N38°20′18.97″, W85°31′17.21″). Note that the micro-bioherm can be detected primarily because of compactional warping of overlying calcareous mudstone.
occurrence; (2) to document the influences that micro-bioherms exerted on the sedimentology, palaeoecology and taphonomy of the Massie Formation; and (3) to comment on the significance of these build-ups to Middle Silurian stratigraphical and palaeoceanographic events.

Locality and stratigraphy

One of the few localities that exposes undolomitized lower Wenlock strata in the Cincinnati Arch region is the New Point Stone quarry, east of the town of Napoleon in Ripley County, southeastern Indiana (N39°12’31.39’’, W85°18’53.74’’; Fig. 2). This locality, which is generally known as the Napoleon quarry, has historically been a focus for Middle Silurian palaeontological research owing to the diverse, abundant and well-preserved macroinvertebrate fauna that has been recovered from units that are devoid of identifiable fossils in nearly all other exposures (e.g. Frest et al. 1999, 2011). The stratigraphical succession at the Napoleon quarry is dominated by clean skeletal carbonates, argillaceous, sparsely fossiliferous micrites and calcareous mudstones deposited in upper ramp settings on the transition from the western margin of the Appalachian Foreland Basin to the Wabash Platform (Spengler & Read 2010).

Much of the stratigraphy of the Napoleon quarry has traditionally been classified as a single unit, the Osgood Formation (Foerste 1897), which Pinsak & Shaver (1964) later downgraded to the lower member of the Salamonie Dolomite, overlain by the Laurel Member. However, in the light of recent high-resolution stratigraphical research that has demonstrated persistence of easily recognizable sedimentary bodies throughout the greater Cincinnati Arch region, an updated lithostratigraphical terminology has been applied to southeastern Indiana (Brett et al. 2012a). The term Salamonie Dolomite was rejected entirely within Ripley County and the ‘Laurel Member’ was returned to full formational status (Fig. 3A). The former ‘Osgood Member’ was split into three individual formation-rank units. The term Osgood Formation was reestablished and restricted to the former ‘lower Osgood shale’ (Fig. 3A), and the former ‘upper Osgood carbonate’ minus the uppermost bed was renamed using Ohio lithostratigraphical terminology to become the Lewisburg Formation (Fig. 3). Likewise, the former ‘upper Osgood shale’ plus the underlying carbonate bed was termed the Massie Formation (Fig. 3).

The sharp contact separating the basal carbonate and overlying mudstone interval of the Massie Formation (i.e. the former contact between the ‘upper Osgood carbonate’ and ‘upper Osgood shale’) represents a major flooding surface that can be traced throughout the Cincinnati Arch region (McLaughlin et al. 2008; Brett et al. 2012a). At the Napoleon

Fig. 2. Location of New Point Stone quarry, ca. 1 km east of Napoleon, Indiana. Modified from Thomka & Brett (2014a).
quarry, this surface represents a hardground that is densely encrusted by pelmatozoan attachment structures and laminar bryozoans (Thomka & Brett 2014a,b) and serves as the source horizon from which micro-bioherms grew (Fig. 3B). The nature of surface and associated fauna and sediments constitutes a primary focus of this study.

Methods

Micro-bioherms at the Napoleon quarry were inspected in the field for physical characteristics; the identity of the fauna comprising the main body of the structure itself; and the presence, identity, and relative abundance of encrusting organisms. Measurements of height and diameter were taken on several build-ups, although this was carried out primarily to determine typical measurements, and quantitative results are not presented here. One large, complete specimen and several incomplete specimens were collected and cut open to expose interior fabrics. The large micro-bioherm was serial-slabbed, producing multiple faces for study.

The portion of the quarry where build-ups are common was recently dug up by a bulldozer, resulting in extensive rubble piles composed of complete and partial micro-bioherms and irregular chunks of immediately surrounding material. This area was searched for fossil material that is not found on the Napoleon hardground where build-ups are absent. Comparisons between taphonomical state, relative abundance and morphology were made between taxa in association with micro-bioherms and on the hardground surface. Faunal counts for quantitative analyses were not taken in part because of the difficulties of obtaining accurate abundance data on disarticulated pelmatozoan echinoderms and trilobites, which are dominant elements in this faunal assemblage.

Several micro-bioherms are preserved in situ at a benched-off surface, corresponding to the hardground under study, at the northern end of the quarry, which permitted direct observation of horizontal cross-sections of the micro-bioherms and sediment immediately surrounding the build-ups.
Based on comparisons with relatively complete micro-bioherms discovered as rubble, it is apparent that much of the middle to upper portions of in situ build-ups was destroyed during removal of overburden. As a result, encrustation patterns are not preserved. In spite of the vertical truncation, micro-bioherms on the benched-off surface nevertheless provided valuable information on the character of lateral margins and immediately surrounding material.

Given that the objectives of this study are to document the stratigraphical setting and palaeontological and sedimentological influences of micro-bioherms on the Massie Formation, petrographic descriptions are not presented here. Analysis of thin sections of micro-bioherms will be presented in a forthcoming paper that focuses on composition and genesis of these build-ups.

Description of micro-bioherms

Micro-bioherms at the Napoleon quarry are roughly domal in cross-sectional shape (Figs 3B, 4A) and typically 20–30 cm high and 50–70 cm in diameter (Fig. 4A, B). Where observed in situ, individual build-ups may be separated from each other by several metres but are more commonly in close proximity. Adjacent micro-bioherms are never laterally linked. The exterior surface is dominated by a crinkled texture with unevenly distributed rod- or pillar-like pustules (Fig. 4A). This reflects the abundance of fistuliporoid bryozoans, likely Fistulipora, in the composition of build-ups (Perry & Hattin 1960). The exterior surfaces of micro-bioherms are densely encrusted by radicular pelmatozoan attachment structures, commonly in clusters (4C). No borings have been observed into either build-ups or the hardground from which they grew (Thomka & Brett 2014a,b). Skeletal elements visible on micro-bioherm exteriors occur alongside ‘patches’ of siliciclastic mud. In some instances, mud appears to have been bound by pelmatozoan attachment structures and/or bryozoan laminae. Based on size, faunal composition and character of sediment, these build-ups appear to be equivalent to bryozoan crust mounds of the classification system of Cuffey (1985; see also Gibson et al. 1988).

The interior fabric of micro-bioherms is dominated by olive-green micrite, massive bryozoan material and fistuliporoid bryozoan laminae, which are more prominent towards the margins of build-ups (Fig. 5). Subordinate elements include radicles of pelmatozoan attachment structures, dark-grey siliciclastic mud and rare articulate brachiopods (Fig. 5). Small calcite-filled void spaces of enigmatic origin are also present, possibly representing burrows (Nose et al. 2006).

Sedimentological effects

The matrix of the hardground from which micro-bioherms at the Napoleon quarry grew is generally well winnowed, being a packstone to grainstone with slightly muddier sediment in topographically negative areas (Thomka & Brett 2014a,b). However, immediately surrounding build-ups is sediment...
characterized by significantly increased siliciclastic mud and micrite contents (Fig. 6A, B). Based on observations of bedding plane exposures of the hard-ground surface, it was determined that this lithology is present only in narrow rings (generally 30–50 cm wide) surrounding micro-bioherms. The increased fine-grained detrital component of these micro-bioherm-marginal deposits likely resulted from: (1) the baffling effects of suspension-feeding organisms comprising and/or encrusting the build-ups (McKinney et al. 1987; McKinney & Jaklin 2001); and (2) the increased production of micrite in micro-bioherm cores that was shed and accumulated in surrounding areas (see also Watts 1988; Nose et al. 2006; Kershaw et al. 2007). Recognition of this build-up-margin sediment is important for properly reconstructing paleoenvironmental parameters of the basal lithofacies of the Massie Formation, as study of isolated slabs of this material or sections that do not permit documentation of lateral relationships of micro-bioherms may lead to flawed interpretations about the otherwise well-winnowed carbonate deposit.

An additional sedimentological effect of build-ups in the Massie Formation is the increased abundance of large-diameter pelmatozoan pluricolumnals in micro-bioherm-marginal deposits (Fig. 6C). These represent bioclasts sourced from the echinoderm fauna that encrusted micro-bioherms, as evidenced primarily by the similarity of columnal morphologies between both substrata. In addition, field (Meyer & Meyer 1986) and laboratory (Blyth Cain 1968; but see Šavarese et al. 1997; Gorzelak & Salamon 2013) studies demonstrated the difficulty in transporting large crinoid bioclasts far from crinoid living sites, and no concentrations of large pluricolumnals are present beyond micro-bioherm margins in spite of the abundance of echinoderm material on the hard-ground surface (Thomka & Brett 2014b). The adjacent, topographically positive micro-bioherms seem...
the most likely source area for accumulations of large pluricolumnals. The increased abundance of large calcareous bioclasts appears to have resulted in decreased physical stability of sediments surrounding build-ups, as inferred by the total absence of pelmatozoan attachment structures or encrusting laminar bryozoans in such deposits. Although the increased influx of fine-grained sediment may have played a role, muddy and presumably unlithified substrata in topographically negative areas of the adjacent hardground are encrusted. This suggests that the coarse, rubbly substrate surrounding microbioherms precluded permanent colonization by sessile organisms, including crinoids with complex dististelar attachment strategies that were capable of occupying other shifting, unstable substrates (Brett 1981, 1984).

**Palaeontological effects**

*Influences on echinoderm palaeoecology, pelmatozoan encrustation of micro-bioherms.* – Thirteen pelmatozoan attachment structures, attributable to crinoids, rhombiferans and diploporites, are present on the micro-bioherm-bearing hardground at the Napoleon quarry, and three of these are unique to build-ups. Micro-bioherm exteriors are densely encrusted by dendritic radix structures (sensu Brett 1981; Figs 4C, 7A, B) characterized by lumina with trilobate, tetralobate and pentalobate configurations. Pentalobate lumen-bearing holdfasts are associated with the common monobathrid crinoid *Eucalyptocrinites* (Halleck 1973; Brett 1981, 1984), trilobate lumen-bearing holdfasts cannot be definitively associated with a specific pelmatozoan taxon (Thomka & Motz 2014).

The density of encrustation by pelmatozoans (Figs 4C, 7A, B) clearly indicates that micro-bioherms represented favourable substrata. The most likely explanation for this is the increased current velocities associated with elevated and topographically irregular surfaces and the decreased likelihood of burial during episodic depositional events. Interestingly, the taxa that encrusted build-ups are those with some of the longest columns of the Massie Formation echinoderm fauna (Brett 1984; Frest et al. 1999) rather than short-stemmed or thecally attached taxa (e.g. holocystitid diploporites, edrioasteroids and cyclocystoids) that would be expected to benefit most from occupation of the highest increased substrate on the seafloor (though Frest et al. 2011 reported diploporite thecal attachments on micro-biohermal masses, apparently from other localities). The unusual nature of this distribution is further highlighted by the partitioning of attachment structure morphotypes on the hardground surface where build-ups are absent: in these areas, holdfasts attributable to long-stemmed taxa are restricted to low areas, whereas increased areas are encrusted exclusively by attachment structures associated with shorter-stemmed taxa.

One explanation for this pattern is that microbioherms served as isolated ‘islands’ of hard substrata during initial burial of the hardground by siliciclastic mud of the overlying mudstone lithofacies of the Massie Formation (Fig. 3). That is, the
upper surfaces of build-ups may have been temporarily disconnected from the surrounding hardground, having been encrusted by long-stemmed pelmatozoans after the hardground was partially or completely buried (Thomka & Brett 2014b). However, micro-bioherms that were cut open have branching radicles identical to those belonging to the holdfasts on exterior surfaces (Fig. 5), indicating that build-ups were occupied by the same (long-stemmed) taxa throughout their growth.

An alternative explanation for this distribution is that pelmatozoan taxa that initially settled on micro-bioherms established and maintained populations on this substrate to the exclusion of others. This is supported by monotypic clustering of radix morphotypes (Figs 4C, 7B), suggesting preferential settling of larvae near members of the same taxon, possibly aided by chemosensory data (Donovan et al. 2007; Donovan & Harper 2010; Jagt et al. 2010). Further, this mechanism accounts for the persistence of the same taxa as encrusters during the entire growth history of build-ups, as well as the identity of encrusters as geographically widespread, eurytopic pelmatozoans (Brett 1984).

Swelling of attachment structures. – One of the most striking features of pelmatozoan holdfasts encrusting micro-bioherms is the severe swelling and thickening of Eucalyptocrinites and Caryocrinites radices by secondary stereom (Fig. 7A, B). Stereomic overgrowths are massive and result in amalgamation of the most proximal portions of radicles and, in some cases, distortion of the symmetry of lumina (Fig. 7A). Some swollen attachment structures are overgrown by amorphous stereom so severely that no radicles are visible, giving the appearance of conical, crustose holdfasts (Fig. 7B), whereas others display tapering, dichotomously branching distal radicles (Fig. 7A).

Dendritic radix structures attributable to taxa encrusting both micro-bioherms and the surrounding hardground are thickened by secondary stereom on the former (Fig. 7A) and characterized by slender radicles on the latter (Fig. 7C). The exact reason(s) for this swelling response on micro-bioherms is unknown. Seilacher & MacClintock (2005) interpreted development of a thick secondary stereomic cortex as a response to increased hydrogen sulphide in sediments occupied by holdfasts; however, we see no evidence for adverse geochemical conditions on micro-bioherm exteriors (Thomka & Brett 2014b). The swelling does also not appear to be a reflection of very old ages for afflicted taxa, as radices of different sizes but belonging to the same taxa are swollen to the same extent. A more likely explanation is that swelling was induced as a response to antagonistic interaction between encrusting pelmatozoans and other organisms, perhaps microbes on the surface of build-ups. The small amount of viscerata within pelmatozoan lumina (see recent discussion in Donovan et al. 2010) would have been easily protected by excessive stereomic overgrowths, and damage to overgrowths would not likely have significantly diminished the health of the organism.

Fig. 7. Selected pelmatozoan attachment structures from the Napoleon quarry. A, severely swollen holdfast of Eucalyptocrinites showing amalgamation of proximal radicles, more distal tendril-like radicles and distorted pentalobate lumen. Scale bar = 0.5 cm. B, external portion of micro-bioherm encrusted by numerous attachment structures (marked by arrows) swollen by secondary stereom growth. Scale bar = 1 cm. C, attachment structure of Eucalyptocrinites on the hardground surface surrounding micro-bioherms. Note the absence of thickening and the clearly visible plate sutures, which are concealed on holdfasts encrusting micro-bioherms. Scale bar = 1 cm.
An intriguing alternative explanation for the swelling of pelmatozoan attachment structures on micro-bioherms at the Napoleon quarry is that this represents purposeful growth of skeletal material to maximize the strength of fixation to increased substrata. Pelmatozoans that occupied build-ups were in a position to benefit from increased food and decreased respiratory stress, permitting these taxa to divert significant amounts of energy away from vital functions and towards growth of larger, stronger holdfasts. Thus, the severe thickening of holdfasts may represent biological investment in skeletal cement precipitated to prevent dislodgement from atop micro-bioherms.

Influences on ichnology, pascichnial traces. – Trace fossils at the Napoleon quarry hardground comprise domichnia (Thalassinoides galleries, minute Trypanites in large bioclasts) reflecting a lithology poor in particulate organic matter. However, in areas immediately surrounding micro-bioherms, a trace characterized by dark-grey mud fill and a horizontally meandering configuration is present (Fig. 8). Although the ichnotaxonomic identity of this trace is currently unclear, we believe that the best candidate for this ichnogenus is a non-looped form of Gordia, which appears a more accurate identification than the superficially similar Planolites and Helmithopsis.

Regardless of ichnogeneric classification, the occurrence of these biogenic sedimentary structures has palaeoenvironmental significance. Meanders represent strong evidence of deposit-feeding/grazing behaviour rather than simple locomotion, making these traces pascichnia rather than repichnia. The paucity of particulate organic matter precluded grazing behaviour on the sediment-starved surface except in the immediate vicinity of micro-bioherms, suggesting a locally increased influx of detrital material surrounding build-ups. Only in the muddy micro-bioherm-margin deposits could organisms adopt a deposit-feeding strategy, whereas elsewhere on the Napoleon hardground, the relatively pure carbonate substrate allowed only suspension feeders to thrive.

Influences ichnology, bioerosion structures. – The Napoleon quarry hardground and associated micro-bioherms are surprisingly devoid of borings (Thomka & Brett 2014b). The abundant large pelmatozoan pluricolumnals that accumulated adjacent to build-ups dramatically increased the number of bioerosion structures, namely the simple boring Trypanites (Fig. 6C). It seems unlikely that this distribution was controlled by palaeoenvironmental parameters other than substrate (i.e. Trypanites-producing organisms almost certainly did not prefer the increased turbidity of micro-bioherm margins). Rather, thick pluricolumnals (Fig. 6) were ideal substrata for boring organisms, resulting in increased abundance of bioerosion structures and fidelity of the record of biotic interactions at the study site.

Influences on trilobite taphonomy, bumastine clusters. – Localized clusters composed entirely of bumastine pygidia, and slightly less abundant cranidia (Fig. 9A, B), are relatively common within the cores of micro-bioherms. Determining the precise size of these clusters is difficult because they are rarely preserved intact as three-dimensional blocks; rather they are typically preserved as fragments in the portion of the quarry where micro-bioherms were exposed by quarrying activity. Trilobite material is
commonly fractured and otherwise damaged, although this may reflect modern weathering processes. Trilobite elements are densely concentrated and commonly display complementary, nested stacking, especially in large clusters (Fig. 9B). Nested pygidia/cranidia are the most commonly oriented concave-up, although it is difficult to determine orientations for many examined clusters. Some clusters are entirely grain-supported, but most are characterized by trilobite grains ‘floating’ in non-fossiliferous sediment. Skeletal material in these clusters occurs within light grey, very argillaceous, otherwise unfossiliferous micrite (Fig. 9A, B). This sediment is clearly distinct from that of micro-bioherm margins, and this fine-grained material occurs in the cores of build-ups. Elements of these large trilobites are rare on the surface of the hardground in between micro-bioherms (although they are abundant in immediately overlying muds), and clusters are restricted to the mounds (Mikulic 1999; D. Bissett, personal communication 2013).

The most logical interpretation is that these clusters represent accumulations within irregular and restricted cavities and/or material swept into undercut platform-like surfaces in micro-bioherms. These are genetically linked to palaeoecological and/or sedimentary processes in carbonate build-ups, as similar features have been described from coeval build-ups in the Irondequoit Limestone-Rochester Shale of New York and Ontario (Sarle 1901; Mikulic 1979; Cuffey & Hewitt 1989; Brett 1999), large mounds on the rim of the Michigan Basin (Mikulic 1976, 1979, 1987), and in Middle Devonian build-ups of the Northern Appalachian Basin, where concentrations of phacopid material have been documented (Speyer & Brett 1986).

Some issues exist with the otherwise parsimonious interpretation that these features represent protected cavities where bumastines moulted (summarized in Mikulic 1976), but the potential role of moulting serves as an important starting point for understanding the nature of clusters of bumastine material in the Napoleon quarry. Discarded exuvial elements would have been readily transported by even low-velocity currents (Mikulic 1990), although episodic storm events seem a more likely explanation for the nested, potentially edgewise orientation of bioclasts and disarticulated state of trilobites. The paucity of other clasts of similar size and shape and dominance of pygidia/cranidia suggests selective hydrodynamic sorting by density (Mikulic 1990). Some behavioural aspect of bumastine trilobites may have also contributed to formation of these clusters, but this behaviour remains unknown.

Influences on trilobite taphonomy, articulated calymenids. – One of the most conspicuous palaeontological associations at the Napoleon quarry occurs between micro-bioherms and articulated calymenid trilobites (Fig. 9C–E). This fauna includes the wide-ranging genus Calymene (Fig. 9D) and the rare, distinctively ornamented spathacalymenids (Fig. 9C, E), which are found only in the Massie Formation. The distribution of trilobites is patchy, but articulated specimens occur only in the vicinity of micro-bioherms, in siliciclastic muds that immediately
order late transgression–early highstand, characterized by increased influx of siliciclastic mud to epeiric ramp settings via episodic storm deposition (Brett 1995; Brett et al. 2012a), leading to burial of the hardground and, eventually, micro-bioherms. The obIgnoring events that entombed spathacalymenids would not have resulted in preferential concentration of specific trilobite taxa near build-ups, but rather would preserve elements of primary spatial relationships (Brett & Baird 1986; Feldman 1989; Brett et al. 1997). Consequently, the hypothesis that calymenids, particularly spathacalymenids, preferentially lived near build-ups is supported. Studies of micro-bioherms in other comparable settings represent a promising prospect for discovery of rare and/ or unusual trilobite faunas.

Discussion

Stratigraphical setting of Napoleon micro-bioherms

Development of micro-bioherms at the hardground within the Massie Formation is related to a termination of clastic sedimentation and static redox boundaries during the most rapid rate of transgression within a third-order sequence (McLaughlin et al. 2008; Brett et al. 2012a; Thomka & Brett 2014b). Low turbidity and the availability of hard substrata during this phase of relative sea-level rise permitted establishment of a biofacies dominated by sessile suspension feeders (see Brett 1995, 1998), including taxa encrusting the hardground surface and incipient build-ups. An abundance of photosynthetic microbes responding to favourable, sediment-starved conditions likely enhanced upward growth of micro-bioherms through increased micrite production (Archer & Feldman 1986; McLaughlin et al. 2008). Micrite almost certainly accumulated close to the site of production (Gischler et al. 2010), having been bound by accreting laminar bryozoans and encrusting peltmatozoans and brachiopods, the skeletal remains of which also contributed to upward growth (Archer & Feldman 1986).

The encrusted hardground and associated micro-bioherms mark the surface of maximum sediment starvation in siliciclastic-carbonate sequences in epeiric seas (Brett 1995, 1998; Schmid et al. 2001; McLaughlin et al. 2008). Consequently, micro-bioherms and similar build-ups commonly occur at the sharp contact between underlying dense carbonates, representing early transgressive conditions, and siliciclastic mudrocks, representing late transgressive to early highstand conditions (Fig. 2). Build-ups pro-
trude upward into the muds, which onlap the topographically positive and palaeoecologically distinct features (Walker & Alberstadt 1975; Brett 1995). This relationship can also be observed in coeval sections at the contact between the Irondequoit Limestone and overlying Rochester Shale in western New York and Ontario (Sarle 1901; Coffey & Hewitt 1989; Brett 1999) as well as within the Middle Devonian succession of New York (Speyer & Brett 1986; Brett 1995).

Micro-bioherms within the Massie Formation occur at a lithologically and sequence stratigraphically analogous position to slightly younger buildups at the hardground contact between the Laurel Limestone and overlying Waldron Shale in the Cincinnati Arch region (Thomka & Brett 2014b; see also Halleck 1973; Ausich 1975; Archer & Feldman 1986). Although many similarities between the Massie and Waldron micro-bioherms have been described in this study, two major differences exist. Firstly, beyond small fenestrae, there is no evidence for late-stage dissolution (e.g. stylolites, recrystallized fossils) in Massie micro-bioherms, in spite of the large proposed role of dissolution in the genetic model for Waldron micro-bioherms developed by Archer & Feldman (1986). Secondly, no tabulate corals or stromatoporoids are present within Massie micro-bioherms, in contrast to Waldron micro-bioherms (Archer & Feldman 1986) and to large Wenlock-age carbonate mounds that grew in shallower water than that interpreted for the Napoleon quarry. Examples of these shallow-water mounds include buildups within the Högklint Formation of Gotland (Watts & Riding 2000), the Muksha Formation of western Ukraine (Jarochowska et al. 2014) and multiple units on the rim of the Michigan Basin (Mikulic 1987; Mikulic & Klussendorf 1999). These differences appear to reflect bathymetric effects, as growth of large, colonial framework elements and diagenetic dissolution are more significant in up-ramp settings, whereas micrite precipitation, siliciclastic mud trapping and organismal binding were more dominant in deeper environments.

**Implications for Middle Silurian palaeoceanographical events**

Although micro-bioherm growth can be fostered by purely sedimentological/stratigraphical phenomena, similar buildups do not occur at every major flooding surface in the Middle Silurian succession of eastern North America. Notably, micro-bioherms are not present at the sharp flooding contact that separates late transgressive carbonate sediments of the Telychian (late Llandovery) Dayton Formation from the overlying highstand muds of the basal Osgood Formation (latest Telychian-earliest Sheinwoodian) in the Cincinnati Arch region. This is unusual because this contact represents a lithologically/stratigraphically analogous setting to the Massie Formation hardground. Further, this surface represents a eustatic event that is largely recognized as the most significant highstand of the Silurian Period (Ross & Ross 1996; Johnson 2006; Loydell 2007). Hence, the conditions responsible for micro-bioherm development were not strictly dictated by third-order scale stratigraphic variations.

The concept of time-specific facies (sensu Brett et al. 2012b) provides a conceptual comparative framework within which distinctive lithological features and faunas can be analysed. The occurrence of micro-bioherms at the flooding surfaces between the basal carbonate and middle mudstone lithofacies of the Massie Formation (and coeval Irondequoit-

![Fig. 10. Micro-bioherm-margin sediment from strongly dolomitized strata of the Cemex quarry, Greene County, southwestern Ohio. The Massie Formation is nearly barren here except for sediment surrounding micro-bioherms. A, slab containing abundant large bioclasts, particularly pelmatozoan pluricolumnals and dististellar attachment structures. Scale bar = 5 cm. B, close-up of pluricolumnal from the slab in Figure 10A showing multiple minute Trypanites borings, characteristically abundant in pelmatozoan material from micro-bioherm flank deposits. Scale bar = 0.5 cm.](image)
Rochester contact) and between the Laurel and Waldron formations, but not at the analogous position between the Dayton and Osgood formations, indicates a previously unrecognized aspect of time specificity. Both the Massie Formation flooding surface and the Laurel-Waldron contact represent micro-biohermal intervals that correspond to globally recognized, positive carbon isotope excursions, namely the lower Sheinwoodian (‘Treviken’) and lower Homerian (‘Mulde’) excursions, respectively (Cramer et al. 2006; McLaughlin et al. 2012). Recently, Thomka et al. (2012) proposed a model for the lower Sheinwoodian excursion and related biological, stratigraphical and geochemical events that linked a brief episode of cooling to changes in eustatic sea level and locally increased palaeoproduction. This ultimately led to a major disruption to the global carbon cycle (manifest in the carbon isotope excursion) and development of a palaeoecologically unusual echinoderm fauna.

We submit that the occurrence of micro-bioherms characterized by a micrite-dominated composition is an additional, far-field reflection of this palaeoclimatic perturbation. Increased micrite production, although commonly associated with warming episodes (Holland & Patzkowsky 1996), would have been fostered by increased productivity even during cool intervals, favoring mud-dominated build-ups over skeletal framework-based build-ups (e.g. Riding 2009). Hence, we suggest that micro-bioherms in the Massie Formation are genetically related to altered palaeoceanographic conditions during the early Sheinwoodian.

Regional faunal patterns

Deposits that are equivalent to the micro-bioherm-bearing unit at Napoleon represent intervals that hold the greatest potential for preserving an invertebrate fossil fauna in sections that have undergone dolomitization. Whereas most of these sections are nearly or completely unfossiliferous, the coarse bioclastic particles and increased argillaceous component characteristic of micro-bioherm margin sediments may make such deposits more resistant to thorough dolomitization. As a test, several dolomitized, micro-bioherm-bearing sections were searched for remnant fossils, with the lithology and position relative to build-ups noted. Sections studied included roadcuts at Madison, Indiana (N38°46'52.85", W83°57'38.86’), Crestwood, Kentucky (Fig. 1A), Mt. Washington, Kentucky (N38°40’11.65”, W85°22’10.17”), on I-71 in Oldham County, Kentucky (Fig. 1D) and a quarry in Greene County, Ohio (N39°46’52.85”, W83°57’38.86’)

In all instances, micro-bioherm-margin sediments contained recognizable fossil material in greatest abundance (Fig. 10A) compared to other lithologies. Further, some of the palaeoecological and taphonomical patterns documented at the Napoleon quarry were present in dolomitized sections. Notably, pelmatozoan pluricolumnals are relatively common surrounding micro-bioherms, and these bioclasts display abundant bioerosion structures (Fig. 10B), allowing recognition of evidence for biotic interactions in deposits where such palaeoecological data are otherwise impossible to document. We suggest that, when attempting to compile faunal data from diagenetically altered sections, sediments immediately surrounding micro-bioherms represent the best options for yielding identifiable macrofossils.

Conclusions

1 An undolomitized Middle Silurian (Wenlock: Sheinwoodian) section at the New Point Stone quarry near Napoleon, Indiana, permitted detailed study of the influence of micro-bioherms on the sedimentology, palaeoecology and taphonomy of a transgressive seafloor. Micro-bioherms, which display a micrite and fistuliporoid-dominated fabric, grew upward from a sediment-starved hardground surface during an episode of rapid sea-level rise.

2 Micro-bioherms are surrounded by material characterized by increased mud content as well as coarse skeletal rubble. This reflects the baffling effects of abundant suspension-feeding organisms and increased micrite production, as well as an increased influx of large-diameter pelmatozoan pluricolumnals shed from build-ups. Mud influx was significant enough to encourage grazing behaviour among vagile benthos, resulting in pascichnial traces. The abundance of pluricolumnals resulted in abundant bioerosion structures.

3 Pelmatozoan attachment structures that encrusted micro-bioherms comprise dendritic radix structures attributable to long-stemmed camerate crinoids and rhombiferans. Holdfasts are swollen by secondary stereom reflecting either a response to some antagonistic interaction or biological investment in strong anchorage to the advantageous position atop micro-bioherms.

4 Clusters of bumastine trilobite material, possibly related to moulting, are known from pockets
contribute to the International Geoscience Program (IGCP) Project kulic (Illinois State Geological Survey) and the constructive with David L. Meyer (University of Cincinnati), Donald G. Mi- nistry of Natural Resources Canada Award to JRT. The owners and management of the New Point Dry Dredgers Paul Sanders Award and Paleontological Research Institute (Burlington, Vermont).


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