‘Intrites’ from the Ediacaran Longmyndian Supergroup, UK: a new form of microbially-induced sedimentary structure (MISS)

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Abstract: Simple discoidal impressions are the only evidence of complex life in some Ediacaran and older rocks, but their interpretation is notoriously difficult. We reassessed a puzzling discoidal form from the c. 560 Ma upper Burway Formation of the Ediacaran Longmyndian Supergroup, Shropshire, UK. The structures, previously described as Intrites punctatus Fedonkin, are found on both the bed tops and soles. They vary in morphology from mounds with central depressions to incomplete rings and pairs of short ridges. Examination of the purported Intrites documented from the Longmyndian in cross-section revealed a torus-shaped structure bounded by microbial mat layers and commonly containing white laminae. We interpret the ‘Longmyndian Intrites’ as a product of microbial trapping, sediment binding and authigenic clay mineral and carbonate precipitation on the flanks of small sediment volcanoes. Subsidence of the ring-like structure into muddy sediments resulted in a torus-shaped microstromatolite. Preferential stromatolitic growth parallel to the prevailing current produced the observed partial rings or parallel ridges and explains their preferential orientation as current alignment. This interpretation of ‘Longmyndian Intrites’ expands the known variety of microbially-induced sedimentary structures (MISS) and emphasizes the importance of considering microbially-induced structures and abiological processes when interpreting discoidal impressions in ancient rocks.

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The enigmatic, soft-bodied Ediacaran macrobiota, which flourished from c. 580 to 541 Ma, is dominated by discoidal impressions. In the absence of more diagnostic features, such as fronds, some Precambrian successions with discoidal markings have been used as evidence for the presence of an Ediacaran macrobiota and thus of probable complex life (e.g. Hofmann et al. 1990; Farmer et al. 1992; Arrouy et al. 2016). It is well known that round impressions may be produced in a variety of ways, including abiogenically by fluid escape (e.g. Cloud 1960; Farmer et al. 1992; Menon et al. 2016). The careful, critical investigation of possible discoidal body fossils is a fundamental prerequisite to an accurate assessment of Ediacaran taxonomic diversity, palaeobiology and palaeoecology.

Discoidal impressions were first observed in rocks of the Ediacaran Longmyndian Supergroup, Shropshire, UK by the Victorian palaeontologist John Salter (Salter 1856, 1857). Subsequent observations revealed widespread evidence for the former presence of microbial mats, including microbially-induced sedimentary structures (MISS) and fossilized remnants of microbial filaments in thin section (Bland 1984; Peat 1984; McIlroy et al. 2005; Callow & Brasier 2009; Callow et al. 2011b). The nature of the Longmyndian discoidal impressions has long been debated (e.g. Cobbold 1900), but they have latterly been regarded as probable evidence for complex Ediacaran life. The discoidal structures were formally described as Medusinites aff. asteroides, Beltanelliformis brunsea, B. minutae and Intrites punctatus (McIlroy et al. 2005). The first three of these structures have been reinterpreted as pseudofossils resulting from sediment injection and loading produced by small-scale fluid escape structures mediated by microbial mats (Menon et al. 2016). These processes are insufficient to explain the remaining disc, described as I. punctatus Fedonkin by McIlroy et al. (2005). A re-examination and reinterpretation of the purported Longmyndian examples of Intrites is the subject of this paper. It should be emphasized that the discussion herein refers purely to material from the Long Mynd. The type material from the White Sea Ediacaran successions (Fedonkin 1980) differs from the

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Longmyndian form in being found only as rows of positive hyporelief impressions and is currently a valid taxon.

Lithology and stratigraphic context

The specimens of Longmyndian Intrites discussed in this paper were collected from rocks of the upper Burway Formation, Stretton Group, Longmyndian Supergroup and were exposed in a disused quarry in Ashes Hollow (Fig. 1). Intrites-like structures (ILS) are found at Ashes Hollow in the Long Mynd, along with other discoidal impressions that have been determined to be fluid-escape structures (Menon et al. 2016), preserved in thinly interlaminated units of mudstone, siltstone and fine-grained sandstone. The fine laminae, <0.2–1 mm thick, show a strong colour contrast between the grey-green of the chloritic mudstone and the dark brown of the hematitic sandstone, allowing a detailed study of the sedimentary structures in polished cross-section. Associated thin white laminae <0.2 mm thickness, previously thought to host microbial filaments preserved in a white aluminosilicate mineral (Callow & Brasier 2009), were found in this investigation to consist entirely of the silicified remains of microbial mat grounds (Fig. 2).

Initial scanning electron microscopy–energy-dispersive X-ray spectrometry investigations of thin sections through these silicified mats indicated a striking absence of sulphur in these rocks. The microbial layers appear to have been limited to a few types of filamentous cyanobacteria without any evidence for underlying assemblages of either sulphur-reducing or sulphur-oxidizing bacteria. Little phosphorus was evident, suggesting nutrient-poor conditions. The Burway Formation has previously been interpreted as shallow marine deltaic sediments and the overlying Cardingmill Grit as a fluvial deposit (Pauley 1986, 1990, 1991).

The age of the upper part of the Burway Formation is constrained by U/Pb geochronology of tuffs from the underlying Stretton Shale Formation and the stratigraphically higher Lightsplot Formation and is estimated to be c. 560 Ma (Compston et al. 2002; Fig. 1; Menon et al. 2016).

Morphologies of Longmyndian Intrites

The discoidal ILS described from the Long Mynd are unusual in occurring with the same morphology on the soles and tops of beds (i.e. they occur in positive epirelief and positive hyporelief; Fig. 3). There is little size variation within the ILS material, which is generally 2–3 mm in diameter, with rare examples reaching 4 mm. This morphotype occurs in a continuum of forms, from a raised mound with a small central depression to broad, low-relief ridges forming an incomplete ring around a wide central flat area (Fig. 4). In some cases, the ILS are found as paired, almost straight, short ridges instead of arcs forming an incomplete ring (Fig. 4c, f; the ‘Are-nicolites didymus’ morph of Salter 1856). Some upper surfaces of beds exhibit counterparts of ILS as negative impressions with a central peak or ridge (Figs 3 & 4d), presumably moulds of positive impressions on the sole of the originally overlying bed. ILS are usually found in clusters on bedding planes. Interestingly, they are not found in association with the ridges of the common Ediacaran MISS Arumberia (McIlroy & Walter 1997; McIlroy et al. 2005), a structure also seen in the Long Mynd. ILS are sometimes seen in association with Medusinites-like pseudofossils preserved in positive hyporelief and, in such cases, the ILS differ only by virtue of having a central depression rather than a pinhead boss. More characteristically, however, ILS occur in dense aggregations on bedding planes as the only circular morphotype present.

Methods

In addition to field observations and the examination of >40 hand specimens, the ILS from the Longmyndian were examined in polished cross-section to gain insights into their nature and as a test of bioge nicity. Fifteen hand specimens from the upper Burway Formation with ILS on either the upper or lower bedding surfaces were sectioned, serially ground and photographed. The resultant photographic database enabled examination in cross-section of >30 examples of ILS on these hand specimens. ILS, along with other sedimentary features and microbial mats, were also studied in 10 thin sections. Work on the microbial mats, including scanning electron microscopy–energy-dispersive X-ray spectrometry, is ongoing, following which the thin sections will be placed in the Oxford University Museum of Natural History, where specimens of ILS previously collected by Richard Callow and examined during this study are deposited (OUMNH Á.02390–Á.02394).

Longmyndian Intrites in cross-section

The ILS on bedding planes can look similar to gas domes or sediment volcanoes as they are raised structures with central depressions, although the crater flanks are more rounded than the conical shape typical of sediment volcanoes. Given the small-scale fluid escape that characterizes these rocks (see Menon et al. 2016), ILS might be expected to be simply sediment volcanoes. In vertical cross-section, however, the ILS consist of two
lobes formed from the pinching and swelling of laminae (Fig. 5). The symmetry of the lobes above and below the horizontal plane explains the identical appearance of the ILS on the sole and top surfaces. Some examples only have upper lobes (e.g. Fig. 5e) and, in some cases, additional laminae drape the upper lobes to form a dome-like structure (Fig. 5g).

Fig. 1. Location and stratigraphic position of Ashes Hollow area of study (after Menon et al. 2016). (a) Simplified geological map of the study area with the site of the specimens indicated. Inset map shows the location of the Long Mynd. (b) Stratigraphy of the Longmyndian Supergroup following the interpretation of Pauley (1990, 1991), with the stratigraphic position of the Ashes Hollow site marked, together with dates measured by Compston et al. (2002).
In three dimensions, the ILS form either a complete, or partially open, torus that is sometimes so open that it forms linear, sub-parallel lobes. ILS have such a characteristic appearance that they are clearly identifiable when entirely within cross-sections, allowing them to be studied in full sedimentological context (Figs 5c & 6).

The ILS in the Longmyndian only occur in association with mudstone laminae, with which they are contiguous, and all are associated with white microbial mat laminae that may be above, below, or sometimes both above and below the ILS (e.g. Fig. 5a). Forms with only upper lobes overlie a thick white microbial mat (Figs 5c, e & 6a). In some examples, an indentation is observed on the bed sole, forming the lower halves of the lobes, but the formation of the upper halves of the lobes appears to have been impeded by an overlying white matground (Fig. 5h).

The ILS sometimes approximately overlie other ILS at lower stratigraphic levels (e.g. Figs 5c & 6b). The central depression of the torus commonly contains sandstone where the ILS are underlain by a white microbial matground (Fig. 6). The sediment is fine-grained within the lobes, commonly paler in colour than the adjacent mudstone laminae, and may contain pale or white laminae (Figs 5d, g & 6a). In thin section, the pale areas within the lobes appear dark, suggesting the presence of micrite (Fig. 7).

**Interpretation**

A variety of sub-millimetre-scale dark sandstone features observed in cross-section in upper Burway Formation rocks have already been explained as...
small-scale fluid-escape structures (Menon et al. 2016). The common occurrence of such fluid-escape structures between the lobes of ILS, just above a white microbial matground lamina (Fig. 6), may provide the key to understanding these ILS. Microbial mat growth and decay may result in gas effusions that have the potential to escape upwards, sometimes in association with fluidized sand (Menon et al. 2016). Fluid-escape columns and disturbances commonly originate at matground laminae. It is considered that gas, and pore fluids, may seep through tears in the matgrounds without leaving any indication of a feeder column below. The ILS may develop around small sediment volcanoes to produce surface features with rounded flanks, rather than the conical flanks expected of a sediment volcano (e.g. Fig. 5f; Reineck & Singh 1973). The indentations on sole surfaces, with local distortion of laminae (e.g. Fig. 5h), suggest failed injections or the narrow seepage of fluids through the structure, with the indentation producing gentle lobes of displaced muddy sediment on either side. Fluid-escape structures with entrained dark sand are sometimes observed to have disrupted the tops of lobes and are inferred to have exploited the pre-existing sediment feeder column that created the ILS (Fig. 8).

It is likely that homogeneous mudstone within the lobes primarily accumulated by baffling and

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**Fig. 4.** Various forms of Longmyndian *Intrites*. (a) On bed sole, both as raised rings with flat centre and as mounds with central depression. (b) On bed top, as raised mound with central depression or two slightly curved parallel ridges. (c) On bed sole as relatively narrow rings and parallel ridges. (d) Counterparts on top surface as shallow negative impressions with central peaks or ridges. (e, f) Close-ups of portions of specimen in (c): sole surface, with complete and near-complete ring-like forms (e); and approximately aligned ridges and pairs of arcs (f) (note different scale for (e) and (f)). Scale bars: (a–d) 1 cm; (e–f) 1 mm.
trapping by microbes and may also include some microbially-mediated authigenic clay mineral precipitation – a process that has been implicated in the exceptional preservation of fossils in lagerstätten such as the Burgess Shale (see Orr et al. 1998; Gabbott et al. 2001; Butterfield et al. 2007; Wacey et al. 2014) and has already been proposed to explain the aluminosilicate preservation of Longmyndian microbes (Callow & Brasier 2009). Both these processes have been described as occurring within days in cyanobacterial biofilms grown in siliciclastic environments with high seawater silica concentrations and suspended clay (Newman et al. 2016).

Trapping and binding, together with the precipitation of authigenic clay minerals and some micritic carbonate on to the extracellular polymeric substances of the microbial mats, may have caused the build-up of laminae (Dupraz et al. 2001; Butterfield et al. 2007; Wacey et al. 2014) and has already been proposed to explain the aluminosilicate preservation of Longmyndian microbes (Callow & Brasier 2009). Both these processes have been described as occurring within days in cyanobacterial biofilms grown in siliciclastic environments with high seawater silica concentrations and suspended clay (Newman et al. 2016).

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Fig. 6. (a) Longmyndian *Intrites* above white microbial mat layer (left, arrowed) showing internal layering and dark sandstone in the dip between lobes; the edge of a further, shallow *Intrites*-like form is seen to the right (right arrow). (b) Two *Intrites*-like structures, arrowed, in approximate vertical alignment. The upper specimen has associated sandstone features, whereas the lower specimen is unusual in having a thick white microbial layer above rather than below, although a thin white layer forms the lower bound. Scale bars: 1 mm.

Fig. 7. (a, b) Thin sections through *Intrites*-like structures in plane polarized light. Note dark areas within lobes in transmitted light, which appear pale in reflected light, suggesting some microbially-mediated carbonate precipitation as micrite. Scale bars: 1 mm.

Fig. 8. Example of Longmyndian *Intrites* on bed sole, with pale layers within the lobes and disruption by fluid escape above, resulting in the distortion of the still soft and unconsolidated mud laminae at the top of the lobes. Scale bar: 1 mm.
Larger microbially-mediated sediment domes and related structures without the central depression would be called stromatolites. The ILS are far smaller than stromatolites – consisting only of several rather than tens of laminae – and appear to lie on the boundary between the predominantly two-dimensional MISS and the mainly three-dimensional stromatolites (see Noffke & Awramik 2013).

The ILS of the Longmyndian are inferred to result from a combination of stromatolite-like microbial trapping and binding of sediment and microbially-mediated clay mineral and carbonate precipitation with the effusion of fluid and fine-grained sediment from a sediment volcano. The raised topography of a shallow sediment volcano would attract cyanobacteria competing for light (Gerdes et al. 1994) and give greater access

Fig. 9. A model for the formation of Longmyndian Intrites by the build-up of stromatolitic laminae on the raised topography of a small sediment volcano produced by injection from below with seepage of fluid through compressed laminae (a, c) or effusions of gas through tears in the matground (b). Scale bar: 1 mm.
to sediment particles sweeping past on a current, thereby enhancing the microbial trapping and binding of sediment together with possible authigenic clay mineral and carbonate precipitation on the crater flanks, resulting in the growth of a torus-shaped ILS around the central vent (Fig. 9). The drawing up of nutrients from below the mat by fluid escape could also attract higher concentrations of cyanobacteria around a sediment volcano (Gerdes et al. 1994; Gerdes 2007). However, such a chemotactic response may be less significant in this example because the environment appears to have been nutrient-poor.

A combination of the sinking of the ILS sediment cone into the underlying muddy sediment and the displacement of sediment at the injection site is inferred to produce the typical full double-lobed form of the ILS in vertical cross-section, with the lower half of the lobes producing Intrites-like rings on bed soles (Fig. 9a). Effusion through small tears in a thick microbial mat may result in the formation of only the upper lobes (Fig. 9b). In some cases, after the cessation of sediment effusion, the build-up of laminae by microbial trapping and binding continued, producing a more typical stromatolite-like dome shape, which overarched the original lobes (Figs 5g & 9c).

Trapping and binding by cyanobacteria tends to cause stromatolitic laminae to preferentially build up parallel to a current (Logan et al. 1964; Garlick 1988; Schieber 1998, 1999). Thus the portions of the Intrites-like ring parallel to the current are more likely to aggrade, resulting in incomplete rings or, in extreme examples, parallel ridges (Fig. 10). This influence of the current may explain the alignment of the double-ridge form of ILS observed on some bedding planes (e.g. Fig. 4c).

Currents may also cause the erosion and redeposition of parts of a raised ring, but erosion does not appear to be a major factor in the formation of the incomplete rings of ILS. Had they been purely

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**Fig. 10.** Preferential build-up of current-parallel sides of a low-relief sediment volcano crater due to trapping and binding by cyanobacteria produces two arcs or parallel ridges on the bedding surface. Equivalent structures on sole surfaces result from the sinking of the stromatolitic structure into soft muddy sediment below. Scale bar: 1 mm.

**Fig. 11.** (a) Salter specimen BGS GSM 49160 showing microbial surface texture and paired pits (example arrowed). (b) Close-up of Salter specimen shown in (a), showing double pits and microbial filaments (arrowed); note the close similarity with the positive Intrites-like structures on bed sole in Figure 3b. Scale bars: (a) 1 cm; (b) 1 mm. Images of Salter’s specimen BGS GSM 49160 reproduced with the permission of the British Geological Survey © NERC. All rights reserved.
the result of the erosion of an originally complete ring-like build-up based on a sediment volcano, then indications should remain below the surface of the sunken parts of the complete ring. This is not borne out by grinding through incomplete ring ILS, however. The structure below the bed top matches the arc-shaped ridges above, thereby favouring localized microbially-mediated sediment aggradation rather than the partial erosion of a ring.

John Salter’s description of paired pits in these rocks, impressions that he interpreted as the twin holes of worm burrows and named *Arenicolites* (Salter 1856, 1857), has subsequently been refuted because close examination indicates that a number of the impressions are not paired nor connected by a U- or J-shaped burrow (Callow *et al.* 2011b; the genus name is retained as a *nomen conservandum* for reasons of nomenclatural stability). The impressions on one of Salter’s specimens are unquestionably paired, however (Fig. 11; Callow *et al.* 2011b). These markings, named by Salter as *Arenicolites didymus* (Salter 1856, 1857), were subsequently described as a form of *Rusophycus* arthropod resting trace (*R. didymus*; Häntzschel 1975). They may, however, now be interpreted as double-ridge Longmyndian ILS, preserved in negative epirelief. (*R. didymus* is also a *nomen conservandum* still in use, despite being first used for this abiogenic structure.)

Pairs of longer parallel ridges or counterpart pits that cannot be explained as the current-parallel sides of an originally ring-like structure are occasionally observed in the Longmyndian rocks (Fig. 12). These markings are otherwise similar to ILS in size and appear in association with them. If the suggestion that microbially build-up may occur preferentially in the direction of the current due to the greater trapping and binding of sediment is correct, then cyanobacteria in neighbouring areas up-current are likely to be drawn to the existing ridge. The ridge may then expand in an up-current direction and merge with other current-aligned ILS. This would explain the occasional extended double-ridge forms and negative counterparts observed in the Long Mynd. The presence of such extended double ridges also argues against microbial chemotaxis towards nutrients brought up from below by fluid escape as the main cause of stromatolitic growth on the flanks of sediment volcanoes in these rocks.

Thus ‘Longmyndian *Intrites*’ can now be understood as a form of torus-shaped microstromatolite that grows from a small, fine-grained sediment volcano. It can be considered as a new form of MISS. As microbial mats are understood to have been widespread in the Ediacaran Period, in the absence of grazing, and the physical processes involved in the formation of ILS are ubiquitous, it may seem surprising that ILS and the other discoidal features observed in the upper Burway Formation (Menon *et al.* 2016) are not commonplace in Ediacaran rocks. However, the environmental conditions under which these Longmyndian markings arose seem to have been unusual, involving the build-up of fine-grained silt layers rich in pore waters and colonized by filamentous cyanobacteria, which formed
Concluding remarks

Our examination of ILS in cross-section demonstrates that the structures are microbially-modified sediment volcanoes that developed above, or between, aluminosilicate-rich microbial matgrounds. The ILS are always associated with microbial matgrounds and fluid-escape processes in a manner similar to that inferred for forms previously described as *Medusinites* and *Beltanelliformis* (McIlroy et al. 2005), but now reinterpreted as pseudofossils (Menon et al. 2016). Our interpretation of ILS as a new form of microstromatolite built up around sediment volcanoes means that all the discoidal impressions in the Ediacaran Longmyndian Supergroup can now be explained by a combination of microbial activity and physical processes. There is therefore no longer any evidence for Ediacaran macrofossils in these rocks.

As the Longmyndian markings have long been regarded as evidence for the presence of a depauperate Ediacaran macrobiota (Salter 1856; Darwin 1859; McIlroy et al. 2005), the discs of the Long Mynd represent a cautionary tale. Microbial matgrounds and activity, in combination with physical processes, can produce a variety of discoidal morphotypes, on bed soles as well as bed tops, that may be mistaken as evidence for the presence of complex life in ancient rocks.

The occurrence of several types of MISS in the Longmyndian succession, including Arumberia, elephant-skin texture, *Medusinites*, *Beltanelliformis* and *Intrites*-like forms (McIlroy et al. 2005; Menon et al. 2016), along with direct evidence for matgrounds and filamentous microfossils (Peat 1984; Callow & Brasier 2009), demonstrates the presence of a microbe-dominated ecosystem in a siliciclastic system of late Ediacaran age devoid of macrobiota that is now in need of significant sedimentological and palaeoenvironmental reassessment.

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