Enigmatic sedimentary structures in the Lower Old Red Sandstone, south Wales, UK: possible microbial influence on surface processes and early terrestrial food webs

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Abstract – Several enigmatic sedimentary structures are present in Upper Silurian and Lower Devonian terrestrial rocks of south Wales. These are millimetre ripples, wrinkle structures, 'cauliflower' and 'molehill' structures, calcretized matgrounds, 'pepper-pots' and 'fairy rings'. Most of the structures occur on fine-grained sandstone bedding surfaces in both inclined and non-inclined red heterolithic deposits that form a large part of the Lower Old Red Sandstone in south Wales. These deposits consist of conspicuous units up to 3 m thick, comprising millimetre- to centimetre-scale laminasets of alternating mudstone and fine-grained sandstone, interpreted as muddy point bars on ephemeral channel margins, crevasse-splay lobes or distal flood-out deposits from ephemeral flow. They are rich in trace fossils reflecting animal locomotion, burrowing, foraging, ploughing and resting. Millimetre ripples and wrinkle structures are related to rapid growth of cyanobacterial mats on wet sediment surfaces, especially in films of standing water, that may have been a critical constituent of the food chain for terrestrial communities. Pustular 'cauliflower' and 'molehill' structures are preserved on tuffs and have been linked to algal blooms formed following an increase in nutrients due to ashfall into floodplain ponds. The tuffs are associated with a diverse ichnofauna indicating that opportunist colonizers took advantage of an abundant food source.

Keywords: Anglo-Welsh Basin, microbially induced sedimentary structures, heterolithic strata, trace fossils.

1. Introduction

The Old Red Sandstone comprises Upper Silurian to Lower Carboniferous sedimentary deposits that border the current North Atlantic (Friend *et al.* 2000; Barclay *et al.* 2005). The Lower Old Red Sandstone of the Anglo-Welsh Basin is dominated by Ludlovian to Emsian sediments representing deposition in a range of terrestrial environments, from ephemeral lakes to alluvial fans. Palaeomagnetic data from the Lower Old Red Sandstone indicate that, at the time, England and Wales lay in sub-tropical latitudes $17 \pm 5°$ S (Channell, McCabe & Woodcock, 1992).

Interpretations of the palaeoclimate have been derived mainly from studies of palaeosols preserved within the sedimentary rocks. Analysis of calcic Vertisols in the Lower Old Red Sandstone led Allen (1974) and Marriott & Wright (1993) to suggest that the climate was warm to hot, semi-arid with seasonal rainfall. Hillier *et al.* (2007), from a study of hydromorphic palaeosols in some Lower Devonian sediments of the region, suggested that there were also periods of prolonged waterlogging. The absence of a dense cover of vegetation, other than in riparian areas, would have contributed to widespread flash flooding and an enhanced sediment yield.

The lithostratigraphy of the Anglo-Welsh Basin has recently been rationalized (Barclay *et al.* in press) and the revised nomenclature is used here. The Milford Haven Subgroup of the Daugleddau Group (Table 1) that forms the basis for this study, crops out in very good exposures around the southwest coast of Pembrokeshire (Fig. 1). It is a mudrock dominated succession of Pridoli to Lochkovian age containing sandstone bodies that show spatial variability in architecture, sediment grade and composition. The thick mudstone intervals between the sandstones reveal a variety of depositional mechanisms (Marriott & Wright, 2004; Hillier & Williams, 2006) and post-depositional alteration by bioturbation and pedogenesis (Marriott & Wright 1993; Morrissey, Hillier & Marriott, 2012).

A range of enigmatic sedimentary structures has been observed in the Milford Haven Subgroup that have similar features to structures that have been interpreted as relating to the activity of microbial communities. These were termed 'microbially induced sedimentary structures' by Noffke *et al.* (2001) and are not well known from the Old Red Sandstone.

Isolated occurrences of freshwater stromatolites have been recorded from the Lower Old Red Sandstone Temeside Mudstone Formation of the Welsh Borderland by Antia (1981), and from the Upper Old Red Sandstone of the Anglo-Welsh Basin in the Abergavenny district (Barclay, 1989). More extensive

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Table 1. Formations of the Milford Haven Subgroup of the Daugleddau Group

| Stage	Stratigraphy	Environment	Sedimentology
Lochkovian	Ridgeway Conglomerate Fm	Alluvial fans	Exotic clast conglomerates, heterolithic complexes, calcretes and associated axial drainage strata
	Freshwater West Fm	*Rat Island Mudstone Mbr*: Dryland ephemeral river systems	Fining-upwards packages intraformational conglomerates, fine sandstones, massive pedogenically altered mudstones, heterolithic complexes, calcretes
		Conigar Pit Sandstone Mbr: Alternating perennial and ephemeral river systems	Sandstone dominated, multi-storey units, fine-grained mud-dominated heterolithic complexes, calcretes
Pridoli	Moor Cliffs Fm	Mud-dominated rivers	Predominantly pedogenically altered red mudstones, (75 %), subordinate fine-grained sandstones and conglomerates, calcretes; ash fall horizons
	Freshwater East Fm	Low-relief coastal plain	Fining-upwards cycles of cobble-grade conglomerates overlain by greenish-grey sandstones, dark/pale green heterolithic complexes and red mudstones
Ludlow	Albion Sands Fm	Braided streams	Interbedded white cross-bedded sandstones and red/brown siltstones, airfall tuffs, calcretes
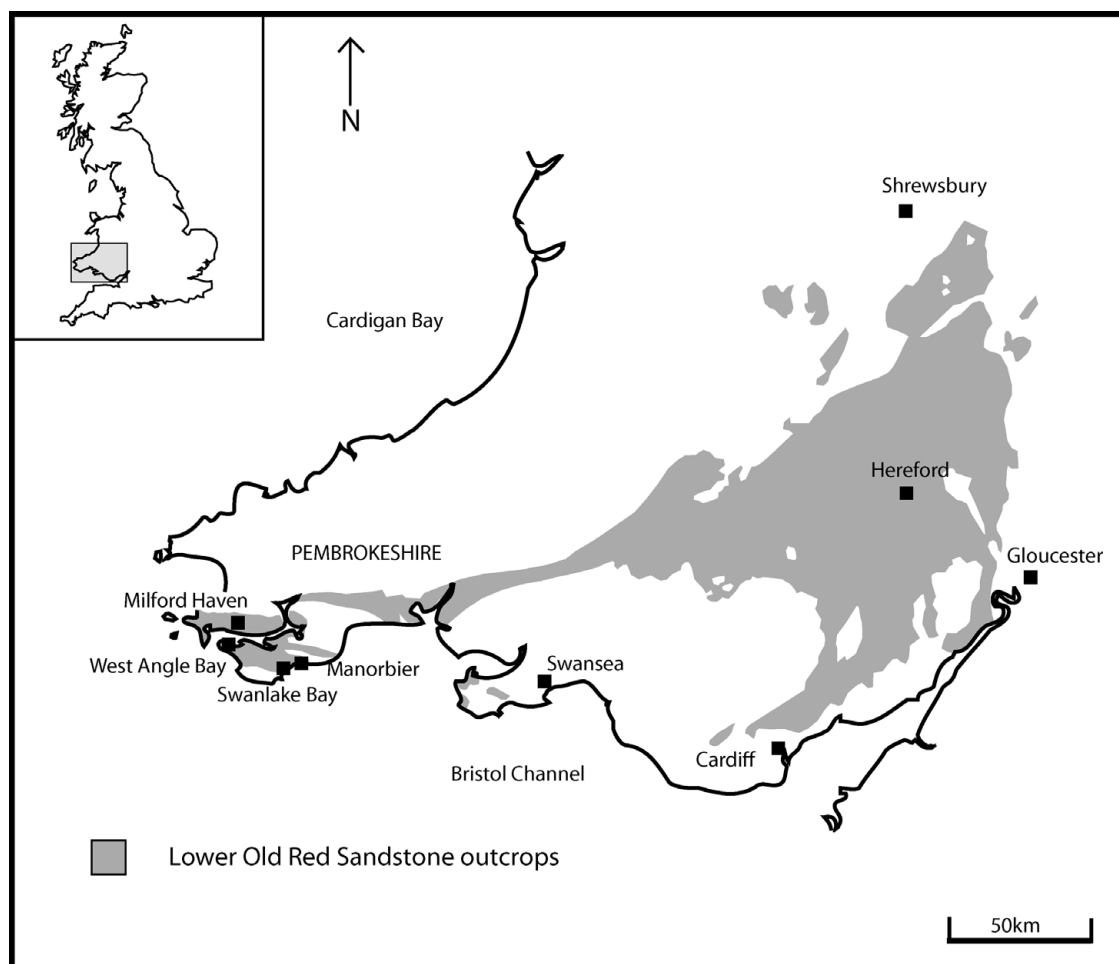
Figure 1. Lower Old Red Sandstone outcrops in SW Wales and locations mentioned in the text.

freshwater stromatolites have been recorded in lacustrine deposits of the Middle Old Red Sandstone of the Orcadian Basin by Fannin (1969), Parnell, Marshall & Astin (1990) and Trewin (1993), who described millimetre-scale hemispheroids and sheets. Trewin commented that in some instances stromatolite growth was related to the desiccation crack morphology, and Fannin (1969) suggested that the frequent association of the stromatolites with desiccation features indicated their development in zones of fluctuating water level, a feature also recorded in modern settings by Gerdes *et al*. (1993). Donovan (1973) described stromatolites, also

from the Orcadian Basin, that formed in spaces between breccia fragments fringing a relatively low-energy lake, cementing them together. He suggested that these cryptocrystalline micritic crusts were precipitated by umbrophile algae that colonized the spaces.

Similar structures in addition to other microbially induced sedimentary structures were recorded from the Late Silurian Ringerike Group (Davies, Sansom & Turner, 2006) and Early Devonian Muth Formation, India (Draganits & Noffke, 2004). The latter deposits were interpreted as representing a barrier-island environment. Draganits & Noffke (2004) also noted the presence of the burrow *Taenidium (Beaconites barretti)* on wrinkle surfaces and interpreted this association as indicative of organisms feeding within microbial mats. Other workers (e.g. Hagadorn & Bottjer, 1997) noted the presence of *Diplichnites* trackways and horizontal burrows on wrinkle surfaces, which is also a feature in the Lower Old Red Sandstone of the Anglo-Welsh Basin.

The aim of this paper is to describe the range of enigmatic sedimentary structures observed in the Milford Haven Subgroup and to discuss the evidence for microbial origin, their associations with ichnofauna and their influence on sedimentary processes in the sub-humid/semi-arid environment of the time.

2. Enigmatic sedimentary structures

This section includes systematic descriptions of the enigmatic sedimentary structures that are thought to represent evidence for microbial mats that once veneered the surface of some deposits, with discussion of related examples from the literature. Although the features are referred to as 'sedimentary structures', they can be regarded as trace fossils because they are evidence of the presence of the microbial mat and indicate the interaction between the sediment and the mat-building bacteria. Schieber (1999, p. 3) suggested that 'laminated sediments produced by microbial mats can be considered the "trace" that reflects the interaction of the mat community with the environment'.

2.a. Millimetre ripples (Fig. 2a–c)

Material. University of Bristol archive (BSRUG) 28576. Field examples: Lower Old Red Sandstone, Daugleddau Group, Moor Cliffs Formation, Priest's Nose, near Manorbier, Pembrokeshire (Fig. 1) [British National Grid Reference SS 060 970].

Description. Millimetre-scale ripple marks preserved as positive hyporelief structures. They most commonly resemble very small wave ripples and are preserved in mudstones and siltstones (Fig. 2a–c). Surfaces may be covered in these ripples forming areas of over a square metre. Wavelengths vary from 3–5 mm, whereas amplitudes are negligible. Patches of ripples sometimes showing differing ripple-crest orientations may be preserved intermittently on a surface. Some surfaces show disorganized ripple

fragments as though the ripples have been broken into small sections and rotated. Individual ripples in bedding-plane view may be separated by conspicuous layers of mica.

Discussion. These structures resemble those described as 'millimeter ripples' by Pflüger (1999) who noted that they had not been reproduced experimentally and were mainly known from Precambrian sediments. Pflüger (1999, p. 33) suggested that they formed within the sediment 'after burial and partial degradation of an interstitial biomat framework, cyclic loading of waves (...) or seismic tremor led to a lateral rearrangement of clay-mineral-wrapped silt packages (...) within individual laminae'. He also suggested that the morphology of millimetre ripples is determined by grain size and bed geometry, and that boundaries between individual laminae withstand liquefaction and allow only internal rearrangement into ripple-like quilts.

The millimetre-scale ripples in the Moor Cliffs Formation occur only in mudstones and siltstones and form regular ripple patterns that suggest that they were formed within the sediment by microbial mats as described by Pflüger (1999), rather than by wave activity. Degradation of the mats after burial and subsequent exposure and desiccation would have led to cracking and allowed reorganization of fragments during subsequent inundation. A further explanation for the patches of different orientation could be related to the stabilizing effect of microbial mats that allow two or more systems of ripples to be produced on the same bedding surface (Pflüger, 1999).

2.b. Wrinkle structures (Fig. 2d)

Material. National Museum of Wales archive (NMW) 2006.13G.1. Field examples: Daugleddau Group, Freshwater West Formation, Tredomen Quarry, Powys (Fig. 1) [SO 116 304]

Description. These are areas of wrinkled, pitted and contorted impressions on bedding planes preserved in both hyporelief and epirelief. Wrinkle structures form mesh-like networks of millimetre-scale ridges and troughs. They may cover several tens of square centimetres of a bedding surface.

Discussion. Wrinkle structures are probably the most well-known sedimentary structures associated with the activity of microbial mats. They have been reported from rocks as old as the Torridonian of NW Scotland (Prave, 2002) and the Vendian–Cambrian of North America (Hagadorn & Bottjer, 1997) and are common throughout the Phanerozoic. Modern microbial mats have contorted, folded, mesh-like and pustulose surfaces and it is thought that many of these wrinkle structures are essentially moulds of these surfaces. Noffke *et al.* (2001) interpreted them as lithified examples of levelled depositional surfaces. Their formation is thought to result from the interaction of the mat and overlying sediment (Noffke, Knoll & Grotzinger, 2002). When buried and under pressure the mat, which is fluid rich, deforms plastically, i.e.
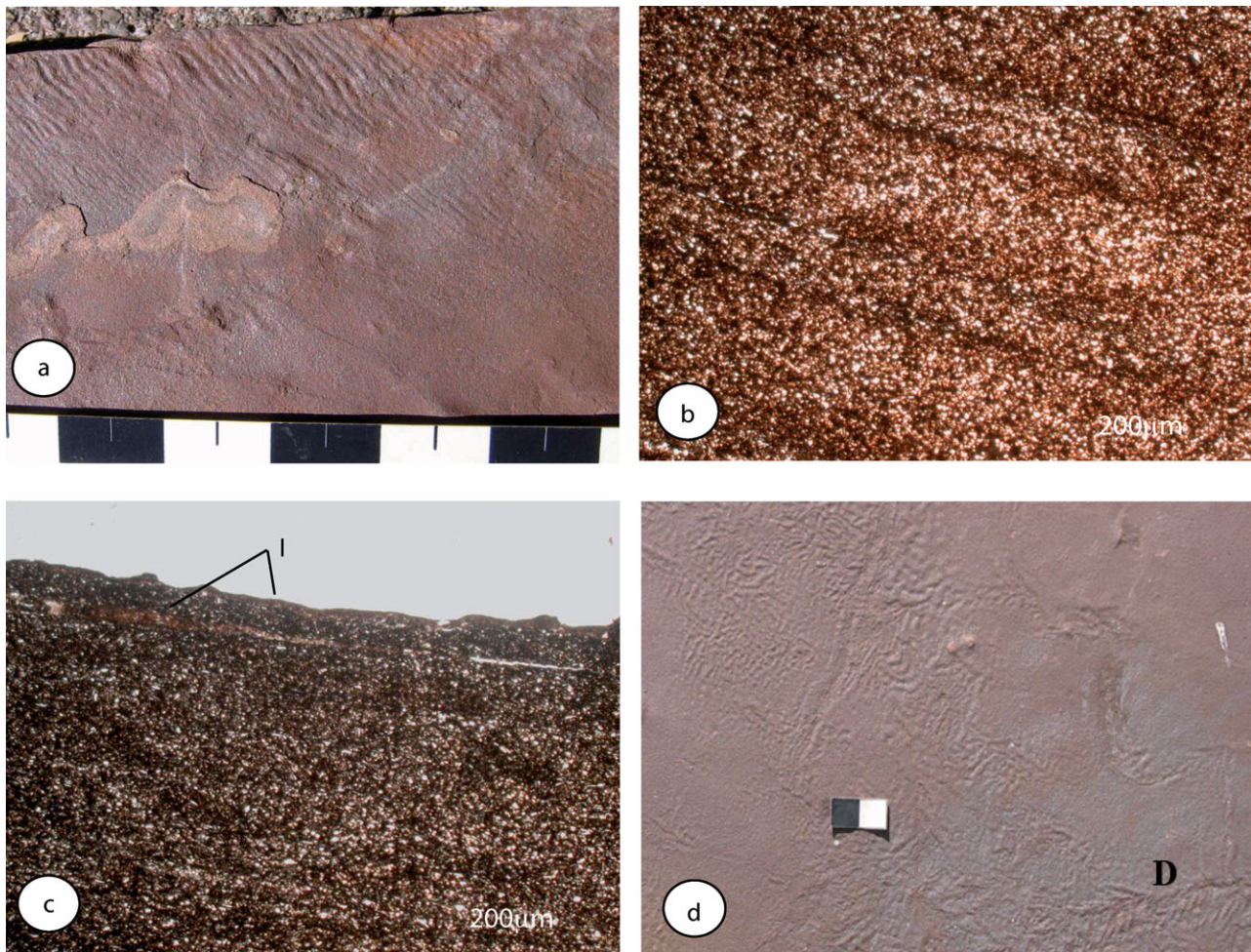
Figure 2. (Colour online) Enigmatic sedimentary structures. (a) Millimetre ripples, scale bar in centimetres. (b) Millimetre ripples in thin-section (BSRUG 28576b) parallel to surface in (a). (c) Thin-section (BSRUG 28576c) perpendicular to surface in (a) and (b) showing light brown coloured organic laminae (l) covering the top surface of the section and a horizon slightly below. (d) Wrinkle structures (NMW2006.13G.1) on very fine sandstone bedding plane including trackway *Diplichnites gouldi* Type B (D); scale bar 2 cm.

differently from the non-colonized sediments, which have lower water content. Owing to depositional loading from overburden, the amount of liquefaction within the mat rises and escaping water subsequently forms protrusions upwards from the mat surface. Therefore, the surface between the mat and the underlying sediment is arranged in casts and moulds.

Allen (1985) described wrinkle structures from sand–mud couplets in a modern intertidal setting. He did not consider the possibility of the structures being associated with microbial mats, though he suggested that they developed owing to differential sediment loading similar to that described by Noffke, Knoll & Grotzinger (2002). Allen's examples were associated with surface trails and feeding traces of annelids, gastropods and amphipods, so a microbial origin for those wrinkle structures cannot be ruled out in view of more recent descriptions (e.g. Noffke *et al.* 2001, Noffke, Gerdes & Klenke, 2003) and the development of microbial mats on North Sea tidal flats described by Gerdes *et al.* (1993). Biofilms grow rapidly during quiet conditions on tidal flats and carpet large areas, sometimes within a few hours (Noffke, 2008), so it is

highly likely that the wrinkles observed by Allen were in sediments bound by microbes. Likewise a microbial origin is preferred for the wrinkle structures in the Freshwater West Formation, because of their scale and their association with trackways and foraging traces (see Section 3.a below).

2.c. Cauliflower structures (Fig. 3a)

Material. Daugleddau Group, Moor Cliffs Formation, Townsend Tuff Bed, Old Castle Head, near Manorbier, Pembrokeshire (Fig. 1) [SS 074 986].

Description. Patterned bedding-plane surface in a volcanic ashfall tuff showing a distinct arrangement of bulbous, low-relief mounds separated by cracks, resulting in a cauliflower-like pattern.

Discussion. Gerdes *et al.* (1993) described a number of physically controlled features that result from microbial mat associations. They noted (Gerdes *et al.* 1993, p. 65, plate 12, no. 1) that shrinkage cracks in modern microbial mats may produce a distinct cauliflower-like pattern that differs from the orthogonally regular desiccation pattern in muds and clays. The pattern
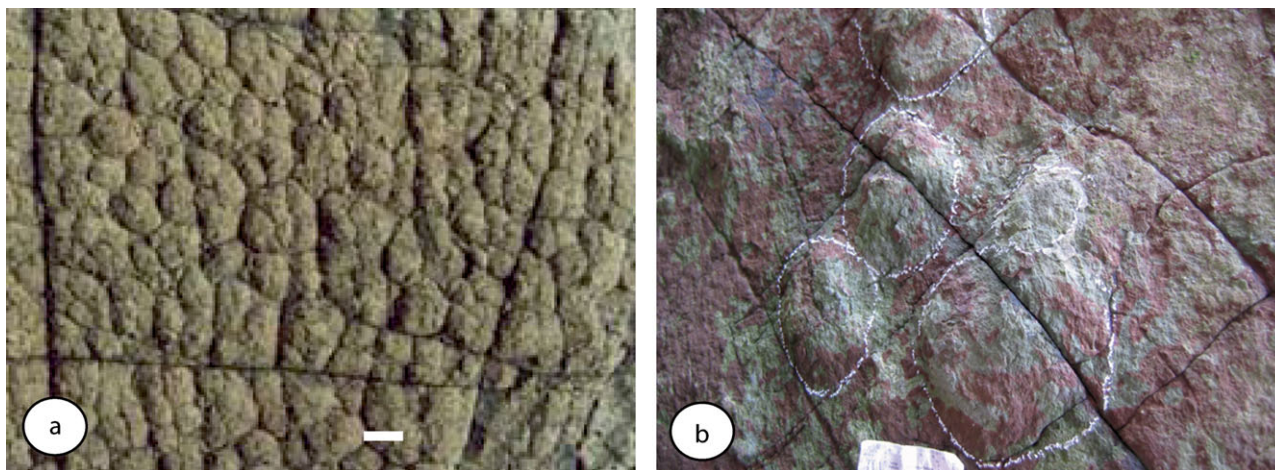
Figure 3. (Colour online) (a) Cauliflower-like pattern on a volcanic ash bedding plane; scale bar 2 cm. (b) Gas mounds in volcanic ash (outlined in white); scale bar 8 cm.

forms owing to small-scale sub-fracturing of crack margins and splitting of larger cracks into smaller ones controlled by fibrillar microbial mats. Edges of the cracks are rounded because cracking allows the mat-forming microbes to overgrow and migrate into the cracks where there might be more humidity and an increase in substrate for colonization. The cauliflower-like pattern seen in the Townsend Tuff Bed does not resemble orthogonal polygons formed by desiccation in clay-rich sediment, which tend to have sharp edges that are slightly raised, giving rise to a concave-upwards surface (see description in Allen, 1987). Instead, the Townsend Tuff structures are domed with rounded edges and form irregular random patterns. A microbial origin is therefore inferred for these cauliflower structures.

2.d. Molehill-like structures (Fig. 3b)

Material. Field examples: Lower Old Red Sandstone, Rook's Cave Tuff Bed, Priest's Nose, near Manorbier, Pembrokeshire (Fig. 1) [SS 060 970].

Description. Structures preserved in convex epirelief comprising circular to oval mounds up to 200 mm in diameter. The mounds may be grouped and stand proud of the surface by up to 80 mm.

Discussion. These structures were reported by Gerdes *et al*. (1993, pl. 13, no.1) from hypersaline salterns of the Canary Islands and supratidal flats of the North Sea coast. They were interpreted as due to domal upheaval because of methane accumulation beneath elastic and deformable microbial mats that were then encrusted by halite or gypsum in the salterns. When the domes are subsequently wetted they are often overgrown by microbial mats forming new surface layers or 'crack tapestries' (Noffke, Gerdes & Klenke, 2003) The methane is thought to have migrated from buried organic deposits (Gerdes *et al.* 1993) Noffke *et al.* (1996) termed these features 'domal upheavals'.

Domed structures of a similar size have been described in beach sand by Shepard (1967), who

considered that they arose owing to air entrapment in the swash zone. It is more likely that the domes in the Townsend Tuff Bed are related to microbial mats, which would have bound the fine-grained muddy tuff material together preventing gas escape. Deposition of the Townsend Tuff Bed is linked to increased algal productivity because of raised nutrient levels. This productivity would have provided organic material as a food source (see Section 4) and as a subsequent source of methane upon burial and decay.

2.e. Calcretized matground (Fig. 4a)

Material. Field examples: Daugleddau Group, Ridgeway Conglomerate Formation, south of West Angle Bay, Pembrokeshire (Fig. 1) [SR 843 029].

Description. Polygonal micrite calcrete sheets are common on some mudstone and fine-grained sandstone bedding surfaces. Polygons are typically 20 to 60 mm in diameter, with the calcrete sheet being up to 20 mm thick. Polygon margins are defined by positive relief overfolds (Hillier & Williams, 2007; Hillier, Marriott & Williams, 2011). Some calcretes display a laminated internal fabric.

Discussion. The overfolded margins are comparable to the petees of Noffke, Gerdes & Klenke (2003) described in evaporitic intertidal environments. The petees occur on the surface of microbial mats (Fig. 4a), with rapid lateral mat growth causing them to ruck up and develop overfolded margins. In the Ridgeway Conglomerate Formation, the calcretized matgrounds occur in sediments deposited at the margins of shallow, probably ephemeral lakes (Hillier & Williams, 2007) in association with root traces.

2.f. Other possible microbial mat indicators

A range of other enigmatic sedimentary structures present in the Lower Old Red Sandstone may also be indicators of microbial mat growth.
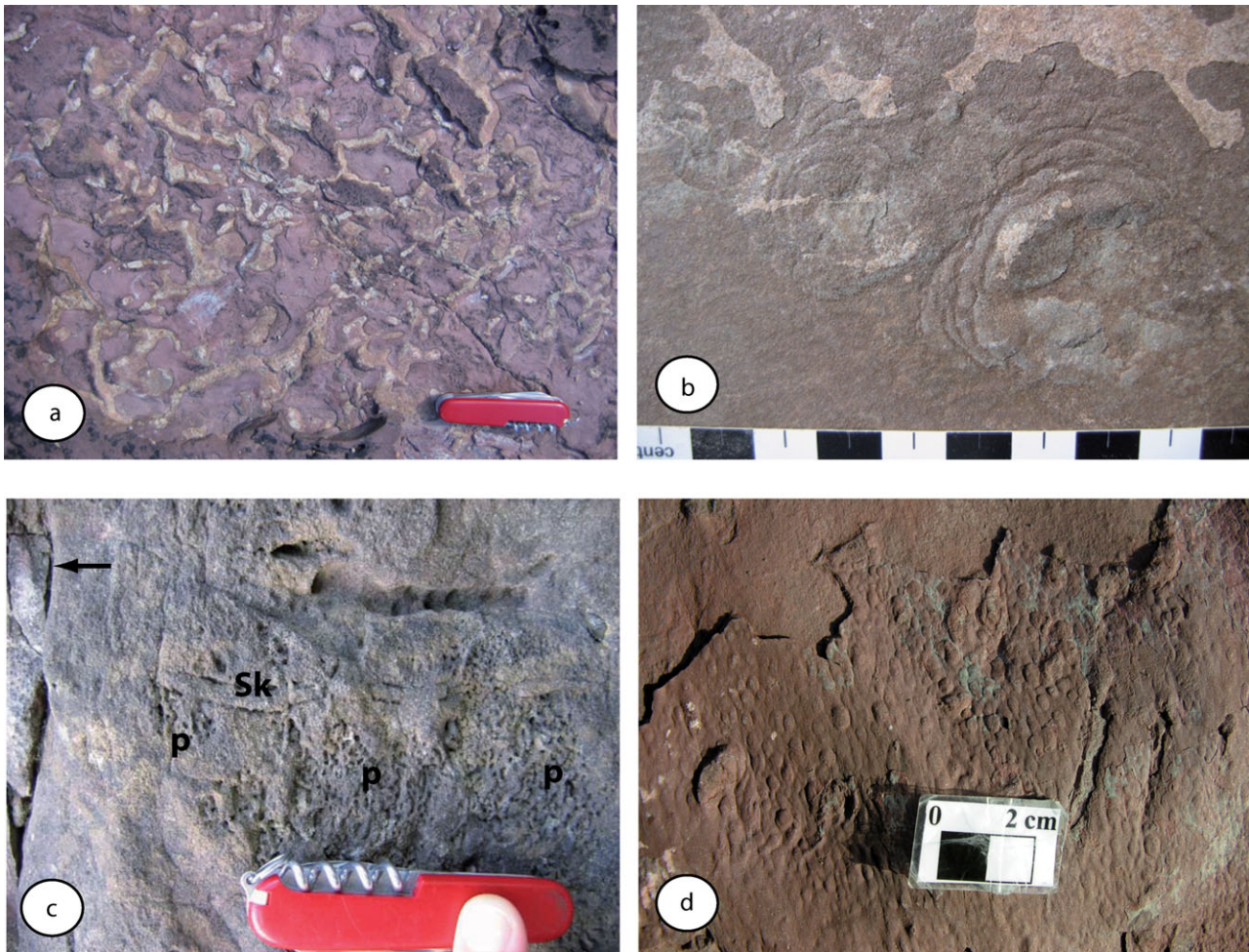
Figure 4. (Colour online) Other possible microbially induced sedimentary structures. (a) Calcrete sheet with polygonal overfolded margins interpreted as a calcretized matground surface; knife is 8.5 cm long. (b) 'Fairy rings' on a fine sandstone surface; scale bar in centimetres. (c) Pepper-pot structures (p) surrounding *Skolithos* (Sk); knife is 8.5 cm long; top of bed indicated by arrow. (d) Oval-spheroidal masses superficially resembling *Beltanelliformis minutae*; scale bar 2 cm.

'Fairy ring' structures were seen on a fine-grained sandstone bedding surface (Fig. 4b). They are preserved in convex epirelief and comprise broadly circular areas of sediment (up to 5 cm in diameter) with the sediment showing concentric laminations around a central zone. These 'fairy rings' may be structures formed on sediment bound by microbial mats by the concentric oscillation of the water surface caused by escaping gas (Gerdes *et al.* 1993, pl. 13, no. 8). In the largest individual seen (Fig. 4b), the concentric laminae appear to be orientated to one side, as though a directional force had been applied to distort the sediment. This is similar to the 'roll-up' structures described from modern cyanobacterially bound intertidal flats and derived experimentally in medium-grained sand, which are produced by currents overturning microbial mats (Noffke *et al.* 2006; Hagadorn & McDowell, 2012). The concentric rings seen in the Old Red Sandstone are likely to be of microbial mat origin, since they show most similarity to those described and figured by Gerdes *et al.* (1993), with the distorted example having been 'rolled up' by directional currents.

'Pepper-pot' structures form discrete patches or areas on bedding planes and, in vertical section, have reticulate patterns. Some of the pepper-pot structures appear as oval patches on the bedding planes composed of concentric laminae (Fig. 4c). These were first described by Croft (1953), who regarded them as only confined to the Senni Formation, and by Ball (*in* Barclay & Wilby, 2003) who referred to them as 'pepper-pot structures'. They are commonly found in association with *Skolithos* in trough cross-bedded sandstones. D. Hawley (pers. comm. 2006) suggested that they may indicate re-burrowing of sediment in and around previous burrows. However, unless the burrower of *Skolithos* was actively storing organic material in its burrow or the animals were frequently entombed by flooding and decayed in the burrow, it is difficult to imagine why other animals would re-burrow the sediment. The pepper-pot structures seen in the Lower Old Red Sandstone resemble some of the '*Kinneyia*' facies, also linked with *Skolithos*, described by Pflüger (1999, fig. 5a, c). These consist of small grooves or pits, which Pflüger linked to gas bubbles trapped beneath microbial mats. Noffke *et al.* (1996)
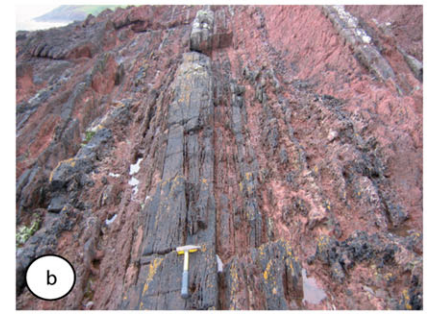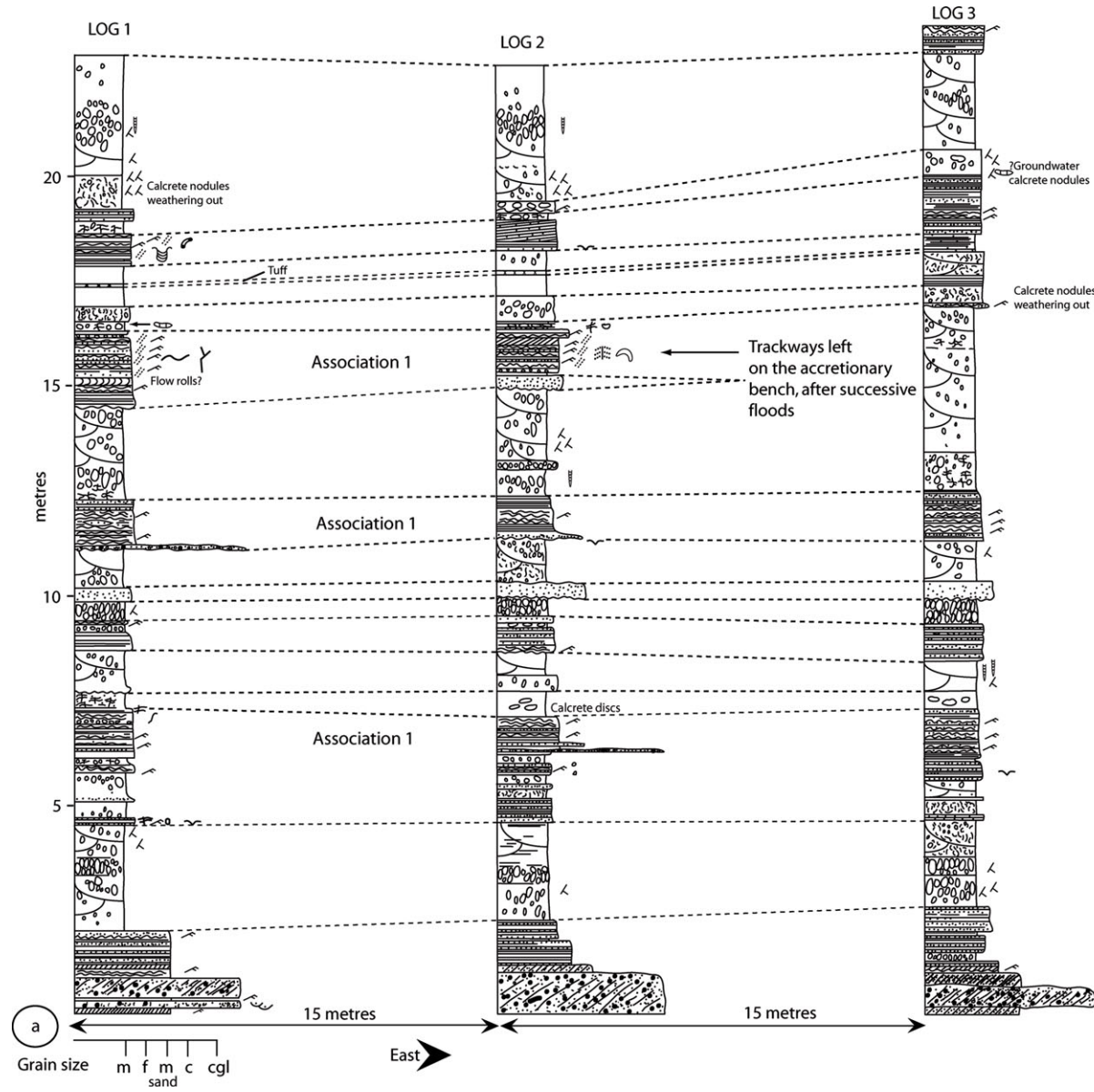
Figure 5. (Colour online) Association 1 in the Rat Island Mudstone Member (Table 1) at Manorbier Bay. (a) Sedimentological log of section showing repeating units of Association 1 in the sequences. (b) Non-inclined heterolithics younging to the right; hammer is 32 cm long. (c) Inclined heterolithics (closing to the west) younging to the right. The unit is about 1 m thick.

Lithology

⬚	Sandstone
⬚	Rubbly mudstone
⬚	Calcrete nodules
x x	Tuff
⬚	Intraformational conglomerate (mud and calcrete clasts)
⬚	Extraformational conglomerate
⬚	Heterolithics (finely bedded)
禾	Calcrete filaments

Sedimentary structures

⌇⌇	Wave ripples
⬚	Current ripple lamination
⬚	Climbing ripple lamination
▤	Planar horizontal lamination
▨	Planar cross-stratification
⬚	Trough cross bedding
⌇	Erosion surface

Other features

⌇	Desiccation cracks
⌇	Drab halo
⬚	Groundwater calcrete mass
⬚	Soft sediment deformation
⬚	Wedge-shaped peds (dashed if poorly developed)

Trace Fossils

● ⬚	*Beaconites antarcticus*
⬚	*Beaconites barretti*
⬚	Calcrete tubule
∿	*Cochlichnus*
⫽	*Diplichnites gouldi* Type A
⫽	*Diplichnites gouldi* Type B
⬚	*Palaeophycus*
⬚	*Paleohelcura*
⬚	Root
⬚	*Selenichnites*
Y	*Treptichnus*
⬚	Wrinkle marks

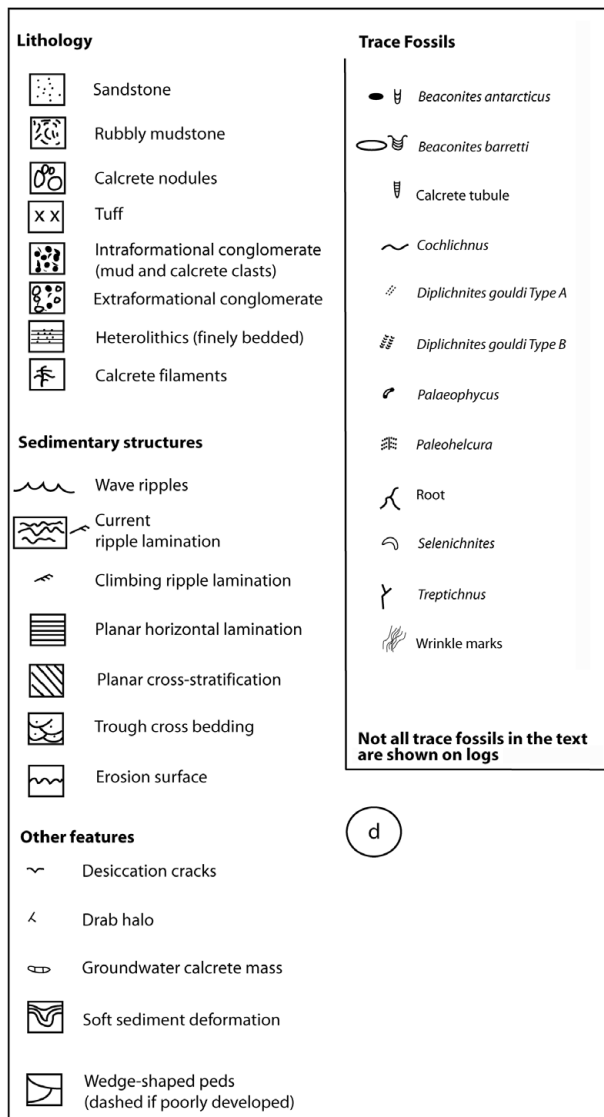**Not all trace fossils in the text are shown on logs**

(d)

Figure 5. (Continued) (d) Key to symbols in Figures 5–7.

described similar features that comprised cavities a few millimetres in diameter in sand layers between sub-recent microbial mats. These were termed 'sponge sand' and originate owing to gas production from the decay of mats in deeper layers. The gas is trapped owing to sealing of overlying layers by newer mat development. The pepper-pot features are therefore interpreted as microbially induced sedimentary structures linked to the 'fairy rings' and 'molehill' structures described above and formed by entrapment of gas produced by decay of microbial mats.

Common in some fine-grained lithologies are oval-spheroidal masses (2–8 mm in diameter), having a 'pustular' appearance preserved in both convex epirelief and hyporelief on bedding surfaces (Fig. 4d). The structures are smooth walled and internally show evidence of concentric laminae. The structures superficially resemble *Beltanelliformis minutae*, described from Ediacaran deposits worldwide, and interpreted as either soft-bodied megafossils or benthic green-algal balls (Xiao *et al*. 2002; McIlroy, Crimes & Pauley,

2005). The spheroidal structures described here may represent similar algal structures, or alternatively faecal pellets or pellets produced by arthropod feeding and/or burrow excavation (Hillier & Williams, 2007).

3. Ichnofacies associations

The terrestrial trace-fossil-bearing Old Red Sandstone deposits of the Anglo-Welsh Basin have been assigned to 12 lithofacies associations based on lithological and ichnological properties and cover a range of sedimentary environments (Morrissey, Hillier & Marriott, 2012). The sedimentary structures described above occur mainly in two lithofacies: (1) red, inclined and non-inclined, fine-grained heterolithic complexes, and (2) tuffaceous horizons.

3.a. Association 1

Description. This association (Lithofacies Association 5 of Morrissey, Hillier & Marriott, 2012) is found in red inclined and non-inclined heterolithic deposits (Figs 5, 6, 7). These deposits form a large part of the Pridolian and Lochkovian successions and consist of conspicuous units, up to 3 m thick, comprising millimetre-to-centimetre-scale lamina sets of alternating mudstone and fine-grained sandstone. Some units are inclined (Fig. 5c) and bedsets close at a low angle to the horizontal (mostly less than 5°), but the majority are horizontal (Fig. 5b). Laminasets are usually 30–50 mm thick and consist of laminae of fine-grained, mica-rich sandstones that are massive, planar- or current-ripple laminated, overlain by a thin mudstone veneer that has a rippled or wavy top. Soft-sediment deformation and desiccation cracks are also common. The surfaces of the units reveal several types of trace fossils and wrinkle structures (see *Ichnology* section below).

Sedimentological interpretation. Marriott & Wright (2004) interpreted the inclined heterolithic deposits as those of muddy point bars or accretionary benches on ephemeral channel margins. The non-inclined heterolithics were interpreted as crevasse-splay lobes or distal flood-out deposits from ephemeral flow in a sub-humid to semi-arid environment and as sediments deposited by sheet flooding in shallow, ephemeral pools in floodplain (Marriott & Wright, 2004) or fan-toe environments (Hillier & Williams, 2007). In the fan-toe environments, the heterolithics contain calcretized matgrounds and spheroidal masses described above. A cephalaspid headshield was recovered from an inclined heterolithic unit (Morrissey *et al*. 2004, fig. 9a), providing further evidence of a fluvial channel origin for these deposits.

Ichnology. Most of the trace fossils in the Pridolian and Lochkovian sequences of the area are preserved in this association. The trace fossils (trackways and burrows) are almost exclusively seen as hyporeliefs on the underside of thin sandstone laminae. In cross-section, heterolithic bedsets are commonly broken by intense bioturbation. Each lamina set probably
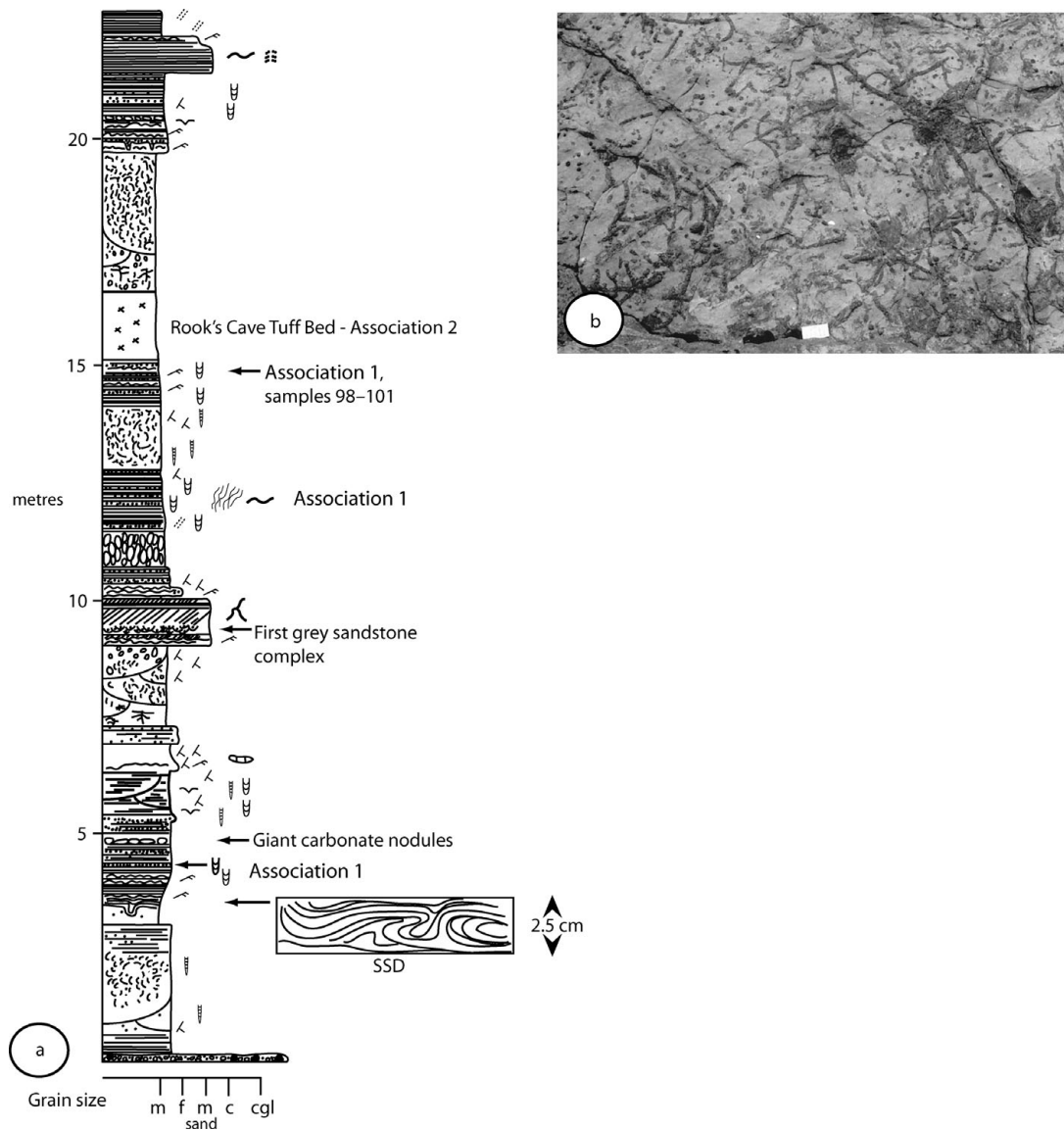
Figure 6. Association 1 in the Moor Cliffs Formation (Table 1) at Priest's Nose, Manorbier. (a) Sedimentological log of section. Samples 98–101 correspond to BSRUG 28560–28563. Key to symbols as in Figure 5d. (b) Intense bioturbation on a bedding surface. Note the broadly circular areas of concentrated burrowing; scale bar 2 cm.

represents a single flood event and animals clearly exploited the fresh sediment, after flooding, to feed. Mudstone surfaces show desiccation cracks, wrinkle structures, arthropod trackways (*Diplichnites gouldi* Type A and Type B Smith *et al.* 2003; *Paleohelcura tridactyla* Gilmore, 1926), single sinusoidal burrows (*Cochlichnus anguiensis* Hitchcock, 1858; *Palaeophycus* Hall, 1847), foraging traces (*Selenichnites* isp. Morrissey & Braddy, 2004; Scratch arrays cf. *Striatichnium* Morrissey & Braddy, 2004), ploughing (bilobed trail cf. *Cruziana* isp.) and resting traces (*Rusophycus* Type B Hall, 1852). Wrinkle structures, some of which are broken, cover bioturbated surfaces. The broken areas may have been due to grazing on algal mats that would have grown quickly as 'green scum' on fresh, wet muddy-bar and channel surfaces, particularly in thin films of standing water. The mats would have been a critical basal constituent of the food chain for these early terrestrial communities. Trackways were

made in the fresh mud and then cast by sand. Root traces are also present in some sections of this association (Hillier, Edwards & Morrissey, 2008).

The commonest components of the heterolithic association are small, horizontal/subvertical backfilled burrows (*Beaconites antarcticus* Vialov, 1962, emended Bradshaw, 1981) (Figs 6, 7). They are well preserved on bedding surfaces, particularly in hyporelief on the underside of contacts between mudstone/sandstone laminae. This evidence of intense, periodic reworking of thin, flood-related bedsets suggests opportunistic colonization by a particular animal that could respond to the acyclical fluvial conditions. It appears that the producer initially moved horizontally through the soft sediment at the mud/sand interface selectively deposit feeding and backfilling unwanted material. Large, circular areas of disturbance (Fig. 6b) could be where multiple burrowers concentrated their activity on one area. Perhaps when sediments began to lose
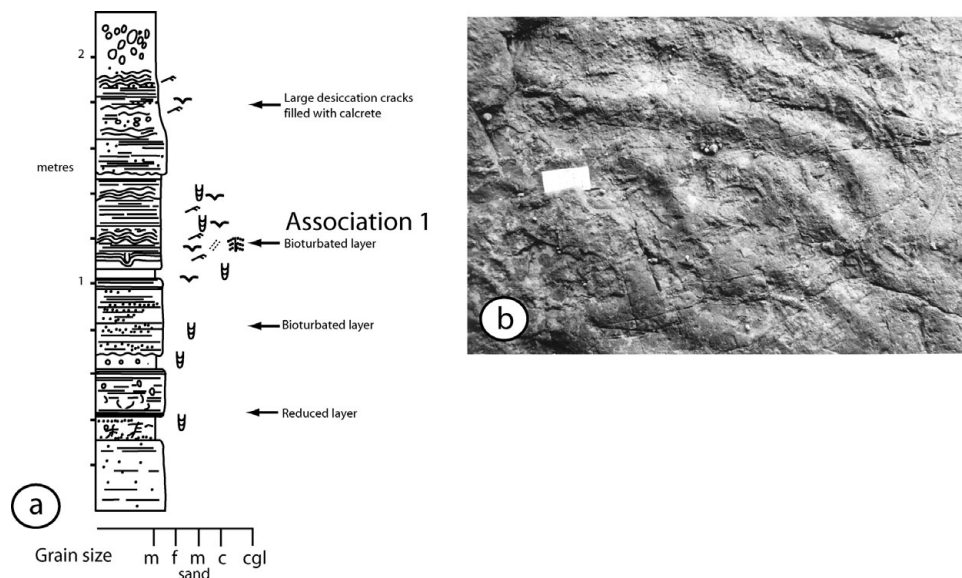
Figure 7. Association 1 in the Moor Cliffs Formation at Swanlake Bay. (a) Sedimentological log of section. Key to symbols as in Figure 5d. (b) Predominantly horizontal *Beaconites antarcticus* on a trochoidal wave-rippled surface (not in log); scale card is 5 cm.

a favourable consistency to the burrower (i.e. during drying), burrowing moved deeper to penetrate previous heterolithic bedsets. Successive periods of burrowing created an overprinted ichnofabric of vertical and horizontal forms. Some trackway sections are obliterated by vertical burrowing. Another possible explanation for the concentration of feeding is that the animals were grazing algal mats, perhaps buried by flooding or broken into patches by shrinkage and erosion by wind or water; some of the wrinkle structure surfaces additionally preserve horizontal *Beaconites antarcticus*. Calcretized and desiccated matgrounds are also found in this association.

3.b. Association 2

Description. This association (Lithofacies Association 9 of Morrissey, Hillier & Marriott, 2012) is found in tuffaceous deposits. There are several tuff beds in the Lower and Upper Pridolian of Pembrokeshire, SW Wales (Allen & Williams, 1981), most of which are thin (5–50 mm). There are, however, three significant tuff beds varying in thickness from 0.5 to 2.5 m, known as the Horse Neck Tuff Bed, the Townsend Tuff Bed and the Rook's Cave Tuff Bed. These comprise layers of pale green and magenta, laminated porcellanite, pale green crystal lithic tuff and reddish muddy or dust tuff. Some horizons, particularly in the Townsend Tuff Bed, locally display wave ripples and lenticular bedding. The sedimentary successions above and below the tuff beds consist of thin, massive red mudstone or red heterolithic deposits (Allen & Williams, 1981; Marriott & Wright, 1993, 2004; Love & Williams, 2000).

Sedimentological interpretation. The lithologies of the tuff beds have been interpreted by Allen & Williams (1981, 1982), Allen, Thomas & Williams (1982) and Marriott, Morrissey & Hillier (2009). The presence of wave ripples and other sedimentary

structures implies either that the ash was reworked by water shortly after deposition or that it settled through standing bodies of water. The varying thickness of the tuffs reflects undulations in the surface on which they were deposited (Love & Williams, 2000). The depositional environment has been interpreted as an areally extensive, uniform coastal mudflat (Allen & Williams, 1981; Williams, Allen & Marshall, 1982) or as a low-gradient floodplain with ponds or cut-offs and gilgai relief due to the development of wedge-shaped peds in the soils formed by shrink-swell mechanisms under a sub-humid/semi-arid climate (Marriott & Wright, 1993, 2004).

Ichnology. Most of the trace fossils in the tuffs are preserved at the tops of individual falls. The top of the Horse Neck Tuff Bed (Fig. 8) records a variety of trace fossils (Fig. 8b–d) including the oldest record of feeding pellets in the Anglo-Welsh Basin, rare *Beaconites antarcticus* and vertical plug-like burrows (cf. *Skolithos*). Other structures may be large burrow tops (Fig. 8c), but are difficult to interpret and are unlike those preserved in the Rook's Cave and Townsend Tuff Beds (see below). They might instead be hollows formed by weathering acting on intersecting fracture planes (Morrissey & Braddy, 2004).

The Rook's Cave Tuff Bed (Fig. 9) has a moderately diverse ichnofauna, comprising abundant feeding pellets spread over some surfaces or lying in the bases of shallow, continuous grooves interpreted as ploughing traces left by an arthropod (Morrissey & Braddy, 2004, fig. 6e). Large oval burrow tops are present, with muddy tuff plugs and pellets of various sizes strewn around the entrances. *Palmichnium antarcticum* Richter, 1954 up to 100 mm across are poorly preserved on the pellet-strewn surfaces (Marriott, Morrissey & Hillier, 2009, figs 7, 9). Other horizons that lack pellets are crossed by foraging trails (*Diplopodichnus biformis* Brady, 1947; *Cruziana* isp.) and one bilobed trail can
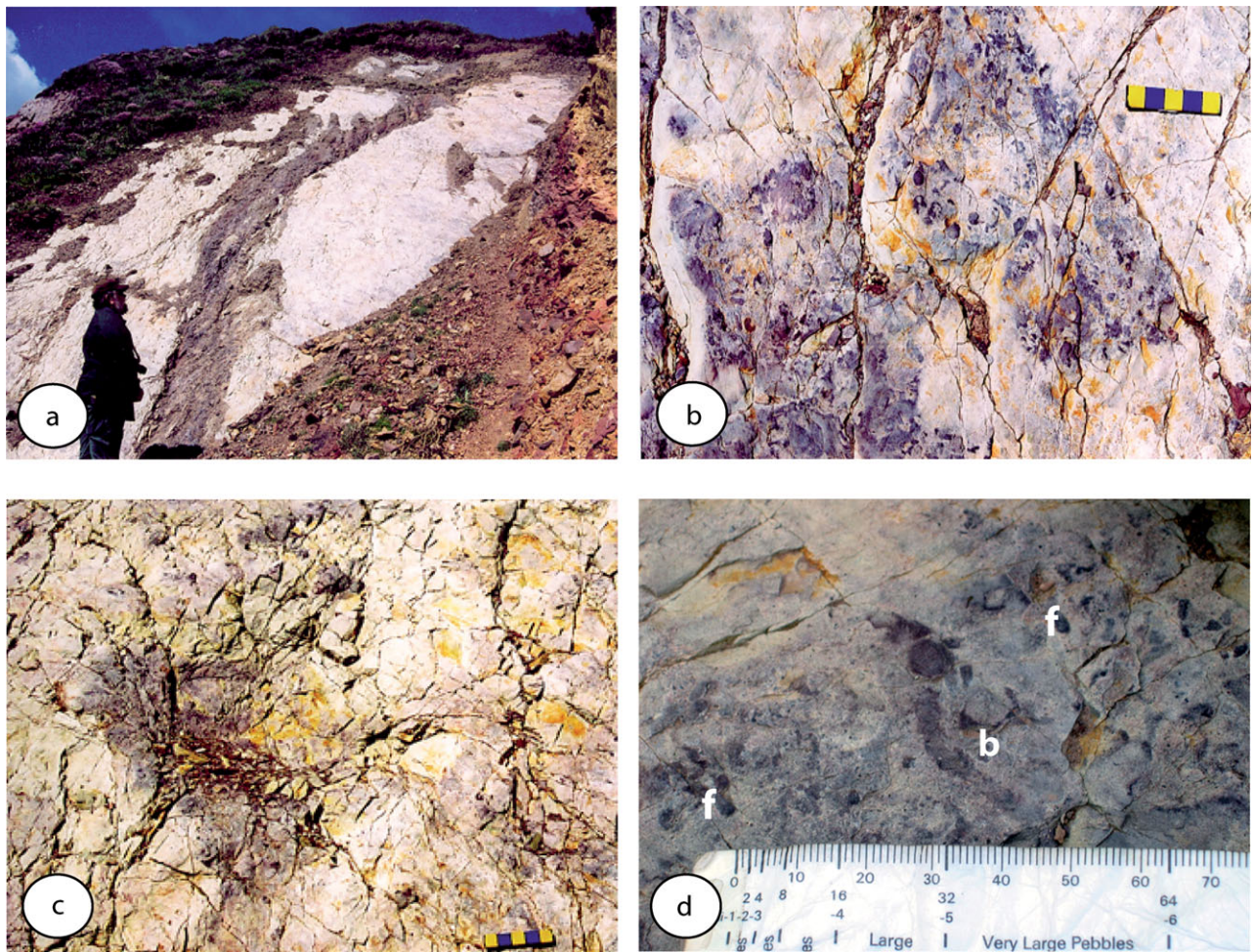
Figure 8. (Colour online) Association 2 in the Horse Neck Tuff Bed (a) View of the upper bedding surface of the Horse Neck Tuff. (b) Purple-stained, circular sections through vertical burrows (?*Skolithos*) and feeding pellets; scale bar 5 cm. (c) Possible burrow tops; scale bar 5 cm. (d) Small backfilled burrow (b, *Beaconites antarcticus*) and feeding pellets (f); scale bar in millimetres.

be observed leading to a burrow. Microbially induced sedimentary structures are also present including 'pepper-pot' structures, pustular surfaces and molehill-like gas mounds (Fig. 9).

A more diverse trace-fossil assemblage is present in the Townsend Tuff Bed (Marriott, Morrissey & Hillier, 2009, figs 7, 12). It comprises foraging trails (*Diplopodichnus biformis*), backfilled burrows (*Beaconites antarcticus*), trumpet-shaped burrows, large circular or oval burrow tops surrounded by feeding pellets, 'bread-roll' marks (Allen & Williams, 1981) and microbially induced cauliflower structures.

4. Discussion

Microbial mats were defined by Gerdes *et al.* (1993, p. 61) as 'fibrillar, slime-supported, coherent coatings on sedimentary and rocky surfaces'. Most mats are built by cyanobacteria (e.g. the blue-green algae *Microcoleus* and *Lyngbya*) and can grow to form significant organic layers that may float on still water. Mats form in a variety of other environments including intertidal mudflats (Noffke, 1998) and lake floors. In some shallow marine and lake settings the interaction

between cyanobacterial growth and sedimentation can form layered columns, generally referred to as stromatolites (Riding, 1999).

It is also important to consider the nature of the substrate, the overall environment and the likelihood that these would support a mat community (N. Noffke, pers. comm. 2010). Microbial communities favour fine-grained sands where quartz grains can be trapped and bound into the mat to channel light deeper into the mat to allow it to increase in depth. Bottom currents must also be sufficient to remove mud that would smother a mat but also weak enough not to remove the mat itself (Noffke, Knoll & Grotzinger, 2002). The interaction of a microbial mat with the sediment on which it lies, and the modification of the surface by the mats in association with other processes such as desiccation, result in a variety of enigmatic sedimentary markings and structures. A variety of problematic sedimentary structures, e.g. wrinkle structures and *Kinneyia* ripples (which are similar to wrinkle structures but have more parallel, flat-topped ridges), have often been thought to represent microbial activity with wrinkle structures formed on mat surfaces and *Kinneyia* ripples formed beneath buried microbial mats (Hagadorn & Bottjer,
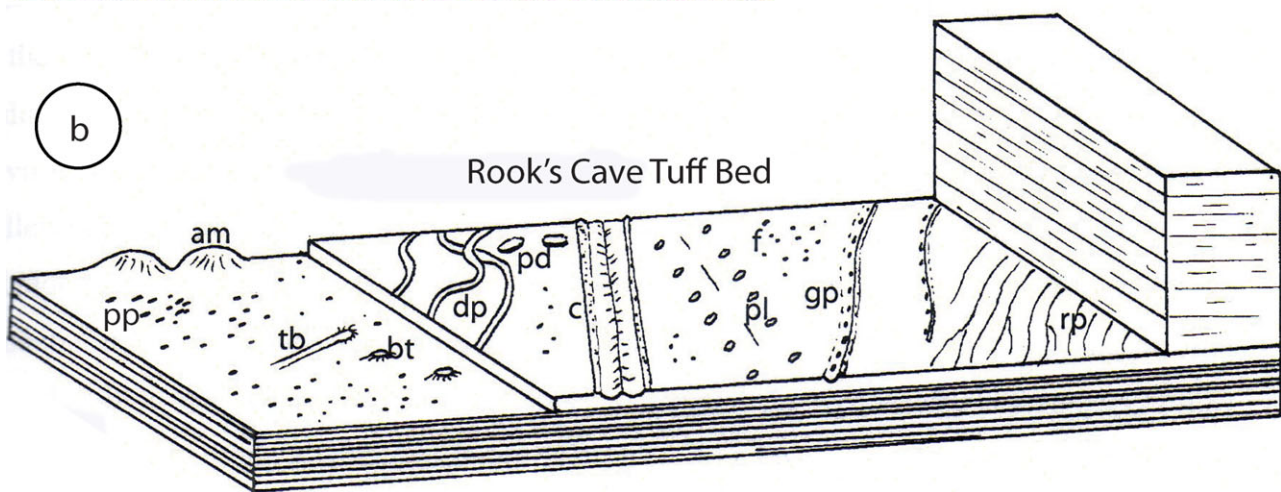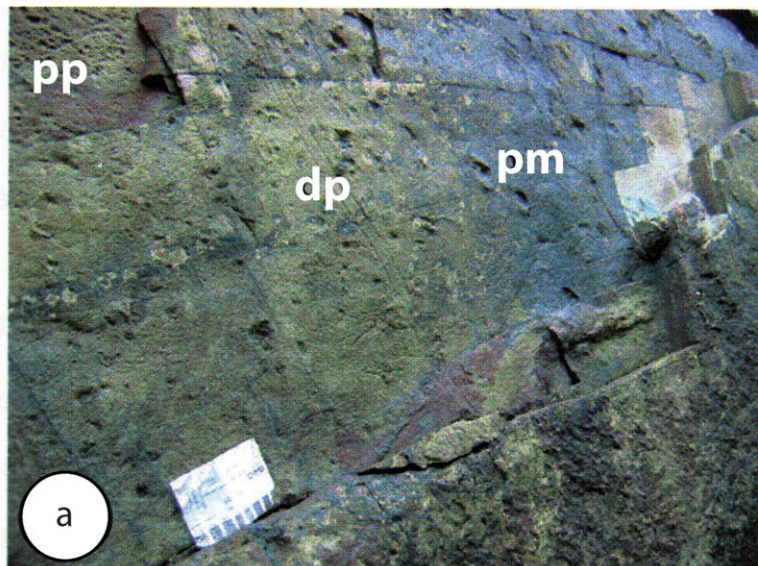
Figure 9. (Colour online) Association 2 in the Rook's Cave Tuff Bed. (a) Surface preserving *Diplopodichnus* (dp), pepper-pot structures (pp) and paired 'paddle marks' (pm); scale bar 8 cm. (b) Cartoon of Rook's Cave Tuff ichnocoenosis: algal mounds (am), burrow top (bt), *Cruziana* isp. (c), *Diplopodichnus* (dp), feeding pellets (f), groove with pellets in base (gp), paddle marks (pd), *Palmichnium* isp. (pl), pepper-pot structures (pp), wave ripples (rp), trail leading to burrow top (tb).

1999). They are common in the fossil record (e.g. Hagadorn & Bottjer, 1997; Schieber, 1999; Prave, 2002; Noffke, Knoll & Grotzinger, 2002; Draganits & Noffke, 2004) and it is only now, through the study of modern interactions between microbial communities and sedimentary surfaces (e.g. Gerdes *et al.* 1993; Noffke, 1998; Noffke *et al.* 2001), that understanding and interpretation of them are improved. Noffke *et al.* (2001) characterized these structures as 'microbially induced sedimentary structures' with cyanobacterial films and mats syndepositionally influencing sediment erosion, deposition and deformation of the substrates that they now occupy (see review in Noffke, Gerdes & Klenke, 2003). These authors recognized several categories of structures: those induced by (1) levelling, (2) biostabilization, (3) microbial grain separation, (4) baffling, trapping and binding, and (5) those imprinted by biofilms. They further distinguished between those structures on bedding planes (e.g. wrinkle structures, multidirectional ripple marks) and those forming internal bedding structures (e.g. gas domes, biolamin-

ites). Descriptions of the latter confirm that the oval-spheroidal masses and molehill structures described in Section 2 are probably internal bedding structures caused by gas produced by the activity of micro-organisms. Similar small-scale, subrounded to elongate bulges have been described from a Neoproterozoic intertidal succession by Porada & Bouougri (2007) and from Cambro-Ordovician quartz arenites by Hilowle, Donaldson & Arnott (2000) with suggestions that the bulges record the subsurface morphology of a microbial mat that has been degraded or removed.

Flat surfaces can also be cryptically affected by microbial activity. In modern semi-arid and arid environments microbial organisms hold together water-stable soil aggregates in cryptobiotic (also known as cryptogamic) crusts (West, 1990) and can thus affect sedimentary processes. Among the primitive organisms involved in forming the crusts are cyanophytes, chlorophytes, fungi and bacteria that contribute to soil stability and the aggregation of soil particles (Brostoff, 2002). Johansen (1993) and Brostoff (2002)

reported that smooth, flat crusts dominated by algae are typically found in areas subject to ephemeral ponding, such as the floodplain pans or pools suggested as likely environments for the ichnofacies associations described in this paper. Brostoff's (2002) studies of dune-pan systems in California found that the algal crusts developed on silt and clay sediments deposited in areas of previously standing water (aquatic remnant crusts), although they were destroyed when the pans were re-inundated. When the dried-out pans have no crust they tend to develop mud-crack polygons. Desiccation crack morphology is also linked to the activity of umbrophile algae and stromatolite growth in lacustrine settings (Donovan, 1973; Gerdes *et al*. 1993; Trewin, 1993).

Marriott & Wright (1996, 2004), Marriott, Wright & Williams (2005) and Hillier *et al*. (2007) interpreted the environment of deposition of the red mudstones and heterolithic complexes (Association 1) of the Moor Cliffs and Freshwater West formations (Table 1). They envisaged that the heterolithic deposits, where inclined, were likely to have formed as accretionary lateral-bench deposits of shallow, sinuous ephemeral channels. Non-inclined heterolithic deposits were interpreted as analogous to intermediate or terminal flood-out deposits as described by Tooth (1999). Some mudstone deposits show pinstripe lamination and vertical burrows and are likely to represent deposition in shallow, ephemeral floodplain ponds. Others are massive and relatively thick (>1 m) and were interpreted as within-channel deposits such as muddy braid bars or ephemeral channel fill of bedload-transported mud aggregates. Sand-sized mud aggregates are produced during the shrinking and swelling episodes that occur in soils with a high smectite content in semi-arid areas. The aggregates can be readily entrained from floodplain surfaces by wind or moving water, although they are not very coherent and break down during lengthy transport (Droppo *et al*. 2005).

Wind erosion is often predominant in semi-arid and arid regions and cryptobiotic crusts can provide an important barrier to wind (and water) erosion, particularly during droughts when vascular plant cover is reduced or absent (Eldridge & Greene, 1994*a*; Eldridge & Leys, 2003). From their studies in semi-arid areas of Australia, Eldridge & Greene (1994*b*) and Eldridge & Leys (2003) found that soil aggregates formed by micro-organisms in soil crusts are more stable than those formed by physical mechanisms from clay shrinking and swelling. They also found that the production of aggregates is volumetrically greater in areas with a cryptobiotic crust than in bare areas. The presence of these types of crust on Lower Old Red Sandstone floodplains helps to explain the integrity of soil aggregates in the massive mudrocks after deposition and burial.

In semi-arid areas, owing to shortage of ground and surface water, the cryptobiotic crusts and mats are likely to shrink and dry out (Krumbein, Paterson & Stal, 1994) and often detach from the underlying sediment.

This then exposes the crust or mat to degradation and erosion by wind, revealing the underlying morphology of elongate bulges and depressions (Porada & Bouougri, 2007).

The evolution of early plant assemblages on the Anglo-Welsh Basin has been described by Edwards & Richardson (2004). The plant material is allochthonous and the distance transported would have affected the size of the fragments, but there is no actual evidence of where the plants grew. Vegetation including rhyniophytoids and cryptospore producers was likely to have grown close to water courses and therefore to have been subjected to periodic inundation and devastation. Other species such as *Zosterophyllum* might have colonized drier areas of the floodplains, further from the river channels (Wellman *et al*. 2000; Lavender & Wellman, 2002). These plants have been considered to be at the base of a terrestrial food chain that was dominated by arthropods (Smith *et al*. 2003; Morrissey & Braddy, 2004). However, the presence of microbial mats, revealed by the microbially induced sedimentary structures described in Section 2, constitutes a lower level in the food chain that was evidently exploited by deposit feeders and grazers in view of the associated ichnofauna (Section 3). In addition, Boyce *et al*. (2007) have suggested that microbial mats may also have been a nutrient source for the enigmatic giant fungus *Prototaxites*. The presence of mats and cryptogamic crusts with irregular surfaces may have also been favourable for the establishment of vascular plants (see discussion in Prasse & Bornkamm, 2000).

In Association 2, deposition of ash would have led to changes in environmental conditions due to an increase in available nutrients such as iron (Banse & English, 1999). In floodplain ponds the presence of iron, which increases algal division rates, is likely to have encouraged blooms of algae and increased productivity in algal mats around the ponds, providing additional food sources for infauna and epifauna (deposit, detritus, suspension feeders and grazers). In the area around Mount St Helens, large algal blooms were reported in some lakes in the summer following the 1980 eruption. The lakes most affected by blooms were outside the blast zone and received ashfall that provided nutrients in the form of nitrates and phosphates (Lee, 1996). Increased phytoplankton production related to iron released from ashfall was also reported following the eruption of the Alaskan volcano Kasatochi in 2008 (Langmann, Zakšek & Hort, 2010).

The enigmatic sedimentary structures described from the Lower Old Red Sandstone therefore help to provide evidence for the existence of a wider diversity of terrestrial life at the time than is available from its body and trace fossils (Marriott, Morrissey & Hillier, 2009).

5. Conclusions

Eight enigmatic sedimentary structures from the Lower Old Red Sandstone of SW Wales are interpreted

as microbially induced. These are mainly found in two particular environments that form ichnofacies associations: inclined and non-inclined heterolithic complexes and airfall tuff beds. In both associations, the microbially induced sedimentary structures occur along with assemblages of arthropod trackways, foraging and ploughing traces and backfilled burrows indicating that microbial mats were exploited as a food source. In association with the emergence of terrestrial plants during Late Silurian time, therefore, algal mats would have provided a lower trophic level for grazing and deposit-feeding animals.

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