A solution to Darwin's dilemma of 1859: exceptional preservation in Salter's material from the late Ediacaran Longmyndian Supergroup, England

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Study of historic and fresh collections from the Longmyndian Supergroup sheds new light on Ediacaran microbial communities and taphonomy. First reported by Salter in 1856, and noted by Darwin in the 'Origin of Species' in 1859, a range of macroscopic bedding plane markings are already well known from the Longmyndian. Here we report filamentous and sphaeromorph microfossils, variously preserved as carbonaceous films, by aluminosilicate permineralization and as bedding plane impressions. This supports a long-suspected link between wrinkle markings and microbes and draws further attention to our hypothesis for a taphonomic bias towards high-quality soft tissue preservation in the Ediacaran Period.

The Precambrian has long been a puzzle for palaeontologists and for many years Precambrian sediments were thought to be unfossiliferous. Charles Darwin saw the lack of a Precambrian fossil record as a potential problem for his theory of natural selection, a problem which has become known as 'Darwin's Dilemma': *"To the question why we do not find records of these vast primordial periods, I can give no satisfactory answer."* (Darwin 1859). Despite this, Darwin appeared confident that life had existed during the Precambrian and that fossils were yet to be identified: *"Consequently, if my theory be true, it is indisputable that before the lowest [Cambrian] stratum was deposited, long periods elapsed, as long, or probably far longer than, the whole interval from the [Cambrian] age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures*." (Darwin 1859). It is around this time that the first reports of Precambrian fossils appeared, as the Geological Survey geologist J.W. Salter described trace fossils (*Arenicolites*) in addition to markings including "rain-prints", "sun-cracks" and "surf-ripples" from the Long Mynd of Shropshire. This important report was cryptically noted by Darwin: *"Traces of life have been detected in the Longmynd beds beneath Barrande's so-called primordial [Cambrian] zone."* (Darwin 1859). Salter's initial discoveries therefore mark the beginning of the study of Precambrian palaeontology and potentially provided Darwin with a solution to his dilemma.

While a variety of unusual bedding plane markings are now well known from the Longmyndian Supergroup, here, we describe a variety of exceptionally preserved microbes, both from Salter's material and from new collections. These microbes are preserved as carbonaceous films, silicate replacements and three-dimensional impressions and reveal that some secrets of the Longmyndian rocks have remained hidden for over 150 years. Exceptionally preserved microbes are well known from Ediacaran carbonaceous (e.g. Miaohe; Xiao et al. 2002), phosphatic (e.g. Doushantuo; Xiao & Knoll 1999) and siliceous (e.g. Doushantuo; Xiao 2004) lagerstätte. However, our observations of microbial preservation by aluminosilicate permineralization and as siliciclastic bedding plane impressions are somewhat unusual and deserving of further description.

Setting and Materials. The Longmyndian Supergroup of Shropshire, England, has been interpreted as an expanded Ediacaran siliciclastic succession, ranging from marine deltaic to alluvial plain or fluvial palaeoenvironments (McIlroy et al. 2005 and references therein). No large Ediacaran frondose macrofossils are known, although an array of unusual bedding plane markings including Salter's putative annelid worm traces (*Arenicolites*), have been described (e.g. Salter 1856, 1857; Greig et al. 1968; Bland 1984; McIlroy et al. 2005). While the biogenicity of Salter's

holotype material for *Arenicolites* has since been disputed (e.g. Greig et al. 1968; McIlroy et al. 2005), markings from the Longmyndian have latterly attracted interpretations ranging from the sedimentary expressions of ancient microbial mats (microbially induced sedimentary structures *sensu* Noffke et al. 2001), to body or even to trace fossil taxa (see McIlroy & Walter 1997; McIlroy et al. 2005).

Microfossils from the Longmyndian were first reported by Timofeyev (1980) while Peat (1984) described carbonized, mat-forming, ribbon-like and sphaeromorph microfossils from petrographic thin sections, which were compared with prokaryotes, eukaryotes and even questionably with metazoans. Here, we report on a fresh study of Salter's historic material, supplemented by new specimens from the Burway Formation at Ashes Hollow and the Lightspout Formation in Carding Mill Valley, Shropshire (see Greig et al. 1968), focusing upon the evidence for exceptional fossil preservation on a microscopic scale.

Longmyndian Fossils. *Description.* Petrographic thin sections through dark carbonaceous siltstones of the Lightspout Formation, reveal abundant black carbonized filaments (Fig. 1), similar to those reported by Peat (1984). The filaments are typically 15-20μm in diameter and up to 1500μm in length and do not show evidence for tapering. They are non-septate and do not appear to show branching of any kind. These filaments are commonly parallel to sub-parallel in orientation and can overlap and form interwoven mat fabrics, much as reported by Peat (1984). Variations in filament diameter along the length of a single filament are here interpreted in part as taphonomic artefacts. We have not yet observed sphaeromorph structures from thin sections. The lower bedding surface of the filament-bearing horizon bears an irregular crinkly texture, similar to putatively microbial markings known as '*Kinneyia*' (e.g. Gerdes 2007). Our observations support the microbial origin of these markings, which is significant given the potential abiogenic modes of formation of wrinkle markings (Porada & Bouougri 2007; McLoughlin et al. 2008) and the often limited evidence for a direct connection between microbial mats and wrinkle markings in the Precambrian.

Sub-millimetre scale examination of siltstone bedding surfaces of the Burway Formation at Ashes Hollow allows us to report a variety of distinctive white filamentous markings, which are preserved within a grey-green siltstone matrix (Fig. 2). Long (mainly >1mm), thin (<20μm) filaments often occur alongside markings attributed to the body fossil *Beltanelliformis minutae* McIlroy and the ichnotaxon *Medusinites* aff. *asteroides* Sprigg, as described by McIlroy et al. (2005). SEM imaging reveals their gentle positive relief and allows us to refute the possibility that they represent surface contaminants. The filaments show no evidence of tapering and are assumed to have been originally circular in cross section. Internal divisions or septation cannot be seen although this may be an artefact of preservation. Significantly, the filaments show unequivocal 'Y'-shaped branching, which may have implications for their biological affinity (Fig. 2C). The filaments can either be found sporadically on bedding planes (Fig. 2B-C) or alternatively they can be observed in extremely high concentrations, where they be either random or parallel in orientation and form dense, interlocking mats within thin (<1mm) sedimentary laminae (Fig. 2A).

Much larger diameter filaments can also be observed on the same bedding planes as the thread-like filaments (Fig. 2D). These can be up to several hundred microns in diameter and 1-2mm in length. The broad filaments are also white in colour and show no evidence for septation or branching nor do they demonstrate a tendency to cluster or form mats. White circular to sub-circular discoidal structures, up to 500μm in diameter, also occur on the same bedding planes, in clusters of up to 20 specimens (Fig. 2E). These discoidal structures show no evidence for internal architecture or evidence for mechanisms of growth. We suggest that these may originally have had a sphaeromorph morphology and may be comparable to the structures reported from thin section by Peat (1984).

In addition to carbonized filaments (Fig. 1) and white filaments and discoids (Fig. 2), we also report the occurrence of filamentous markings, which are preserved as impressions and moulds in three-dimensions, likewise on bedding planes. Straight to sinuous, narrow (c. 200μm),

thread-like features are relatively common in Salter's specimens labelled "Yearling Hill, Church Stretton" (Fig. 3). These samples are thought to be from the Burway/Synalds Formation at Yearlet Hill (Greig et al. 1968), although our field investigations have not revealed the exact locality of these samples. These filamentous markings occur either in positive or negative relief and are often found in close spatial association with (or even superimposed upon) features referred to *Beltanelliformis minutae* (c.f. McIlroy et al. 2005). Features referred to *B. minutae* are also found in the opposite sense of relief to the thread-like impressions (Fig. 3). These markings may be comparable to the somewhat smaller "hair-like" structures reported by McIlroy et al. (2005), which have been used as an indicator for ancient microbial mats. Typically the thread-like markings are rather sinuous and randomly oriented. In other cases, parallel-oriented filaments may reflect a palaeocurrent direction. Together, these observations are not easily interpreted as minute trace fossils or even as abiogenic structures such as shrinkage cracks, current lineations or groove casts and we suggest that these markings may represent the external moulds of large, mat-building, microbial filaments.

Biological Affinities. A wide range of microbial morphologies are present in the Longmyndian, which supports the presence of a diverse late Ediacaran microbial community. Resolving the biological affinities of these microbes is difficult however, given the lack of characteristic and diagnostic biological or morphological features. The shallow marine to fluvial depositional environment of these sediments means, of course, that either a photoautotrophic or heterotrophic mode of life remains possible. Potential biological affinities to be considered for these microbes include cyanobacteria, eukaryotic algae, fungal hyphae or a variety of other filamentous autotrophic and heterotrophic bacteria. Although many filamentous microfossils have previously been interpreted largely on the basis of size (e.g. Schopf 1992), our investigations of modern and ancient filaments suggest that determining the biological affinities of fossil microbes using filament diameter is highly problematic.

The smallest (c. 20μm) carbonized and permineralized filaments (Fig. 1, 2A-C) overlap with the size ranges reported from modern and putative fossil cyanobacteria (see Schopf 1992 fig. 5.4.27) and branching could also be compatible with cyanobacteria. Wrinkle markings observed from the Longmyndian (e.g. elephant skin texture) can also be compared with microbially induced sedimentary structures found within living cyanobacterial mats (e.g. McIlroy et al. 2005; Gerdes 2007). We have not definitively observed features such as 'H'-shaped branching or hyphal fusion which would support a fungal affinity (e.g. Butterfield 2005). Therefore, although we suggest that a cyanobacterial affinity is possible, we are unable to reject eukaryotic algal or other microbial possibilities. The larger white filaments (Fig. 2D) and the filamentous impressions (Fig. 3) could also be explained as large cyanobacterial sheaths, as bundles of microbial filaments, or as eukaryotic algae. Determining the biological affinities of discoidal microfossils is equally problematic, although it may be interesting to speculate whether they are comparable to the Precambrian possible prokaryote *Chuaria*, which is more commonly preserved as a carbonaceous film (e.g. Steiner 1994).

We are currently unable to satisfactorily resolve the affinities of the Longmyndian microbes, although we suggest that future sampling combined with further morphological and geochemical (e.g. biomarker) analysis may yet help to distinguish between the various possibilities.

Taphonomy. As we have described, the Longmyndian microbes are preserved within three distinct taphonomic modes. In the first case, microbes are preserved as carbonaceous films (Fig. 1). This style of preservation is well known from Proterozoic mudrocks (e.g. Hofmann 1994; Steiner 1994) and ranges through the Ediacaran and into the Cambrian (e.g. Lower Cambrian *Sabellidites*; Urbanek and Rozanov 1983 and the Middle Cambrian Burgess Shale; Butterfield et al. 2007) but subsequently disappears from the marine fossil record as a significant mode of preservation (Butterfield 1995).

In the second mode, the microbes are preserved three dimensionally by a distinctive white mineral (Fig. 2). Energy Dispersive X-Ray (EDX) analysis reveals this to be an iron and potassium aluminosilicate mineral. The fine grain size means that is not possible to observe the structure of this microcrystalline mineral and the exact mineralogy remains speculative. Precambrian permineralized microbes are well known to occur in lagerstätten where silica, phosphate and even pyrite replace soft tissues (Grazhdankin & Gerdes 2007; Brasier et al. in press), but not hitherto preserved in aluminosilicates. Preservation of soft tissues in aluminosilicate clay minerals has been described from Phanerozoic lagerstätte including the Burgess Shale (Orr et al. 1998; Butterfield et al. 2007) and the Ordovician Soom Shale (Gabbott et al. 2001), although the exact mechanisms of aluminosilicification are not yet fully resolved. For example, it has been suggested that Burgess Shale aluminosilicates were formed during late stage diagenesis/metamorphism by replacement of a precursor phase (Butterfield et al. 2007). We have not, however, observed any evidence for the replacement of a mineral precursor phase in the Longmyndian. It has also been proposed that aluminosilicates (phyllosilicates) may be formed during the low grade metamorphic devolatilization of carbonaceous films (e.g. Page et al. in press). The presence of unaltered carbonaceous filaments in Longmyndian sediments is, however, less easily explained by this hypothesis. In the Soom Shale it has been suggested that organic tissues acted as templates for the adsorption of colloidal clay minerals, leading to their replication by aluminosilicates (Gabbott et al. 2001). In this case it is the most labile organic tissues which are preserved in the greatest detail. Such an observation matches our discovery of the preservation of labile microbial materials by aluminosilicates. We also draw attention to the well known affinity of quartz and colloidal clay particles for organic materials (Konhauser & Urrutia 1999; Martin et al. 2004). We therefore propose that very early diagenetic aluminosilicate permineralization was a key factor for the preservation of the Longmyndian filaments.

In the third mode, filaments are not preserved as carbonaceous remains, or replaced by a diagenetic mineral, but are preserved as impressions and moulds by the siliciclastic sediment itself. These filaments are therefore found on bedding planes as sharp positive ridges (Fig. 3A) or their counterpart negative impressions (Fig. 3B). In the Ediacaran Period, this type of preservation is more commonly known from large macrofossils such as *Charnia* (Narbonne 2005). In comparison with the Precambrian, the preservation of soft tissues within siliciclastic sediments is also notably rare from the Cambrian onwards (see Brasier et al. in press). Our investigations from the Longmyndian and other Ediacaran lagerstätten suggest that this style of preservation is reliant upon the rapid lithification of bedding plane interfaces. It is noteworthy that while microbial mats are often invoked as important factors in the preservation of Ediacaran macrofossils (Gehling 1999), there is currently no obvious explanation for the preservation of microbes themselves in the same taphonomic mode.

Conclusion. The palaeontological importance of the Longmyndian Supergroup has been recognized for over 150 years, but its microbial lagerstätten have not been widely reported until now. We find that Longmyndian microbes are preserved as carbonaceous films, as aluminosilicate permineralized filaments and as moulds and impressions on bedding planes. These observations reinforce the hypothesis (Brasier & Callow 2007; Brasier et al. in press) that the Ediacaran fossil record appears to be biased towards the high quality preservation of soft tissues. The relative scarcity of such exceptional preservation at later times, in a variety of taphonomic modes suggests that these unusual taphonomic windows significantly narrowed following the Ediacaran-Cambrian transition.

Salter's discoveries have been important from two perspectives in addressing the paradox known as 'Darwin's dilemma'. Firstly, his keen macroscopic observations revealed the first evidence for an Ediacaran fossil record, an observation of particular interest to Charles Darwin 150 years ago. Secondly, these same rocks have been found by us to contain microbial preservation at a resolution that scientists including Charles Darwin could not have dared to predict.

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References.

Bland, B.H., 1984. *Arumberia* Glaessner & Walter, a review of its potential for correlation in the region of the Precambrian-Cambrian boundary. *Geological Magazine*, **121(6)**, 625-633.

Brasier, M.D., & Callow, R.H.T., 2007. Changes in the patterns of phosphatic preservation across the Proterozoic-Cambrian transition. *Memoirs of the Association of Australasian Palaeontologists*, **34**, 377-389.

Brasier, M.D., Antcliffe, J.B., & Callow, R.H.T., *In Press*. Evolutionary trends in remarkable preservation across the Ediacaran-Cambrian transition: the impact of metazoan mixing. In: P.A. Allison & D.J. Bottjer, *Taphonomy: Process and bias through time.*

Butterfield, N., 1995. Secular distribution of Burgess Shale-type preservation. *Lethaia*, **28(1)**, 1-13.

Butterfield, N., 2005. Probable Proterozoic fungi. *Palaeobiology*, **31(1)**, 165-182.

Butterfield, N., Balthasar, U., & Wilson, L.A., 2007. Fossil diagenesis in the Burgess Shale. *Palaeontology*, **50(3)**, 537-543.

Darwin, C.R., 1859*. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. John Murray, London, 502 p.

Gabbott, S.E., Hou, X.G., Norry, N.J., & Siveter, D.J., 2001. Preservation of fossils in clay minerals; a unique example from the Upper Ordovician Soom Shale of South Africa. *Proceedings of the Yorkshire Geological Society*, **53**, 237-244.

Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios*, **14**, 40-57.

Gerdes, G., 2007. Structures left by modern microbial mats in their host sediments. *In:* Schieber, J., Bose, P.K., Eriksson, P.G., Banerjee, S., Sarkar, S., Altermann, W., & Catuneanu, O. (eds) *Atlas of microbial mat features preserved within the siliciclastic rock record*. Atlases in Geoscience, 2. Elsevier, Amsterdam, pp. 5-38.

Grazhdankin, D., & Gerdes, G., 2007. Ediacaran microbial colonies. *Lethaia*, **40**, 201-210.

Greig, D.C., Wright, J.E., Hains, B.A., & Mitchell, G.H., 1968. *Geology of the country around Church Stretton, Craven Arms, Wenlock Edge and Brown Clee*. Memoir of the Geological Survey of Great Britain, H.M.S.O, London, 379 p.

Hofmann, H.J., 1994. Proterozoic carbonaceous compressions ("metaphytes" and "worms"). *In:* Bengtson, S., (ed) *Early life on Earth. Nobel Symposium No. 84*. Columbia University Press, New York, pp.342-357.

Konhauser, K.O., & Urrutia, M.M., 1999. Bacterial clay authigenesis: a common biogeochemical process. *Chemical Geology*, **161**, 399-413.

Martin, D., Briggs, D.E.G. & Parkes, R.J., 2005. Decay and mineralization of invertebrate eggs. *Palaios*, **20(6)**, 562-572.

McIlroy, D., Walter, R., 1997. A reconsideration of the biogenicity of *Arumberia banksi* Glaessner & Walter. *Alcheringa*, **21**, 79-80.

McIlroy, D., Crimes, T.P., & Pauley, J.C., 2005. Fossils and matgrounds from the Neoproterozoic Longmyndian Supergroup, Shropshire, UK. *Geological Magazine*, **142(4)**, 441-455.

McLoughlin, N., Wilson, L.A., & Brasier, M.D., 2008. Growth of synthetic stromatolites and wrinkle structures in the absence of microbes – implications for the early fossil record. *Geobiology*, **6(2)**, 95-105.

Narbonne, G., M., 2005. The Ediacara Biota: Neoproterozoic origin of animals and their ecosystems. *Annual Review of Earth and Planetary Sciences*, **33**, 421 – 442.

Noffke, N., Gerdes, G., Klenke, T., & Krumbein, W.E., 2001. Microbially induced sedimentary structures – a new category within the classification of primary sedimentary structures. *Journal of Sedimentary Research*, **71**, 649-656.

Orr, P.J., Briggs, D.E.G. & Kearns, S.L., 1998. Cambrian Burgess Shale animals replicated in clay minerals. *Science*, **281**, 1173-1175.

Page, A., Gabbott, S.E., Wilby, P.R., Zalasiewicz, A., *In Press*. Ubiquitous Burgess Shale-style 'clay templates' in low grade metamorphic mudrocks. *Geology*.

Peat, C., 1984. Precambrian microfossils from the Longmyndian of Shropshire. *Proceedings of the Geologists' Association*, **5**, 17-22.

Porada, H., & Bouougri, E.H., 2007. Wrinkle structures – a critical review. *Earth Science Reviews*, **81**, 199-215.

Salter, J.W., 1856. On fossil remains in the Cambrian rocks of the Longmynd and North Wales. *Quarterly Journal of the Geological Society*, **12**, 246-251.

Salter, J.W., 1857. On annelide burrows and surface markings from the Cambrian rocks of the Longmynd. *Quarterly Journal of the Geological Society*, **13**, 199-207.

Schopf, J.W., 1992. Proterozoic prokaryotes: affinities, geologic distribution, and evolutionary trends. In: Schopf, J.W., Klein, C. (eds) *The Proterozoic Biosphere: a multidisciplinary study*, Cambridge University Press, Cambridge, pp. 195-218.

Steiner, M., 1994. Die neoproterozoischen Megaalgen Sudchinas. Berliner *geowissenschaftliche Abhandlungen (E)*, **15**, 1-146. (In German).

Timofeyev, B.V., Choubert, G., & Faure-Muret, A., 1980. Acritarchs of the Precambrian in mobile zones. *Earth Science Reviews*, **16**, 249-255.

Urbanek, A., & Rozanov, A.Yu., 1983. *Upper Precambrian and Cambrian Palaeontology of the East-European Platform*. Publishing House, Wydawnictwa Geologiczne, Warszawa, 158pp, 94pls.

Xiao, S., 2004. New multicellular algal fossils and acritarchs in Doushantuo chert nodules (Neoproterozoic, Yangtze Gorges, South China). *Journal of Paleontology*, **78(2)**, 393-401.

Xiao, S., & Knoll, A.H., 1999. Fossil preservation in the Neoproterozoic Doushantuo phosphorite lagerstätte, South China. *Lethaia*, **32**, 219-240.

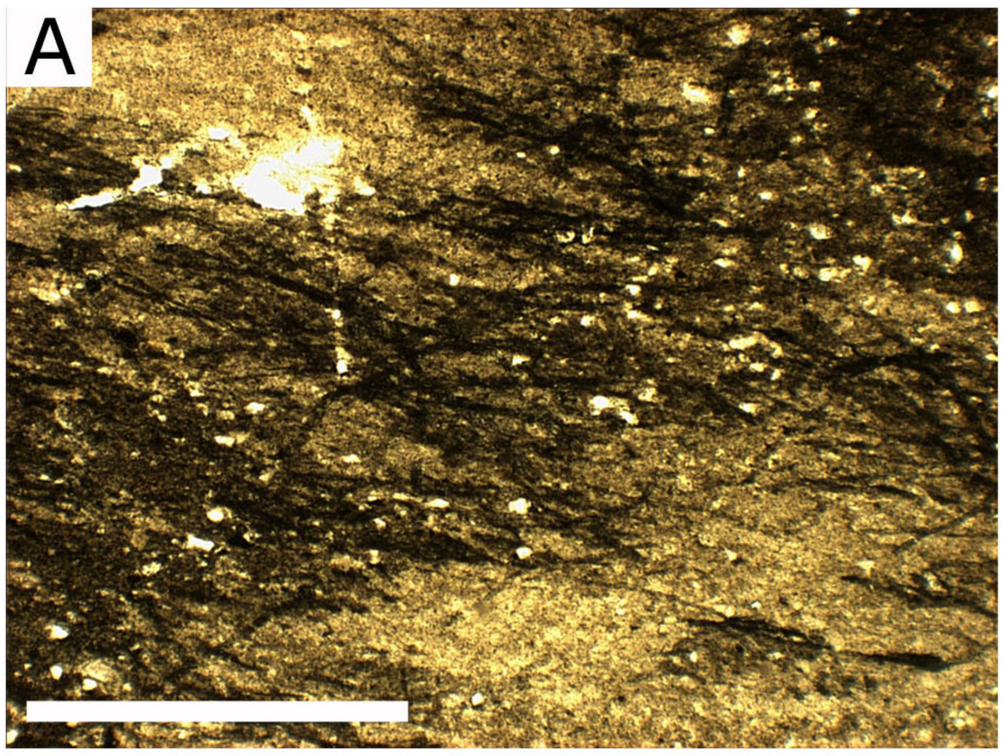
Xiao, S, Yuan, X., Steiner, M., & Knoll, A.H., 2002. Macroscopic carbonaceous compressions in a terminal Proterozoic shale: A systematic reassessment of the Miaohe Biota, South China. *Journal of Paleontology*, **76(2)**, 347-376.

Figure Descriptions

Fig. 1. Carbonaceous microbial filaments preserved as carbonaceous compressions from petrographic thin sections of the Lightspout Formation, Longmyndian Supergroup at Carding Mill Valley, Shropshire. (a) Densely interwoven parallel to sub-parallel filaments forming a laminated microbial mat fabric (Scale bar 1mm). (b) Dark black filamentous carbonaceous filaments (Scale bar 400µm).

Fig. 2. Microbial filaments preserved in aluminosilicate minerals from the Burway Formation at Ashes Hollow, Shropshire. (a) Dense network of randomly oriented straight filaments forming a microbial mat. (b) Bedding plane with much lower density of filaments. (c) Filaments showing 'Y'-shaped branching (arrowed) and cross-cutting relationships. (d) Larger diameter filament with one distinctively rounded apex. (e) A cluster of discoidal bedding plane structures. (Scale bar 1mm for A-B; 0.5mm for C and E; 0.25mm for D).

Fig. 3. Three-dimensionally preserved microbial impressions on Salter's specimens from Yearling (Yearlet?) Hill, Church Stretton, Shropshire. (a) British Geological Survey Specimen 49151, originally figured by Salter, 1857 Pl. V, fig. 1, and described as "rain-prints on rippled surface with Annelide-burrows (*Arenicolites sparsus*; young) in the hollows of the ripple". The shallow negative relief depressions (Salter's rain prints) contrast with the sharp positive moulds of microbial filaments (Scale bar 1cm). (b) Specimen BGS 49157 (counterpart of 49151) showing sharp positive relief pustules (counterparts of *A. sparsus* of Salter) and broad, gentle positive relief markings (counterparts of Salter's rain prints) with abundant narrow, sinuous negative relief impressions of microbial filaments (Scale bar 1cm). n.b., the pale markings are a secondary weathering phenomenon.



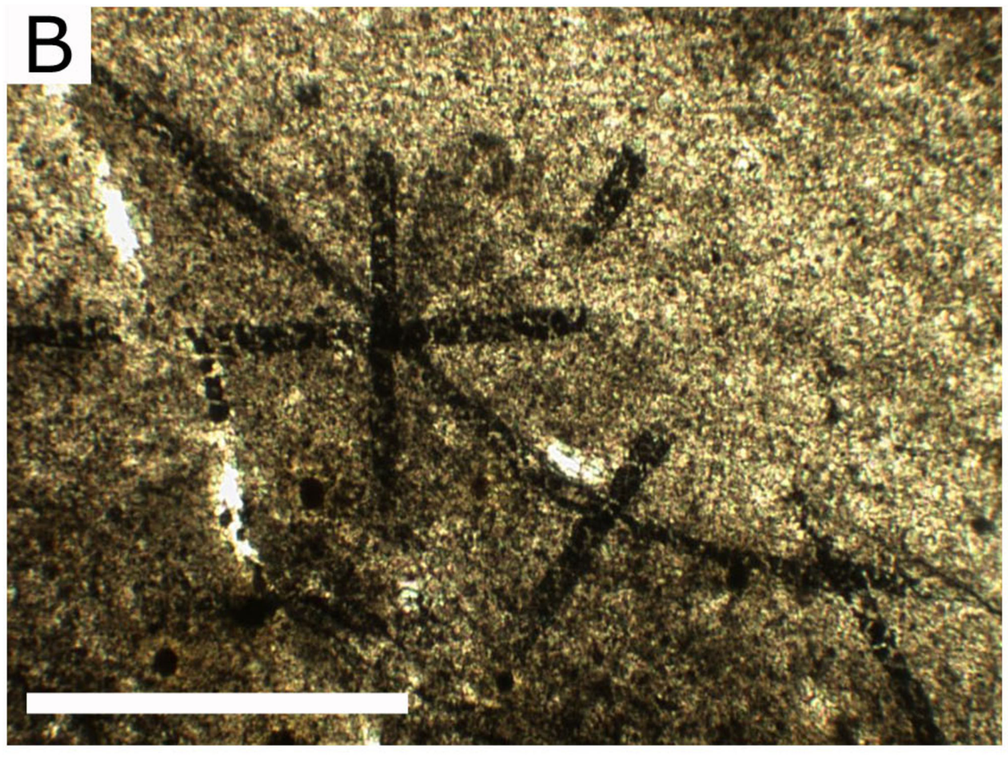


Fig. 1

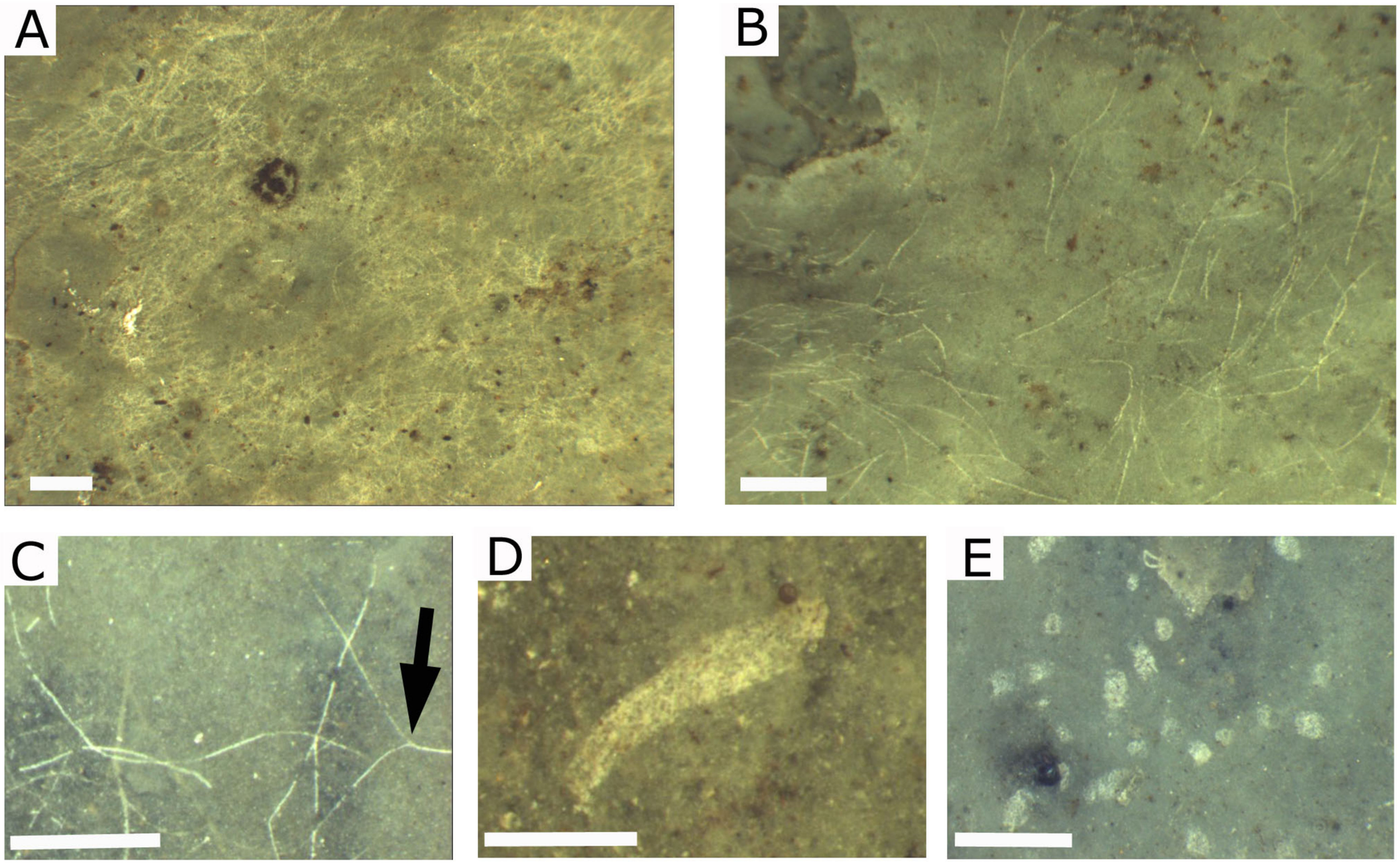


Fig. 2

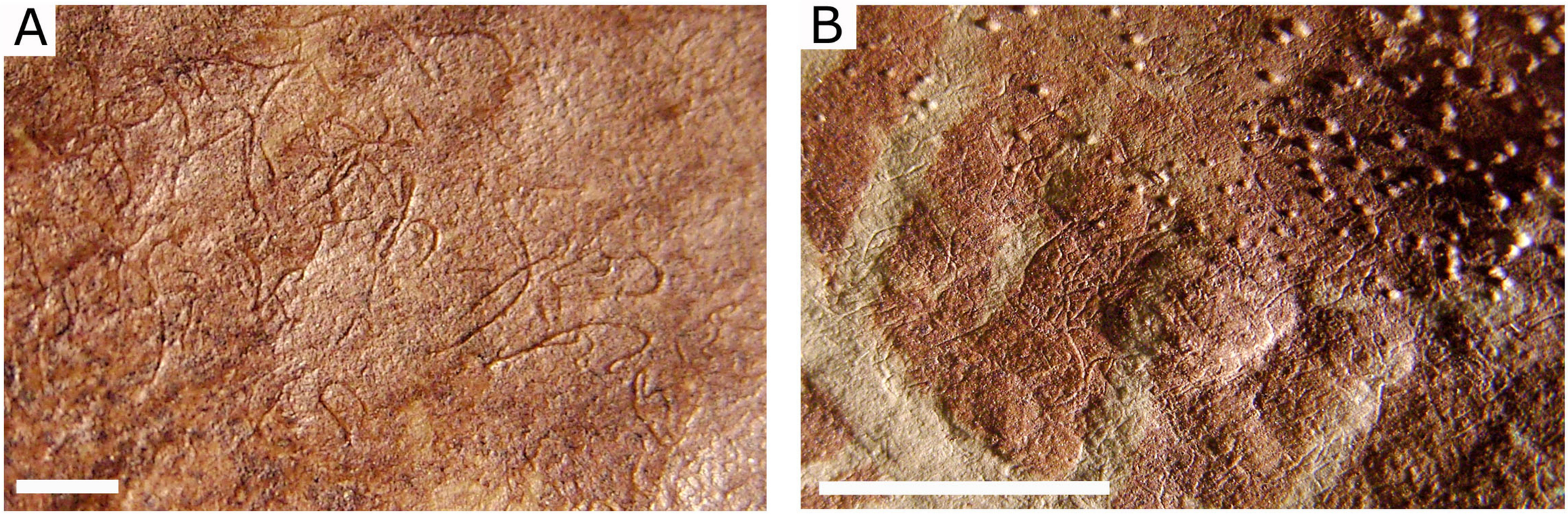


Fig. 3