

Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, UK

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Abstract – Body and trace fossils of Ediacaran affinity are described from strata of the late Neoproterozoic Longmyndian Supergroup exposed near Church Stretton, Shropshire, UK. The almost spherical soft-bodied Ediacaran fossil *Beltanelliformis brunsae* Menner occurs rarely in the Burway Formation, but much smaller, simpler, discoidal structures are common in both the Burway and Synalds formations and are referred to *Beltanelliformis minutae* sp. nov. Similar discoidal structures, but with a distinct central depression, are included in *Intrites punctatus* Fedonkin and are common at several horizons. Two blocks with numerous examples of *Medusinites* aff. *asteroides* (Sprigg) Glaessner & Wade were recovered from the Burway Formation. The purported Ediacaran body fossil 'Arumberia' Glaessner & Walter is common at several horizons but its biogenicity is not accepted herein. 'Arumberia' is thus treated along with evidence for microbially bound sediment surfaces or matgrounds that have been suggested by several authors to be necessary for some types of Ediacaran preservation. The assemblage of simple trace and body fossils along with matgrounds is typical of latest Neoproterozoic time, though some elements range into the Phanerozoic.

Keywords: Neoproterozoic, Ediacaran fauna, palaeontology, pseudofossils, matgrounds.

1. Introduction

Macroscopic organic remains have been reported repeatedly from the Longmyndian Supergroup of the Welsh Borderlands (Fig. 1) (Salter, 1856, 1857; Cobbold, 1900; Watts, 1925; Bland, 1984), but their organic nature has been contested (e.g. J. H. James, unpub. M.Sc. thesis, Univ. Bristol, 1952; Greig *et al.* 1968; McIlroy & Walter, 1997). The Longmyndian has recently been demonstrated by sedimentological/provenance and geochronological studies to be at least partly contemporaneous with the Uriconian (Greig *et al.* 1968; Thorogood, 1990; Pauley, 1991; Compston, Wright & Toghil, 2002). The age of the Longmyndian succession is constrained by dates from minor volcanic rocks within this dominantly siliciclastic succession (Fig. 2). A lapilli tuff at the base of the Stretton Shale Formation has been dated at 566.6 ± 2.9 Ma and another from within the Longmyndian succession at the base of the Lightspout Formation at 555.9 ± 3.5 were dated by Compston, Wright & Toghil (2002). It has also recently been proposed that the Wentnor Group is unconformable on the Stretton Group (Compston, Wright & Toghil, 2002), but no new evidence was presented and is not reconcilable with our field observations (Pauley, 1990, 1991; McIlroy & Horák, in press). The Uriconian is, however, in unconformable contact with the overlying Wrekin Quartzite, which is estimated at about 530 Ma, with the local marine Cambrian

transgression thus being estimated as spanning 520–530 Ma (Wright *et al.* 1993). This indicates, therefore, that the 6000 m thick Longmyndian Supergroup is an expanded late Neoproterozoic (Ediacaran) succession. The upper part of the succession can thus be inferred to lie close to the Neoproterozoic–Cambrian boundary (dated at around 543–545 Ma: e.g. Grotzinger *et al.* 1995), and gives greater interest and importance to the supposed organic structures within it.

The most common Longmyndian structure considered to be organic consists of small circular or, where deformed, elliptical mounds on the soles of bedding planes and corresponding pits on the upper surfaces. Structures of this type were recorded as *Arenicolites didyma* Salter 1856 and *Arenicolites sparsus* Salter 1857, in the mistaken belief by Salter (1856, 1857) that they were the tops of U-tubes. The same author described other forms as rain prints (Salter, 1857, pp. 202–3, pl. 5, fig. 10). Similar mounds and pits have been found to be widely distributed and locally abundant within the Longmyndian Supergroup (Cobbold, 1900; Bland, 1984; J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986). Elsewhere, structures resembling these types have been recorded from around the world from Neoproterozoic (Ediacaran) strata and ascribed to various body and trace fossil taxa including *Beltanelliformis*, *Intrites*, *Medusinites*, *Nemiana*, *Sekwia* and *Vendella* (Palij, 1976; Palij, Posti & Fedonkin, 1979; Fedonkin, 1981, 1983, 1985; Hofmann, Fritz & Narbonne, 1983; Bekker, 1985; Gureev, 1987; Narbonne & Hofmann, 1987). Similar

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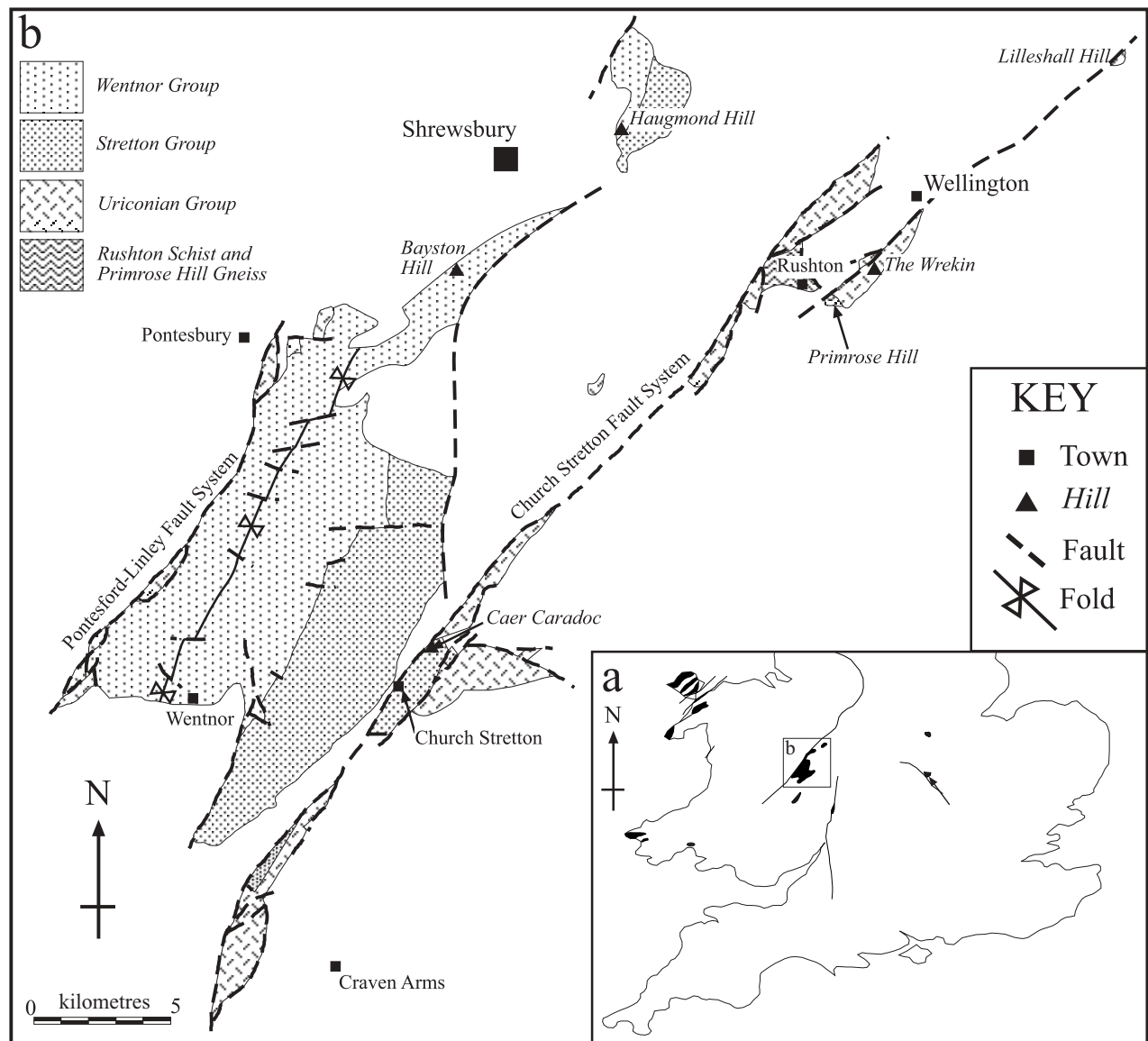


Figure 1. The distribution of Neoproterozoic rocks in the Longmynd inlier (redrawn from Pauley, 1990). Black areas on the inset map (a) represent the Neoproterozoic–Cambrian outcrops of England and Wales.

simple discoidal forms have also been described from the Cambrian of Ireland and Norway (Crimes, Insole & Williams, 1995; Crimes & McIlroy, 1999).

Recent investigations by the present authors in the Longmyndian Supergroup have produced abundant new material of this type, many specimens being collected by Pauley between 1982 and 1986. The purpose of this paper is to describe this new material and to discuss the nature and significance of these structures.

2. The nature of the supposed organic structures

The most common organic structures in the Longmyndian are the pits and mounds that were described as paired burrows of *Arenicolites didyma* and *Arenicolites sparsus* by Salter (1856, 1857). Their paired nature has been refuted by most subsequent workers (J. H. James,

unpub. M.Sc. thesis, Univ. Bristol, 1952; James, 1956; Greig *et al.* 1968; J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986), and does not even seem to accord with Salter's own specimens (Salter, 1856, pl. 4, fig. 1a; 1857, pl. 5, figs 3–4). The 'pits and mounds' are particularly abundant within the Synalds Formation but also occur in the Portway and Lightspout formations and possibly the Bridges Formation (Cobbold, 1900; J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986, p. 159). Remarkably similar structures have been described as rain prints by both Salter (1857, pp. 202–3, pl. 5, fig. 10) and James (1952, 1956, J. H. James, unpub. M.Sc. thesis, Univ. Bristol, 1952).

An interpretation of some or all of these structures as rain prints can be dismissed for the following reasons:

(a) The part of the Burway Formation in which some of the structures were found has been shown on

Stratigraphy	Sedimentology	Palaeontology & geochronology
<p style="writing-mode: vertical-rl; transform: rotate(180deg);">Wentnor Group</p>	<p>Bridges Formation</p> <p>The basal contact of this formation is gradational but marked. The cross-stratified sandstones of the Bayston-Oakwood Formation become interbedded with heterolithic purple siltstones and thin ripple cross-laminated sandstones. Thick cross-bedded sandstones with sharp erosional bases are also recorded, and are interpreted as fluvial channels associated with mud-rich alluvial plain deposits.</p>	
	<p>Bayston-Oakwood Formation</p> <p>This formation comprises mainly fine- to medium-grained cross-stratified sandstones with mudstone rip-up clasts and sub-rounded lithic clasts. These are interbedded with cross-laminated finer-grained sandstones in subtle upward-fining successions.</p> <p>The formation also contains locally developed conglomeratic members that are variably clast- to matrix-supported, containing sub-rounded lithic clasts and sub-angular clasts of sedimentary origin. These conglomerates are interpreted as braided fluvial deposits.</p> <p>No fossils are recorded from this unit.</p>	
<p style="writing-mode: vertical-rl; transform: rotate(180deg);">Longmyndian Supergroup</p> <p style="writing-mode: vertical-rl; transform: rotate(180deg);">Stretton Group</p>	<p>Portway Formation</p> <p>Red mudstones and siltstones interbedded with fine-grained sandstone. Sandier and coarser than the underlying Synalds and Lightspout formations but also interpreted as alluvial plain and fluvial deposits. Possibly with marine incursions associated with fossil bearing horizons. The base is marked by a minor conglomerate (Huckster Conglomerate) deposited in a braided fluvial palaeoenvironment.</p>	<p><i>B. minutae</i> 'Arumberia'</p>
	<p>Lightspout Formation</p> <p>Upward coarsening succession of laminated mudstones and upward-fining sandstones interpreted as alluvial plain, fluvial and ?deltaic deposits.</p>	<p><i>B. minutae</i> 'Arumberia' 555.9 ± 3.5</p>
	<p>Synalds Formation</p> <p>Mudstones with interbedded laminated and cross-stratified sandstones interpreted as alluvial plain, fluvial and ?deltaic deposits. Mudstones green at the base and red at the top with rare matgrounds, mudcracks, tuffs and possibly marine incursions associated with fossiliferous horizons.</p>	<p><i>B. brunsae</i> <i>B. minutae</i> 'Arumberia' 'Elephant-skin texture'</p>
	<p>Burway Formation</p> <p>The base of the Burway Formation is taken at the base of the rhyolitic tuffs of the Buxton Rock Member. The Burway Formation shows a coarsening-upward trend from thin to thick bedded turbidite lobe facies followed by shallow marine mudstones and deltaic sandstones. The Cardingmill Grit at the top is interpreted as a fluvial deposit.</p>	<p><i>B. brunsae</i> <i>B. minutae</i> <i>Intrites punctatus</i> <i>M. aff. asteroides</i></p>
	<p>Stretton Shale Formation</p> <p>The Stretton Shale is grey/green with normally graded siltstone beds and is interpreted as distal turbidite and basin floor facies. The Helmeth Grit marks the base of the formation and comprises medium-grained sandstone similar in composition to the underlying Ragleth Tuff Formation.</p>	<p>566 ± 2.9</p>
<p>Ragleth Tuff Formation</p> <p>Coarse epiclastic sediments that may pass laterally and stratigraphically upward into the Helmeth Grit. Contacts are faulted and stratigraphic position tentative.</p>		

Figure 2. Stratigraphy and sedimentology of the Longmyndian Supergroup showing palaeontology and geochronology (redrawn from Pauley, 1990).

detailed sedimentological evidence (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986) to have been deposited in sub-aqueous environments. Thus the sediment surface was not subject to the subaerial conditions necessary for rain to produce preservable impressions.

(b) Many of the structures are from 0.5 to 2.0 mm in diameter and some blocks have many tens of examples with none more than 1 mm; as such they are far too small and uniform for rain prints.

(c) Despite their abundance on some bedding planes, these structures rarely coalesce, even though they may touch, whereas, as Twenhofel (1921) has observed, 'after only a few minutes of rain a mud surface becomes thoroughly sculptured through the presence of a multiplicity of coalescing pits'.

Some of these features have been interpreted by Greig *et al.* (1968) as bubble impressions due to floating wave-foam bubbles. However, foam impressions generally occur as clusters of coalescent pits with a wide range of sizes on the same surface (Reineck & Singh, 1975, p. 52) without raised rims. The Longmyndian pits, in contrast, are normally discrete and of a broadly similar size on any given surface.

It has also been suggested by Greig *et al.* (1968, p. 70) that some of these structures are similar to sand domes found on modern beaches (Greig *et al.* 1968, pl. 5B). However, sand domes are positive features on the tops of beds, whereas most of these structures are positive features on the soles of beds and are normally represented only as corresponding hollows on the underlying (upper) bedding plane surface.

Structures caused by dewatering/degassing of water-saturated muds, known as pit and mound structures (see review in Shrock, 1948), bear some similarities to taxa described herein, especially *Medusinites*. The structures can be generated in fluid mud deposits, a common feature of estuarine muds (e.g. McIlroy, 2004), though their preservation potential is poor. A central tubular conduit is located in the centre of the pit, but collapses upon cessation of fluid flow to the surface. Our material shows no signs of having been formed in soupy sediments and seems to have a central sandy tube preserved. While improved knowledge of the formation of pit and mound structures would doubtless be valuable in assessing the biogenicity of Ediacaran fossils, it is considered that the internal structure of the present material is indicative of a biogenic origin.

It has also been considered that the circular structures may represent trapped gas bubbles within microbial mats. While it is likely that gases were formed in such microbial mats as are associated with the Ediacara fauna, similar conditions are likely to extend much further back into the Proterozoic where there is little if any convincing evidence for dense associations of circular impressions. In addition, we have no good examples for coalescing structures making sausage-like impressions that would be expected from the presence of gas bubbles (cf. Pflüger, 1999).

The most compelling argument against an inorganic origin for most or all of these structures is, however, their abundance on some surfaces and recurrence in different facies through thousands of metres of sediments. Similar structures are common at approximately the same stratigraphic horizon in strata of latest Neoproterozoic (Ediacaran) age at localities worldwide, including Russia, Ukraine, Australia and Canada (e.g. Fedonkin, 1985; Wade, 1969; Narbonne & Hofmann, 1987; Gehling, Narbonne & Anderson, 2000). The structures will, therefore, be described as biological taxa and, in the course of these descriptions, further evidence will be adduced for their organic origins.

Disc-like or spheroidal structures of this type have been considered both to be body fossils (e.g. Fedonkin, 1985; Narbonne & Hofmann, 1987) and trace fossils (e.g. Crimes & Germs, 1982; Fedonkin & Runnegar, 1992). The approach adopted herein is that forms in which the three-dimensional morphology of the organism can be deduced and in which there is no evidence for movement are described as body fossils. Only that material in which there is some evidence for activity of the organism is interpreted as being trace fossil.

In contrast to the biological affinities of the circular impressions in the Longmyndian, the radiating surface impression 'Arumberia' has been regarded as inorganic by several recent studies (Jenkins, Plummer & Moriarty, 1981; Runnegar, 1993, p. 1001; McIlroy & Walter, 1997). These authors have focused on similarities between 'Arumberia' and flute marks. The most recent work (McIlroy & Walter, 1997) concluded from re-examination of the type material that the linear grooves were formed by currents acting on microbially bound sedimentary surfaces with flute marks. These authors noted that 'Arumberia' grooves occur in arrays and radiate in a manner that reflects the pattern of current flow associated with the formation of flute marks (Allen, 1982). The lineations typical of 'Arumberia' are therefore interpreted as being formed in a firm sediment by action of a scouring current. 'Arumberia' is thus considered a pseudofossil, but does represent a peculiar sedimentary fabric that is typical of this latest Neoproterozoic interval. Thus the name is retained but not as a Linnean term.

Herein, we describe 'Arumberia'-like material from the Longmyndian, and review the case for it being a body fossil but, according to our interpretation, it is discussed along with other evidence for microbial structures and matgrounds. Evidence for the presence of numerous non-actualistic sedimentary structures in the Proterozoic has been mounting in recent years (McIlroy & Walter, 1997; Hagadorn & Bottjer, 1999; Pflüger, 1999; Seilacher, 1999), and their demise in the Phanerozoic has been typically linked to the evolution of pervasive bioturbators in the Neoproterozoic–Cambrian transition (e.g. McIlroy & Logan, 1999).

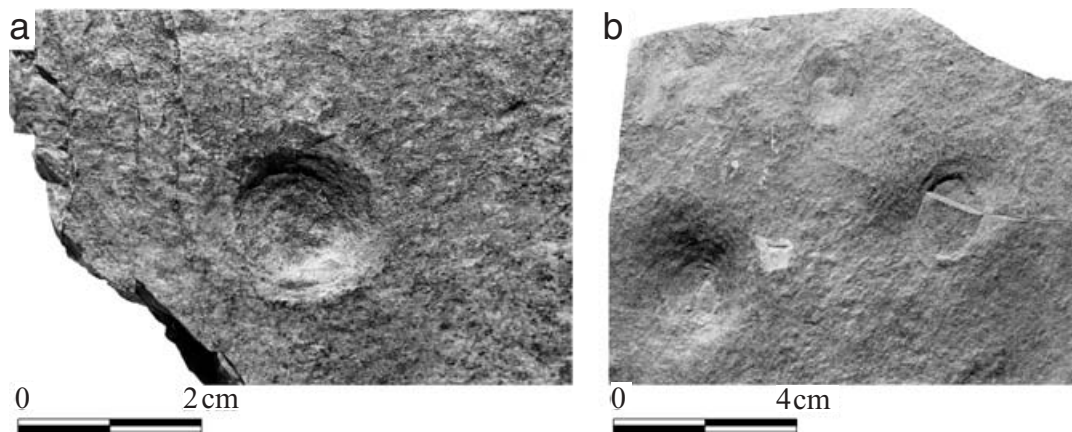


Figure 3. Morphology of *Beltanelliformis brunsa* from the top of the Burway Formation at Ashes Hollow. (a) Negative epirelief of a specimen on sample 82/12/8/2 showing concentric ornamentation. (b) Negative epirelief of specimen 82/12/8/1 showing three associated specimens.

3. Systematic palaeontology

In recent years a number of authors have taken a conservative view of taxonomy of Ediacaran disc-like fossils, which recognizes the importance of preservation on the morphology of such forms (Jenkins, 1992; Gehling, Narbonne & Anderson, 2000). One of the intrinsic difficulties in attempting to classify Ediacaran discs is the limited number of morphological features preserved. While we acknowledge that there is a continuum between several types of simple Ediacaran body fossil, we do not advocate the wholesale synonymization of many similar morphotypes. In particular we suggest that size-range is an important feature of Ediacaran disc-like assemblages that can be used to distinguish discrete taxa. For example, while the size of *Aspidella* overlaps with that of *Ediacaria* in the Fermeuse Formation of Newfoundland (Gehling, Narbonne & Anderson, 2000), *Aspidella* never reaches the maximum size of *Ediacaria*. Whether morphological differences/similarities are a result of taphonomic processes or original biology is almost impossible to determine. Thus in this paper the body fossil taxa under consideration are form taxa that are morphologically separate from each other. We prefer this approach in that it retains maximal information about the fossils; whether that information is sedimentological or biological in nature remains one of the frontiers in Ediacaran palaeontology.

The material described here is lodged in the Oxford University Museum of Natural History and numbered OUM Á.02284 to OUM Á.02293.

3.a. Body fossils

Genus *Beltanelliformis* Menner
 Type species *Beltanelliformis brunsa* Menner
Beltanelliformis brunsa Menner
 Figure 3a,b

Material. OUM Á.02284 and OUM Á.02285

Description. Preserved as negative epireliefs consisting of a circular depression 10–20 mm in diameter and approximately 1–2 mm high. Some show narrow concentric rings at the transition from the raised outer margin to the central depression. The two collected blocks have five complete specimens and one partial specimen (Fig. 3a,b).

Remarks. *Beltanelliformis brunsa* is more typically preserved in positive hyporelief, although it has also been recorded in negative epirelief and negative hyporelief (Narbonne & Hofmann, 1987, pp. 665–6, pl. 75, figs 3,5). It is of widespread occurrence in late Neoproterozoic strata and has been found in the Ukraine (Palij, 1976; Palij, Posti & Fedonkin, 1979; Gureev, 1985), Russia (Keller *et al.* 1974; Fedonkin, 1981, 1985; Bekker, 1985) and Canada (Hofmann, Fritz & Narbonne, 1983; Narbonne & Hofmann, 1987). Germs (G. J. B. Germs, unpub. Ph.D. thesis, Univ. of Capetown, 1972, pp. 218–19, pl. 29, figs 2–4) also described, as ‘Pseudo-*Bergaueria*’, specimens from the late Neoproterozoic Kuibis Formation of Namibia, which may well be referable to this taxon. The distinctions between *Beltanelliformis* and *Bergaueria* are far from clear but of obvious importance because of the much greater stratigraphic range of the latter taxon (cf. Pickerill, 1989). It has been suggested by Palij, Posti & Fedonkin (1979) that *Nemiana* (= *Beltanelliformis*) can be distinguished from *Bergaueria* by (1) the presence of numerous wrinkles and folds resulting from deformation of a soft bodied organism following burial, (2) the absence of an overlying vertical cylinder and (3) by the observation that adjacent specimens never cross-cut each other. Narbonne & Hofmann (1987, p. 666) also point out that the preservation of specimens in concave hyporelief suggests that *Beltanelliformis* represents the impression of a soft-bodied organism rather than a hemispherical burrow fill. These lines of evidence are not completely compelling and certainly some *Bergaueria* show wrinkles and folds

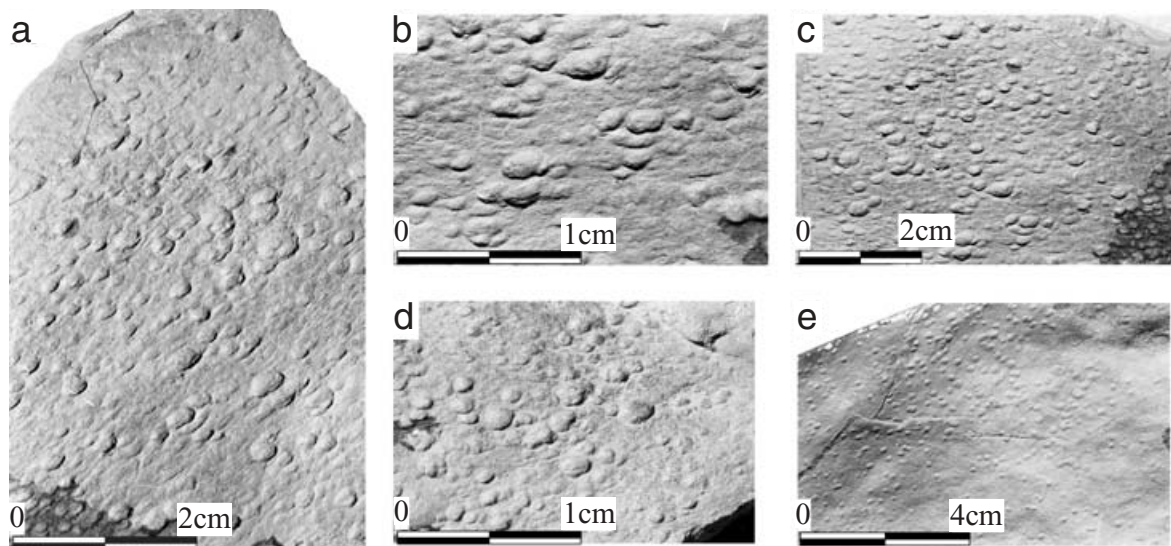


Figure 4. Specimens of *Beltanelliformis minutae* sp. nov. from the Longmyndian. (a–e) Syntypes of *Beltanelliformis minutae* sp. nov. from the Synalds Formation at Ashes Hollow.

(see Arai & McGugan, 1968, pl. 36, fig. 3; Pickerill, 1989, fig. 3) while there is not normally any vertical cylinder. Cross-cutting relationships are also rare in *Bergaueria*, even when specimens are closely crowded as in the material of Arai & McGugan (1968, pl. 36, fig. 12).

Recent suggestions that *Beltanelliformis* may be related to the megascopic acritarchs *Chuarua* and *Tawuia* (Steiner, 1997) is not supported by the observations herein or by Xiao *et al.* (2002). Although all three fossil genera are simple sphaeroidal forms, the similarity breaks down due to the complete absence of organic material in association with the margins of *Beltanelliformis* despite the good preservation of organic matter in the Longmyndian matground horizons (discussed below). Preservation in negative hyporelief (Narbonne & Hofmann, 1987 and herein) is also considered unlikely for such thin-walled organic fossils. The taxonomic status of the genus *Beltanelliformis* is somewhat in a state of disarray with some workers uncritically including large organic walled taxa previously included in the invalid genus *Beltanelloides* in *Beltanelliformis* with the consequence that *Beltanelliformis* is commonly considered to be coenocytic green alga (Gureev, 1985; Narbonne & Hofmann, 1987; Steiner, 1994; Xiao *et al.* 2002). Re-investigation of the type material is thus required. The probability of both small smooth rounded Ediacaran fossils and similar-sized round organic walled algal fossils in the late Precambrian is high. Broadening an existing taxon to encompass large thick-walled organic fossils is considered unwise by the present authors.

Occurrence. Near the top of the Burway Formation, Longmyndian Supergroup, Ashes Hollow, near Church Stretton, Shropshire. It is interesting to note that *B. brunsa* has not been found in association with

Intrites and *Medusinites* in the Longmyndian and is generally rare.

Beltanelliformis minutae sp. nov.

Figure 4a–e

- 1856 *Arenicolites didyma* Salter, pp. 248–9, pl. 4, fig. 1a,b.
 1857 *Arenicolites sparsus* Salter, p. 203, pl. 4, figs 1–4.
 1969 [?] ‘minute fossils’ Wade, p. 359, pl. 69, fig. 7.
 1984 ‘Spheroid impressions’ Bland, pp. 625–6, figs 1a,b, 2a–c.
 1987 [?] ‘Dubiofossil C’ Narbonne & Hofmann, p. 672, text fig. 10i.

Material. OUM Á.02284 and OUM Á.02285

Diagnosis. Small circular to elliptical impressions without concentric or radial markings that are commonly found in large numbers on bedding planes. Individual specimens are rarely greater than 4 mm in diameter and hyporeliefs are usually less than 1 mm in depth. The impressions are generally found in positive hyporelief and, more rarely, as negative epireliefs.

Syntypes. The numerous examples on the sole of specimen OUM Á.02286.

Etymology. Named from the small size of the fossils.

Type locality and horizon. Synalds Formation (Longmyndian Supergroup), Ashes Hollow, near Church Stretton, Shropshire.

Description. The syntypes are numerous examples on a block that was sectioned during study. Specimens are preserved as sub-circular to elliptical positive hyporeliefs on the sole of a fine-grained brown

sandstone. There is no discernible ornament or other markings. The structures are mostly elongate in a direction parallel to the local bedding/cleavage intersection lineation and therefore reflect a combination of fine-grained lithology and thus increased tectonic deformation. Original shapes would approximate to circular and be about 0.5–4.0 mm in diameter, although some now have long axes as much as 6 mm. Depth is typically less than 1 mm.

Remarks. *Beltanelliformis minutae* can be distinguished from *B. brunsa* not only on account of its smaller size but also because it lacks any circular or radial ornament. *B. minutae* is the most common organic structure to be found in these strata. In addition to the syntypes, numerous other specimens have been examined at the type locality but also at the same horizon in the nearby Cardingmill Valley and locally in the Portway, Lightspout and Bridges formations. They are commonly found crowded on bedding planes, each of which may show hundreds of specimens. Most examples are preserved in positive hyporelief, but some occur as hollow pits. This reflects negative hyporelief preservation, so indicating burial of specimens in their entirety in a firm mudstone, followed by decay to leave a mouldic cavity. In section, specimens preserved in positive hyporelief on the soles of the beds are infilled with siltstone, and muddy horizons drape over the structure (Fig. 6c).

Similar hemispherical bodies, probably to be included in *B. minutae*, have been recorded from late Neoproterozoic strata in many parts of the world. Wade (1969, pl. 69, fig. 7) records ‘minute fossils’ preserved in positive hyporelief on a slab of sandstone from the Neoproterozoic of the Central Mount Stuart Beds, central Australia. The ‘hypichnial casts’ 1–2 mm in diameter described from the Neoproterozoic Innerelv Member, Finnmark, northern Norway, by Banks (1970, pl. 1a) were described as ‘passively filled simple vertical burrows’ but are probably pseudofossils (Farmer *et al.* 1992). Examples described as ‘Dubiofossil C’ and suggested to be possibly small *Beltanelliformis*, were recorded from late Neoproterozoic strata of the Wernecke Mountains, Yukon, Canada by Narbonne & Hofmann (1987, text fig. 10i). The figured blocks show large numbers of specimens, exactly as in much of our material. It is also possible that some of the small, unornamented, simple hemispherical bodies included in *Nemiana* (= *Beltanelliformis*) *simplex* might better be included in *B. minutae* (e.g. Fedonkin, 1985, pl. 29, fig. 6).

Bland (1984) has also illustrated ‘spheroid impressions’, which appear to be examples of *B. minutae*, from the Lightspout Group of the Longmyndian Supergroup at the Longmynd. He also figures two similar specimens collected by Salter (1856, 1857) that are housed in the British Geological Survey Museum. Examples from the late Neoproterozoic Gibbett Hill Formation, St

John’s, Newfoundland and from strata of a similar age at Bréhec in northern France were also figured (Bland, 1984). Bland documented some examples where these spheroids occur within the arrays of ‘Arumberia’ and suggested that they are its dispersible resting stage. As discussed above, ‘Arumberia’ is now considered a problematical structure best interpreted as a pseudofossil, and we can find no compelling reason to conclude that the two are associated, except by chance in some specimens. Structures associated with *B. minutae* in our material include hair-like straight to sinuous, short linear structures that occur with profusion on some specimens including that illustrated here as Figure 4a–e. Although individual strands are too small to see clearly, the surface has an irregular texture that may represent a microbial mat (see Narbonne & Dalrymple, 1992; Fedonkin, Yochelson & Horodyski, 1994; Hagadorn & Bottjer, 1999 for discussion). Similar surfaces have been identified as being microbial mats by Fedonkin, Yochelson & Horodyski (1994, p. 206, fig. 7), and the surface texture is referred to as ‘elephant-skin texture’. It would therefore appear that there is evidence to link preservation of *B. minutae* with matground conditions and microbial growth. In addition, Peat (1984) described cryptarchs from associated finely laminated dark shales and siltstones in the Lightspout Formation, and Pauley (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986, pp. 179–81) described figured mats formed of filamentous cryptarchs and disseminated organic matter within similar lithologies from the Lightspout, Synalds and Portway formations.

Despite its simple form, *B. minutae* is a distinctive structure whose globular shape readily distinguishes it from the bedding plane intersections of vertical burrows. Its common occurrence crowded on bedding planes is also distinctive. To date, no examples are known to the authors from above the late Neoproterozoic and as such, this taxon may prove to be a useful index fossil.

Specimens of *B. minutae* were used by Salter to define two ichnospecies of the vertical U-shaped burrow *Arenicolites*, based on purported pairing of depressions in material from the Longmynd. Re-examination of the type material refutes this interpretation; the impressions are neither demonstrably paired, nor is there a strong vertical component to the impressions. Rare specimens of *B. minutae* found during our field studies show deformation/poor preservation that gives the superficial appearance of bilobation. Salter’s two species of *Arenicolites* from the Longmynd (*A. sparsus* Salter 1856 and *A. didyma* Salter 1857, housed at the British Geological Survey Museum) are therefore transferred to *Beltanelliformis minutae*.

Lastly, the occurrences of *B. minutae* in the Lightspout and Portway formations appear to be associated with dominantly non-marine strata (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986).

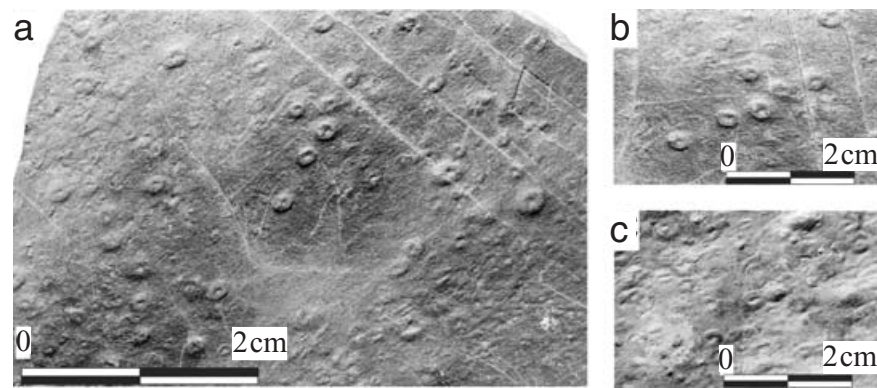


Figure 5. Specimens of *Intrites punctatus* from the Burway Formation and Lightspout Formation at Ashes Hollow and Callow Hollow showing the gregarious nature of the fossils. (a, b) specimen 22/1/1/84; (c) specimen 13/9/2/84 E.

At this stage, however, their association with marine incursions cannot be ruled out.

Occurrence. Documented from the Burway, Synalds, Lightspout and Portway formations. Where present it is commonly superabundant as monotypic assemblages, sometimes in (chance) association with the pseudo-fossil 'Arumberia'.

Genus *Intrites* Fedonkin

Type species *Intrites punctatus* Fedonkin

Intrites punctatus Fedonkin

Figures 5a–c, 6a

- 1980 *Intrites punctatus* Fedonkin, pp. 44–5, pl. 2, fig. 1.
 1982 *Bergaueria* sp. Crimes & Germs, pp. 893–4, pl. 1, fig. 1a.
 1985 *Intrites punctatus* Fedonkin, pl. 26, fig. 7.
 1991 'Dubiofossil E', Hofmann, Mountjoy & Teitz, p. 1548, fig. 8G.
 1992 *Intrites punctatus* Fedonkin & Runnegar, p. 391, fig. 7.6.4b.
 1992 *Intrites punctatus* Bekker, p. 21, pl. 1, figs 5–7.
 1995 [?] '*Neonereites*' *renarius* Fedonkin; Jenkins, p. 56, pl. 1d.
 2003 non *Intrites* Seilacher, Grazhdankin & Legouta, p. 49, fig. 9.

Material. OUM Á.02288 and OUM Á.02289

Description. Numerous specimens preserved mainly in positive hyporelief and negative epirelief, occasionally in positive epirelief and negative hyporelief. The fossil thus consists of a circular protrusion with a shallow, well-defined, circular central depression only 1–7 mm diameter and with height always less than diameter. The central depression is typically a fraction of a millimetre in diameter but may be up to 2 mm. In negative hyporelief the trace comprises a circular moat-like depression several millimetres in diameter with a central protuberance up to 1 mm in diameter. None of

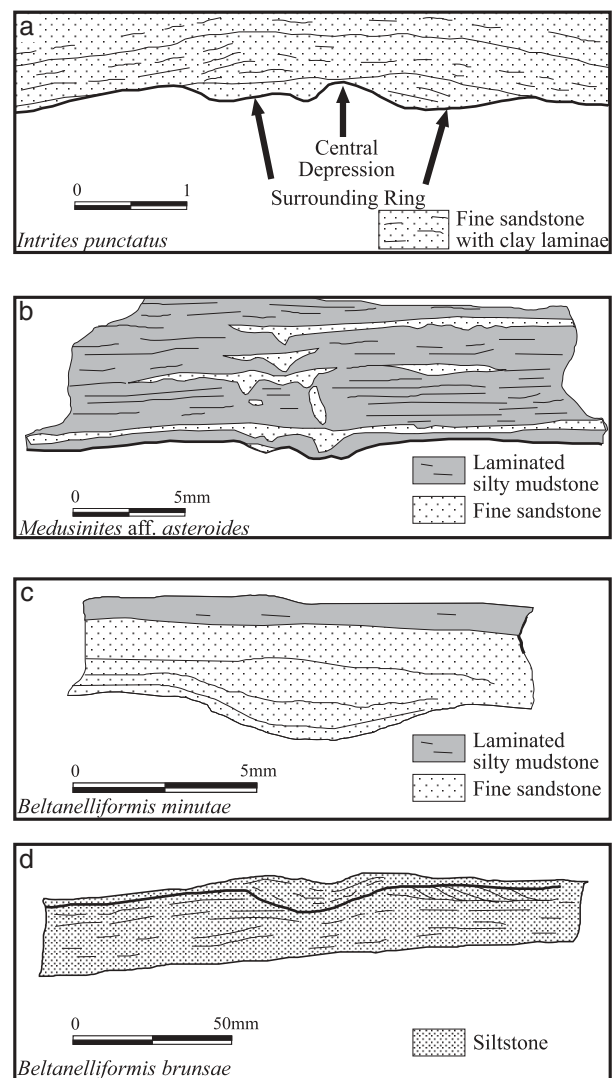


Figure 6. Illustrated cross-sections through the trace fossil and Ediacaran body fossil and trace fossil taxa: *Intrites punctatus* (a); *Medusinites* aff. *asteroides* (b); *Beltanelliformis minutae* sp. nov. (c); and *Beltanelliformis brunsa* (d). The line drawings are based on polished cross-sections.

the fossils bear any ornament and they commonly occur in profusion. Fill is similar to under- or overlying sediment. In polished vertical section (Fig. 6a) the traces are seen to be infilled with parallel and cross-laminated very fine sandstones and mudstones overlain by parallel-laminated or disturbed alternating siltstones and mudstones.

Remarks. *Intrites punctatus* was first described as a trace fossil by Fedonkin (1980) from the Valdai Series of Vendian (= Ediacaran) age on the shores of the White Sea in northern Russia for a series of small casts with an indent in the middle of each one, preserved on the underside of beds (positive hyporelief) and resembling a doughnut. The diameter of the hyporeliefs was 1.5 to 7 mm and the depth 0.5 to 2.5 mm, which compares closely with the examples described here. As mentioned by Fedonkin (1980), the traces bear some superficial resemblance to the trace fossil *Neonereites*, but some of the abundant examples described herein show little tendency to a close-packed linear arrangement. The diagnostic central depression is present in almost every Longmyndian example studied and is not a character associated with the ichnogenus *Neonereites*.

Material collected from float and described by Crimes & Germs (1982, p. 893, pl. 1, fig. 1) as *Bergaueria* isp. consists of cylindrical sacs (1–5 mm wide), with rounded lower ends and a shallow circular central depression. Crimes & Germs mentioned (1982, p. 893) that the traces closely resembled *Intrites punctatus* in morphology and size. It is now considered that these traces should be included in *Intrites punctatus*. This genus has also been described from Vendian (Ediacaran) strata in the Ural Mountains, Russia (Bekker, 1992, p. 21, figs 5–7). Cruse & Harris (1994, pp. 6–7, fig. 4) describe as *Bergaueria*, 24 examples of discs 4–8 mm in diameter, 1.5–2.0 mm high and with a central depression, from the Stirling Range Formation of Western Australia that are dated at between 2016 and 1215 Ma (Rasmussen *et al.* 2002). This material resembles *Intrites* but requires close re-investigation owing to its great antiquity.

Hofmann, Mountjoy & Teitz (1991, p. 1548, fig. 8G) describe, as Dubiofossil E, small circular, randomly scattered mounds, 3 mm in diameter and 0.2 to 0.3 mm high, with a 1 mm wide central depression from float of the late Neoproterozoic Miette Group of Mount Fitzwilliam area, British Columbia (Canada). These small doughnut-like bodies are indistinguishable from the examples of *Intrites punctatus* described here and should be included within it. The age of the upper part of the Miette Group, containing these structures, is considered to be Ediacaran and they are accompanied by an Ediacara-type fauna including *Beltanella*, *Charniodiscus?*, *Irridinitus* and *Nimbia*. The most recent discussion on *Intrites* in Seilacher, Grazhdankin & Legouta (2003) unfortunately is based

upon a specimen of the trace fossil *Palaeopascichnus delicatus*.

There is some doubt about the orientation of some of our *Intrites*, since some were collected from float or from areas of poor exposure and structural complexity, which rendered the way-up of specimens uncertain. Some material found *in situ*, including blocks where way-up is known, contained numerous examples, all in positive hyporelief. Specimens described by Greig *et al.* (1968, p. 70) as ‘pit and mound structures’ from Ashes Hollow, are probably examples of *Intrites* and they suggest that positive doughnut-like bodies occur on the tops of the beds. We incline to the view that at least some may be symmetrical, forming true doughnuts, and as such are closer to body fossils than trace fossils. Most specimens, however, appear to be impressions of the lower surface of an organism that was largely sessile but which had some propensity for limited movement to create the typical linear arrangements of impression. It may also, however, be that the movement was passive (induced by currents) rather than through active locomotion. No wall structure can be determined in our material and a protistan affinity cannot currently be tested.

Occurrence. Within the Longmyndian Supergroup (late Neoproterozoic) exposed to the west of Church Stretton, in the Burway Formation at Callow Hollow but also at Ashes Hollow, where they are comparatively rare. Material attributable to *Intrites punctatus* was recovered from a horizon tentatively attributed to the Lightspout Formation, though due to structural complexities the exact level cannot be determined with confidence.

3.b. Trace fossils

Ichnogenus *Medusinites* Glaessner & Wade
Type species *Medusinites asteroides* (Sprigg)
Medusinites aff. *asteroides* (Sprigg)
Figures 6b, 7a, b

Material. OUM Á.02290 and OUM Á.02291

Description. Two blocks showing numerous circular or sub-circular positive hyporeliefs, composed of a minute smooth pimple at the centre of a smooth mound. The diameter of the pimple is less than one millimetre, while that of the complete structure is 1–3 mm. Relief is typically approximately 1 mm.

Remarks. A detailed synonymy of *Medusinites asteroides* (Sprigg) has been given by Narbonne & Hofmann (1987) who figure three examples, all much greater (9.0–25.6 mm) in diameter than those described here. They also show a more distinct outer margin but lack the radial elements and marginal flange present in the holotype (Glaessner & Wade, 1966, pl. 97, fig. 3). However, radial elements are absent in the two hypotypes illustrated in Glaessner & Wade (1966, pl. 97,

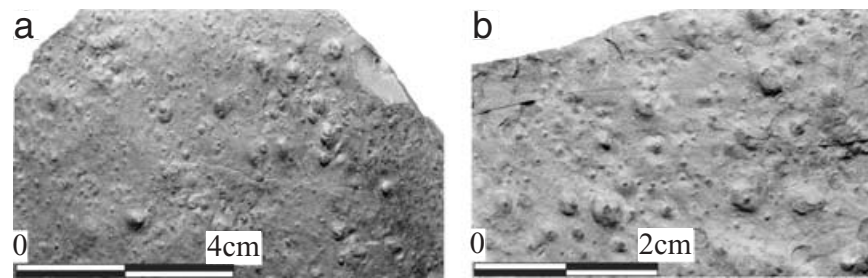


Figure 7. *Medusinites* aff. *asteroides* from the upper part of the Burway Formation at Ashes Hollow. (a) Showing the densely populated sediment surface with the circular hyporeliefs containing a small central pimple. (b) Detailed morphology of *Medusinites* aff. *asteroides*.

figs 1, 2). Most of our material lacks both the marginal flange and radial elements, but the latter feature is present in one specimen from the same unit and locality figured in Pauley (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986, fig. 28B). In view of their exceedingly small size, well below the stated 10–50 mm diameter of the type material (Glaessner & Wade, 1966, p. 606) and the absence of both a flange and radial elements in most specimens, we only consider this material to have affinities with the type. Examples similar to those described here, but rather larger, have been described as *Medusinites asteroides* by Gureev (1987, fig. 10) and Riabenko, Assayeba & Furtes (1988, pl. 9, figs 1–4). Cross-sections normal to bedding (Fig. 6b) show that the mound is infilled with coarse silt and fine sand, similar in composition to, and in continuity with, the adjacent laminae. A thin tube, less than one millimetre diameter, infilled with fine sand, extends upwards above the mound, cuts through laminae in the silty mud and appears to connect several mounds, which are stacked one above the other. This suggests that the animal migrated upwards with sediment accumulation and tends to imply that the structures are trace fossils rather than body fossils. It is, however, highly probable that the morphology of the trace strongly reflects the lower surface of the trace-maker.

Occurrence. The few specimens recovered came from the Burway Formation, Longmyndian Super-group, Ashes Hollow, near Church Stretton, Shropshire, from a horizon also yielding *Intrites punctatus*.

3.c. Microbially modified sedimentary structures

Pseudofossil ‘Arumberia’

Figure 8b

- 1856 Marks of -?Salter, p. 250, pl. 4, fig. 4.
- 1856 Ripple marks (with thin mud-coating?); Salter, p. 250, pl. 4, figs 5, 6.
- 1857 Surf lines, Salter, p. 202, pl. 5, fig. 8.
- 1968 Raised mounds and rills on sand ridges, Greig *et al.* p. xi, pl. 5E.
- 1968 Groove casts and raised mounds, Greig *et al.* p. xi, pl. 5F.

- 1975 *Arumberia banksi* Glaessner & Walter, figs 1–3.
- 1980 *Arumberia banksi* Bekker, pp. 235–7, fig. 2.
- 1981 *Arumberia banksi* Liu, p. 74, pl. 1, figs 3a,b, pls 2c, 4.
- 1984 *Arumberia banksi* Glaessner, p. 73, fig. 2.9.
- 1984 *Arumberia* sp. Bland, pp. 625–32, figs 1, 2.
- 1985 *Arumberia banksi* Bekker, pp. 127–8, fig. 5.
- 1997 ‘*Arumberia*’ McIlroy & Walter, pp. 79–80, figs 1–3.

Material. OUM Á.02292

Description. Subparallel, raised linear ridges both in positive epirelief and hyporelief, typically less than 1 mm wide and separated by flat to gently concave furrows with a width of 0.5–3.0 mm. Relief from ridge-top to furrow-bottom is normally less than 0.5 m. Ridges are commonly several centimetres long but may continue for tens of centimetres. As the ridge spacing increases, their relief tends to increase. Ridges are usually parallel but some diverge and bifurcate whereas others converge. Transverse sculpture is rarely present and crosses some ridges, and in some examples this is sufficiently frequent and prominent to produce a network (see Fig. 8a).

Remarks. ‘*Arumberia*’ has been the subject of much contention and its organic nature contested (e.g. Jenkins, Plummer & Moriarty, 1981; Runnegar, 1993; McIlroy & Walter, 1997). ‘*Arumberia*’ was first described by Glaessner & Walter (1975), based on material collected by J. Banks, from the Arumbera Sandstone in the Northern Territory, Australia. The type material shows arrangements of many fine subparallel ridges with some converging to small apical areas. Bifurcation of the ridges was also observed and transverse sculpture was seen crossing the intervening ribs. The ribs in some specimens radiate in all directions from an apex, but never equally. The ridges were shown mainly to occur on the soles of beds (positive hyporelief), but a few were noted as grooves on the tops (negative epirelief) and so differ from some of the Longmyndian structures which are mainly in positive epirelief. Glaessner & Walter (1975) noted that there was evidence of current scour parallel to these structures but they considered that their

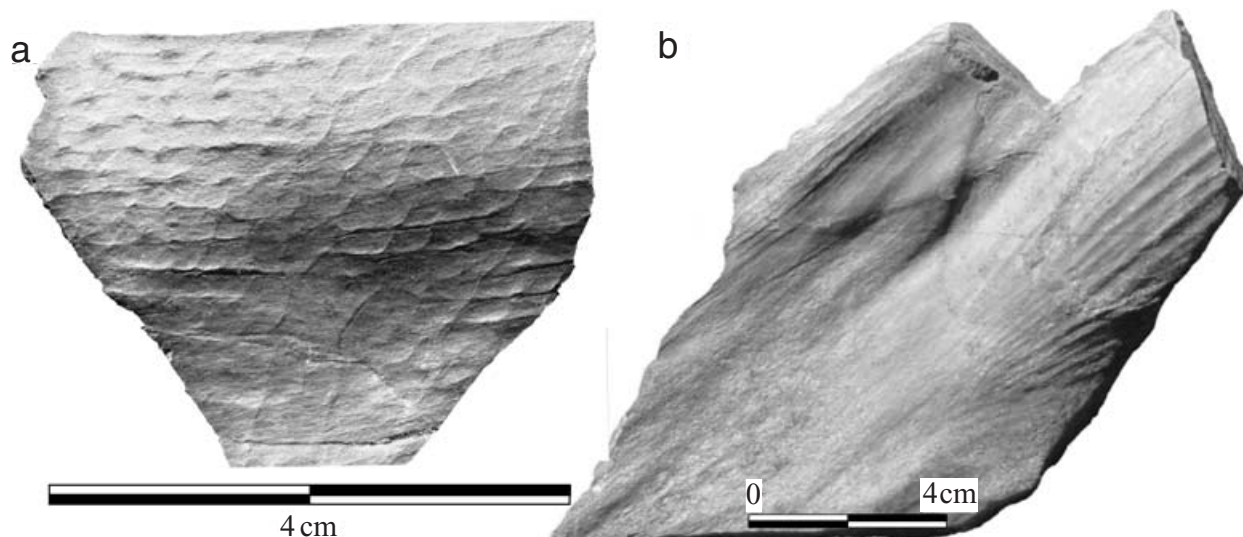


Figure 8. The non-actualistic sedimentary structures 'Arumberia' and 'Elephant-skin texture' from the Synalds, Lightspout and Portway formations. (a) Net-like/reticulate 'elephant-skin texture' from the Synalds Formation at Ashes Hollow (specimen 20/4/1/85). (b) Radiating 'Arumberia' associated with a shallow groove from the top of the Lightspout Formation at Deadmans Batch (specimen 82/6/10/3).

overall form, and particularly their radiating tendency, were quite unlike any known mechanical lineations or drag or prod marks. In response to the critical appraisal of 'Arumberia' by Jenkins, Plummer & Moriarty (1981), who questioned their organic nature, Glaessner (1984, p. 73) suggested that mechanical current lineations on bedding planes never radiate from hollows as do the ribs on many of the figured specimens of 'Arumberia' and thus he maintained their interpretation as a body fossil. The presence of tool marks associated with the scouring currents is common in a variety of sedimentary structures including gutter cast and they do not always have longitudinal orientations (Whitaker, 1972), but reflect flow patterns as suggested by McIlroy & Walter (1997).

In some of the material described herein both a transverse and longitudinal sculpture is developed (Fig. 8a, OUM Á.02292) that also has no counterpart in inorganic sedimentary structures, but bears some resemblance to material described by Runnegar & Fedonkin (1992) and Gehling (1999) as 'elephant skin texture'. This elephant skin texture is also attributed to microbially bound surfaces and strongly linked with the Ediacaran-type of soft-bodied preservation by Gehling (1999).

'Arumberia' has been recorded from many other late Neoproterozoic sequences. Bekker (1980) has described examples from a late Neoproterozoic sequence in the Urals that also contains an Ediacara-type fauna. Additional well-preserved material in the All Union Geological Institute in St Petersburg has been examined by TPC. Liu (1981) has described and illustrated 'Arumberia' from the Mashan Group, which he considers to be of late Neoproterozoic age, in

the Heilongjiang Province, China. Glaessner (reported in Bland, 1984, p. 629) examined 'Arumberia' from China and considered some, at least, to be correctly designated. Forms described as *Jixiella capistratus* by Liu (1981) may well also be pseudofossils related to Arumberia.

In a wide-ranging paper, Bland (1984) reviewed published data on 'Arumberia', described some new material and discussed its potential for correlation of late Neoproterozoic/Early Cambrian strata. He recorded, but did not illustrate, material from the Bonney Sandstone of late Neoproterozoic age in South Australia and from the Early Cambrian Billy Creek Formation in the same area. 'Arumberia' was also recorded from a Neoproterozoic/Cambrian sequence in Erquy and Bréhec in northern France (Bland, 1984, p. 629, fig. 2b) and from a late Neoproterozoic sequence in the Signal Hill Group of St John's, Newfoundland, Canada. Attention was also drawn to Salter's material from the Longmyndian Supergroup which was assigned to 'Arumberia' (Bland, 1984, fig. 1a,b). Further material was described from the Lightspout Group (Bland, 1984, fig. 2c).

In the Longmyndian there are lineations in the same sequences where 'Arumberia' has been recorded that are of tectonic or sedimentary origin, in particular a very prominent bedding/cleavage intersection lineation (Fig. 8b). These confuse the interpretation of 'Arumberia' in the Longmyndian. Although *in situ* specimens are found in positive epirelief, the way-up of some specimens is uncertain either due to retrieval from float or to structural complexity.

An association of 'Arumberia' with *Beltanelliformis minutae* (referred to as 'spheroids' by Bland) led Bland (1984, p. 631) to consider the latter to be a dispersible

resting stage of the former. However, *Beltanelliformis* is not intimately associated with 'Arumberia' in the type material (Glaessner & Walter, 1975), material from the Urals (Bekker, 1980) or from China (Liu, 1981). We have found some specimens where the two are associated, but in most cases they are not and the arrangement of spheroids and ridges is probably fortuitous. The two forms appear to be distinct from each other but may occur in the same stratigraphic interval.

Occurrence. Synalds, Lightspout and Portway formations of the Longmyndian Supergroup in some cases associated with apparently non-marine lithofacies (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986).

4. Discussion

The fossils described herein are typically found elsewhere in association with the so-called 'soft bodied' Ediacara fauna. We take this as circumstantial evidence for the Neoproterozoic age of this section along with the absence of pervasive bioturbation that characterizes similar environments to those of the Longmyndian in rocks of Phanerozoic age (e.g. McIlroy & Logan, 1999).

Much recent literature has focused on alternative explanations of the Ediacara fauna, all of which have proven to be highly controversial. These include: comparison with modern faunas (e.g. Glaessner, 1984; Jenkins, 1992); erection of new phyla (Pflug, 1970, 1972; Fedonkin, 1985; Gureev, 1985; Seilacher, 1992; Buss & Seilacher, 1994); comparisons with fungi (Retallack, 1994); comparisons with protists (Zhuravlev, 1993; Crimes & Fedonkin, 1996 and popularized by Seilacher, Grazhdankin & Legouta, 2003); and comparisons with microbial colonies (Grazhdankin, 2001; Steiner & Reitner, 2001) among others. Many authors accept that there is a strong link between matgrounds and preservation of the Ediacara fauna (Gehling, 1991, 1999). What is becoming clear is that at least some elements of the Ediacara fauna persist into the Phanerozoic, as asserted by Crimes & Fedonkin (1996), albeit in reduced numbers.

The association of our Ediacaran fossils with microbial mats, 'Arumberia' and simple trace fossils is in keeping with the 'death mask' model of Gehling (1991, 1999). Our fossils show no evidence of having pervasively grown through the sediment and as such appear not to be protists or microbial colonies. Despite the preservation of abundant organic matter at several levels in the Longmyndian (J. C. Pauley, unpub. Ph.D. thesis, Univ. Liverpool, 1986), no organic matter is preserved in association with any of the macrofossils. Such low diversity Ediacaran assemblages are common in Avalonia, Baltica and Laurentia during the Ediacaran and provide a good marker for rocks of this age.

The demise of the Ediacara fauna has been suggested by a number of authors to be linked to the destruction of the matgrounds that are commonly invoked in

preserving the Ediacara fauna (Gehling, 1991, 1999), by increased grazing and bioturbation following the 'Cambrian explosion' (Seilacher & Pflüger, 1994). Study of temporal trends in the intensity of bioturbation predicts that an escalation in the intensity of bioturbation began in an offshore setting, only reaching near-shore environments later in the Cambrian (McIlroy & Logan, 1999). It is this time lag that probably accounts for the persistence of the Ediacara fauna in the shallowest water environments well into the Cambrian (Narbonne *et al.* 1991; Jensen, Gehling & Droser, 1998; Crimes & McIlroy, 1999; Hagadorn, Dott & Damrow, 2002).

5. Conclusion

The following conclusions can be drawn from this study:

1. The late Neoproterozoic (Ediacaran) Longmyndian Supergroup of the U.K. contains abundant hemispherical bodies, mostly a few millimetres in diameter and normally preserved as mounds on lower bedding surfaces and pits on upper surfaces.
2. Most or all of these bodies are shown to be of organic origin and can be assigned to one of the following taxa: *Beltanelliformis brunsa*, *B. minutae* sp. nov., *Intrites punctatus* and *Medusinites asteroides*.
3. Linear net-like structures occur in the same strata and are, in places, associated with the hemispherical bodies. Linear 'Arumberia' structures are attributed to microbial binding of sedimentary surfaces following McIlroy & Walter (1997) or as tectonic lineations and, as such, their association with the pits is presumed to be fortuitous.
4. Structures of these types are being increasingly recognized worldwide in strata of late Neoproterozoic (Ediacaran) age and may be useful in correlation.

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