

The sequestration of trace metals preserved in pyritized burrows

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Abstract

Pyritized burrows from three localities were analysed using LA-ICP-MS to determine their trace element content and assess their ability to sequester trace elements. Pyritic burrows from Hock Cliff (Jurassic), Wren's Nest (Silurian) and Southerham Grey Pit (Cretaceous) have anomalous levels of Se, Cu and Pb and are enriched relative to their host sediments. Sequestration rates were calculated using sedimentation rates from similar depositional environments. Results show that pyritic burrows, mediated by bacterial sulphate reduction, can sequester Se, Cu and Pb up to 3 orders of magnitude greater than the rate of Fe-Mn crusts, which are considered rich sources of trace elements, demonstrating that bioturbated marine sediments are significant sinks of trace elements.

Keywords: Bioturbation, burrows, pyrite, trace elements, sequestration, selenium

1 Introduction

Burrows are one of a large range of trace fossils, which can be defined as a biogenic sedimentary structure created in sediment by the activity of a burrowing animal (Bromley, 1996). The burrows analysed in this study are cylindrical or tube-line sedimentary features which are present in all orientations (vertical to horizontal) in shallow marine environments and which are generally oxidised.

22 Burrowing evolved particularly at the Ediacaran-Cambrian boundary during a major increase in animal
23 diversification and modes of life (Buatois et al., 2020; Mángano and Buatois, 2014). Burrowing in the
24 Ediacaran was restricted to very small horizontal traces, commonly associated with firm, erosion-
25 resistant algal mats (Jensen et al., 2006; Seilacher et al., 1999). The Cambrian Period is characterised
26 by an increase in penetrative, vertical burrowing promoting the exchange of fluids and OM between
27 the water column and the sediment, increasing habitability, known as the 'agronomic revolution'
28 (Seilacher et al., 1999).

29 Sulphate-reducing bacteria control the composition of OM in shallow marine sediments under anoxic
30 conditions, and higher microbial activity is coupled with decreasing sulphate levels and an increase of
31 sulphide and OM degradation (Sturdivant and Shimizu, 2017). Burrows are commonly enriched in
32 organic matter and a range of nutrients including nitrogen, potassium, phosphorus, sulphur, and trace
33 elements as burrowing organisms such as worms, secrete mucus to pass easily through the sediment
34 (Ayoola and Olayiwola, 2014; Bromley, 1996). The mucus in the burrow walls can be used as a
35 feedstock for sulphate-reducing bacteria which promotes localised hydrogen sulphide (H₂S), and early
36 diagenetic pyrite (Virtasalo and Kotilainen, 2013; Virtasalo et al., 2010). Pyritization would most likely
37 take place after the death of the organism, as a live organism would create an oxic environment which
38 would prohibit pyritization (Jørgensen, 1977). The decomposition of the mucus walls and the
39 burrowing organism creates a reducing environment which favours pyrite formation (Thomsen and
40 Vorren, 1984).

41 The reworking of sediments by animal activity prior to compaction alters the substrate significantly.
42 Burrowing organisms such as worms can have subsurface burrows as deep as 2 m and affect several
43 square kilometres of sediment (Gingras et al., 2015; Weaver and Schultheiss, 1983). Burrowing can
44 highlight erosional features in fine grained sediments such as black shales, which reveals information
45 on bottom currents, water-column mixing and oxygenation (Schieber, 2003). It can disturb sediment
46 layering which enables the exchange of minerals and fluids between sedimentary layers; cause an

47 increase or decrease in organic matter and change the pore fluid chemistry. These changes have
48 knock-on effects on porosity and permeability, which is why bioturbation is an important area of
49 research for the oil industry, as it can affect oil recovery (Gingras et al., 2015; Pemberton and Gingras,
50 2005).

51 Bioturbation also has implications for trace element sequestration and concentration. Pyrite is a
52 major residence of trace elements in sedimentary rocks. It is more common for pyrite to precipitate
53 in sediments such as black shales that are clearly anoxic (Hu and Gao, 2008; Large et al., 2015, 2014;
54 Parnell et al., 2016). However, pyrite also precipitates in anoxic/sub-oxic microenvironments within
55 otherwise oxic environments (Jørgensen, 1977; Mitchell, 1968; Thomsen and Vorren, 1984), such as
56 the burrows investigated here. Pyritic burrows from three localities in the UK, representing a range of
57 geological ages were analysed to investigate their trace metal element and sequestration rate.

58 The objectives were to determine:

- 59 (i) If the burrow pyrite contains anomalous concentrations of trace elements. Pyrite in black
60 shale can concentrate trace elements first located in organic matter in the carbonaceous
61 sediment, but this reservoir is not available in many other sediments so enrichment in
62 pyrite might not occur.
- 63 (ii) If trace elements in the burrow pyrite represent concentrations relative to the host
64 sediment.
- 65 (iii) If the pyrite caused an overall sequestration of trace elements into the host bed.

66 2 Methods

67 Pyritized burrows were collected from three localities throughout the UK (Fig. 1); Wren's Nest, Dudley
68 (Silurian), Hock Cliff, Fretherne (Jurassic) and Southerham Grey Pit, Lewes (Cretaceous). Wren's Nest,
69 Dudley, part of the Much Wenlock Limestone Formation, hosts extremely well preserved Silurian fossil
70 biota including pyritized burrows, which are concentrated in the Nodular Beds Member (Ray and

71 Thomas, 2007). The Blue Lias Formation, exposed at Hock Cliff, Fretherne, has alternating mudstones,
72 shales and limestones, with vertical pyritized burrows preserved in dark, grey shale beds (Simms et
73 al., 2004). Southerham Grey Pit, Lewes, has abundant 'worm' tubes, which are pyritized or have
74 pyritized nodules spatially associated with them, found in the Zig Zag Chalk Formation (Jeans et al.,
75 2016).

76 Mm-scale burrows from each locality were analysed by laser ablation-inductively coupled plasma-
77 mass spectrometry (LA-ICP-MS) to produce enrichment maps. The LA-ICP-MS method is described in
78 detail in Parnell et al. (2017). This approach was used to map the distribution of Fe, Se, Cu and Pb.
79 These elements were chosen because they are commonly found in pyrite in black shales.

80 Average trace element values from Fe-Mn rich crusts and Neoproterozoic Gwna Group shales were
81 used as a comparison with the new data presented here, given that both are regarded as rich sources
82 of trace elements and the Gwna Group shales were studied at the same laboratory at the University
83 of Aberdeen.

84 Bulk trace metal content was determined by inductively coupled plasma-atomic emission
85 spectrometry (ICP-AES) and inductively coupled plasma-mass spectrometry (ICP-MS), at ALS
86 Laboratories, Loughrea, Ireland. Each sample was agate milled and homogenised and 0.5 g was
87 partially digested using aqua regia.

88 Scanning electron microscopy was performed on a Zeiss Gemini-300 FEG-SEM, to investigate
89 mineralisation within the burrows.

90 3 Results

91 3.1 LA-ICP-MS

92 Burrows were analysed with LA-ICP-MS to determine the enrichment and the distribution of elements
93 within an area of interest e.g. cross-section of a burrow. The trace metal content of the samples and

94 average shale and carbonate values are summarised in Table 1, and are plotted in Fig. 2. Average spot
95 analyses from Hock Cliff burrows show a Se content of 8.2 & 7.7 ppm (A & B respectively). Mean shale
96 Se content is 1.3 ppm (Stüeken et al., 2015). The average Pb content at Hock Cliff is 669 ppm in burrow
97 A & 297 ppm in burrow B, which is up to 30 times higher than the global mean shale Pb content of
98 19.5 ppm (Hu and Gao, 2008). The average Cu content is 494 ppm in burrow A & 215 ppm in burrow
99 B, which is up to 10 times higher than the global mean shale Cu content of 36.5 ppm (Hu and Gao,
100 2008). The host rock has a Se value of 0.7 ppm, a Cu value of 10.7 ppm, and a Pb value of 6.24 ppm.

101 Fe, Se, Cu and Pb LA-ICP-MS maps from Hock Cliff are shown in Fig. 3 below. Se and Pb are
102 concentrated in the rim of both burrows suggesting they occur in the same mineral phase. In burrow
103 A, Fe is more concentrated in the rim, suggesting there is some weathering in the burrow core. Cu is
104 more evenly distributed but appears slightly depleted in the burrow rim.

105 Fe, Cu and Pb maps from Wren's Nest are shown in Fig. 4, below. The concentrations of Cu and Pb are
106 more evenly distributed throughout the burrow, compared with Hock cliff where the Se and Pb are
107 concentrated in a halo towards the edge of the burrow. Another notable feature is the lack of Se
108 present within the burrow. Cu and Pb are concentrated in similar amounts compared with Hock Cliff.

109 Average spot analyses show a Cu content of 210 ppm, which is 5 times that of the global mean shale
110 Cu content, and a Pb content of 198, which is 10 times that of the global mean shale Pb content (Hu
111 and Gao, 2008). The Wren's nest host rock has a Cu content of 4 ppm, and a Pb content of 4.19 ppm.

112 Southerham burrows are extremely weathered and the majority of them display a weathered burrow
113 core, which could not be analysed by LA-ICP-MS as the surface was not flat. The burrows are large
114 enough to be extracted for bulk analysis at ALS laboratories which is comparable to LA-ICP-MS. The
115 results are summarised in Table 1.

116 Pyritized burrow from Southerham have a Se value of 4.5 ppm, Cu of 66 ppm, and Pb of 329 ppm.
117 These measured values are up to 15 times greater than the average shale values, and up to 2 orders
118 of magnitude greater than the host rock values (Hu and Gao, 2008).

119 4 Discussion

120 4.1 Metal enrichment in burrows

121 A summary of the burrow forming process and metal enrichment is shown in Fig. 5 below. Trace metals
122 are incorporated in to burrows during diagenesis. Trace metal-rich seas deposit a range of elements
123 including Se, Pb and Cu on the seafloor. Iron-oxides present in the seafloor sediments act as a sink,
124 and many trace elements are adsorbed on the Fe-oxides. Organic matter accumulates on the seafloor
125 through the decomposition of marine organisms and land-derived detritus (e.g. plant material).
126 Burrowing organisms introduce organic matter, Fe (oxyhydr)oxides and trace metal oxyanions into the
127 burrow from the seafloor (Berner, 1984; Virtasalo and Kotilainen, 2013). The act of burrowing requires
128 a lubricant; therefore, organisms secrete mucus to ease passage through the sediment which decays
129 creating a localised reducing environment (Bromley, 1996). Lalonde et al. (2010) demonstrated that
130 mucus linings were more reactive than other organic compounds in marine sediment, increasing the
131 potential of burrows as metal sinks. Mucus trails preserved by pyritization are found in the Cretaceous
132 Ingersoll shale where body fossils are not as common, emphasising the reactivity of mucus secreted
133 by organisms (Savrda et al., 2016). Burrows preserve a range of nutrients such as nitrogen, potassium,
134 phosphorus, sulphur, and trace elements as a result of the burrowing organism (Ayoola and Olayiwola,
135 2014).

136 The introduction of “super-reactive” organic carbon in the form of extracellular polysaccharides (EPS)
137 bioturbation within the burrow system, through mucus lining of the burrower drives sulphate
138 reduction and OM degradation (Harazim et al., 2020; Sturdivant and Shimizu, 2017; Sutherland, 2006).
139 Early localised sulphate-reducing bacteria exploit OM in the burrow as a feedstock, reducing sea water

140 sulphate to hydrogen sulphide (H₂S). The H₂S reacts with iron minerals which are rich in trace metals
141 to form pyrite. This process is dependent on a balance between carbon, sulphur, and iron.
142 Bioturbation in iron-rich sediments rapidly oxidises OM through iron-reducing bacteria. Where no
143 bioturbation occurs, sediments become sulphide rich, mediated by sulphate reducing bacteria. In Fe-
144 rich sediments, the supply of ferrous iron exceeds the supply of sulphide and ferrous iron reacts with
145 H₂S and sequesters it to monosulfide, which detoxifies the sediment, promoting bioturbation (Antler
146 et al., 2019). At depth sediments become dominated by sulphide which is poisonous to bioturbating
147 organisms and reduced ventilation from sediment mixing, inhibits the reoxidation of ferrous Fe,
148 promoting pyrite formation (Antler et al., 2019). The trace metals present in the pyrite reflect the
149 trace metals present in the iron minerals in the sediment (Mitchell, 1968). After diagenesis the burrow
150 is completely pyritized and enriched in trace metals. Au, Cd, Cu, Pb and Zn are commonly found
151 adsorbed onto naturally occurring Fe sulphides, and this process could be significant in the
152 concentration of metals and the formation of ore deposits (Huerta-diaz et al., 1998; Jean and Bancroft,
153 1986).

154 The control that bioturbation has for mobility of redox-sensitive trace elements (i.e. Fe, V, Cr, Mn, Co,
155 Ni, Cu, and As) has been addressed by Harazim et al., (2015). The authors found that the average TOC
156 was 1.0 wt. % higher in sediment from within burrows compared with the surrounding sediment, and
157 that pyrite found within burrows correlated with an increased level of Co, Ni, Cu and Zn. The rarity of
158 the pyrite and persistence of organic carbon suggest that in this case the carbon was too refractory to
159 be used as a feedstock for bacterial sulphate reduction (Widerlund and Davison, 2007). The lack of
160 organic matter reactivity means that these elements are incorporated into silicates rather than pyrite
161 or organic matter. The localities selected for this study were abundant in pyritized burrows suggesting
162 that the bioavailability of the organic matter in the burrows was not a limiting factor.

163 Examples of lacustrine pyritic burrows are also found in the literature. Virtasalo et al. (2010), analysed
164 small burrow-like and irregularly shaped concretions in Holocene postglacial lacustrine clays in the

165 northern Baltic Sea. The burrows here experienced a transition from a freshwater lacustrine
166 environment to a more brackish environment due to increasing influx of saline water from the Baltic
167 Sea. The burrows reported are pyritic and show a range of crystal textures including framboidal,
168 euhedral, microcrystalline masses and framboids with overgrowths of marcasite crystals. The
169 framboidal texture indicates sufficient space for the crystals to grow so pyrite precipitation would
170 occur in an open space (Thomsen and Vorren, 1984). Trace metal concentration was not the scope of
171 this work but given the concentration of pyritic burrows within the sediments, lacustrine settings could
172 sequester significant levels of trace metals.

173 *4.2 Burrow enrichment relative to host sediment*

174 The burrows discussed here all show an enrichment in trace elements relative to their host sediment
175 as shown in Figure 2. Se mineralisation in Hock cliff burrows are 10 times richer than its host sediment,
176 and Southerham burrows are around 4 times that of their host sediment. The burrows at Wren's nest
177 did not show any Se mineralisation. Cu concentrations at both Wren's Nest and Hock Cliff burrows
178 were 50 times greater than their host sediment, and Southerham burrows was 20 times that of its
179 host sediment. Pb concentrations at both Wren's Nest and Southerham were 50 times greater than
180 trace elements recorded in the host sediment. The Hock Cliff burrows were up to 100 times richer in
181 Pb than its host sediment.

182 This shows that there is anomalous enrichment of trace elements in pyritic burrows relative to their
183 hosts sediments. Trace element enrichment in burrows exceed the average values recorded for shale
184 and carbonates and are comparable to values of the Gwna Group shales, which are regarded as
185 protoliths to ore deposits.

186 *4.3 Pyrite mineralisation*

187 Burrows from Southerham and Hock cliff display framboidal textures, indicating that the pyrite had
188 space to grow, and is also considered a signature of early stage microbial sulphate reduction (Fig. 6A

189 & B) (Schoonen, 2004; Virtasalo and Kotilainen, 2013). Early diagenetic framboidal pyrite in
190 bioturbations have been shown to be richer in trace elements compared with pyrite not found in
191 bioturbations (Lerouge et al., 2011). Southerham pyritic burrows show pyrite framboids with euhedral
192 overgrowths (Fig. 6A). Euhedral pyrites are a secondary feature to the framboids and formed during
193 diagenesis, recrystallising the original pyrite. Similar features are observed in SEM micrographs from
194 Armstrong et al. (2018) and Virtasalo et al. (2010), which show framboidal pyrite with euhedral
195 overgrowths.

196 The distribution of the metals within the burrows can give information about the timing of pyrite
197 mineralisation. In the Hock Cliff burrows, as Pb and Se are concentrated in the burrow rim it is likely
198 that they are from the same mineral phase. Lead selenide (clausthalite) is a common mineral phase
199 found in pyrites. As Pb and Se are concentrated in the rim it suggests that it was enriched at a later
200 stage, after early stage pyritization mediated by sulphate-reducing bacteria. Similar features are
201 described by Parnell et al. (2017) and are attributed to hydrothermal Pb mineralisation during
202 metamorphism. Fe and Cu are more evenly distributed throughout the burrow but are depleted at the
203 burrow rim. This suggests that Cu was originally incorporated into the burrow at an early stage.

204 *4.4 Oxidation of burrows and implication on metal concentration*

205 The pyritic burrows reported here and elsewhere in the literature tend to be altered to Fe-oxide, as
206 pyrite is commonly oxidized in the sedimentary environment (Rimstidt and Vaughan, 2003), giving the
207 burrows a rusty colouration. Primarily this oxidation is only on surface exposures but in some cases,
208 this weathering can penetrate to the core of the burrow. This has the potential to affect the
209 distribution of trace metals, by remobilising trace metals which are soluble in oxidising conditions.
210 Perez et al. (2019) demonstrated through LA-ICP-MS analysis of weathered pyrites that some trace
211 elements were concentrated in a halo around the edge of the pyrite crystal, suggesting that certain
212 trace elements are more persistent under oxidising conditions. Laser maps from Hock Cliff show that

213 Se & Pb are concentrated in a halo on the edge of the burrow and are depleted in the core of the
214 burrow, which could be a result of preferential oxidation, redistributing Se within the burrow.

215 Regardless of the redistribution of metals, results shown here demonstrate that trace elements are
216 preserved within burrows after oxidation, and therefore bioturbated sediments still represent a
217 significant sink for trace metals, even after oxidative weathering.

218 *4.5 Sequestration rates*

219 Seafloor mining operations have focussed on deep marine Fe-Mn crusts as they are abundant in Se,
220 Te and other trace elements. Although Fe-Mn crusts are rich sources of trace elements, they
221 accumulate extremely slowly at 1-10 mm/Ma (Hein, 2000). Recent work by Armstrong et al. (2018)
222 demonstrated that the black shales of the Gwna group have a Te sequestration rate greater than that
223 of Fe-Mn crusts, highlighting the value of black shale for trace element sequestration.

224 The sequestration rates of Se, Pb & Cu were calculated using; the accumulation rates of each locality,
225 which was calculated using the thickness and age of the unit they were sampled from; the measured
226 density of each sample and the concentration of the element (in ppm) determined by LA-ICP-MS
227 analysis. This information is summarised in table 1. Accumulation rates for each depositional
228 environment were collated from existing literature and used to calculate sequestration ranges for the
229 selected elements. This information is summarised in supplementary table 1.

230 Accumulation rates for a Cretaceous shallow shelf sea environment ranges from 6.4-100 m/Ma
231 (Damholt and Surlyk, 2004; Friedman et al., 2016; Hopson, 2005; Kennedy and Garrison, 1975;
232 Lauridsen et al., 2009; Puckett, 1991; Surlyk and Lykke-andersen, 2007). Sequestration rates based on
233 these accumulation rates and a measured density of 2.44 g/cm³ are 900-13900 nmols/yr⁻¹ for Se,
234 16300-253400 nmols/yr⁻¹ for Cu and 24900-387400 nmols/yr⁻¹ for Pb.

235 Accumulation rates for a Jurassic hemipelagic/pelagic environment ranges from 1.5-40 m/Ma
236 (DeCelles and Currie, 1996; Hinnov and Park, 1999; Mattioli and Pittet, 2002; Simms et al., 2004).
237 Sequestration rates based on these accumulation rates and a measured density of 2.72 g/cm³ are 400-
238 10600 nmols/yr⁻¹ for Se, 31100-368100 nmols/yr⁻¹ for Cu, and 6300-156000 nmols/yr⁻¹ for Pb.

239 Accumulation rates for a Silurian carbonate platform environment ranges from 5.8-79 m/Ma
240 (Bosscher and Schlager, 1993; Calner and Jeppsson, 2003; Cocks, 2004; Narbonne and Dixon, 1984;
241 Soja, 1993). Sequestration rates based on these accumulation rates and a measured density of 2.87
242 g/cm³ are 55000-745200 nmols/yr⁻¹ for Cu and 15900-215500 nmols/yr⁻¹ for Pb.

243 The sequestration rates of Se, Cu & Pb in Fe-Mn crusts are 0.5, 200 & 100, respectively. Conservative
244 estimates of sequestration rates for all three depositional environments exceed those of Fe-Mn crusts.
245 On average pyritic burrows sequester Se up to three orders of magnitude faster than Fe-Mn crusts.
246 Cu and Pb are sequestered in pyritic burrows at two orders of magnitude greater than Fe-Mn crusts.
247 Pb sequestration rates in pyritic burrows is the only element discussed here that is comparable to
248 sequestration rates of Gwna Group sediments. Se and Cu burrow sequestration rates are two orders
249 of magnitude lower than that of the Gwna Group. This shows that bioturbation can sequester metals
250 more efficiently than Fe-Mn crusts, and bioturbated marine sediments could be regarded as a
251 significant sink for trace elements.

252 5 Conclusion

253 The trace element data shows that bioturbated marine sediments have anomalous levels of trace
254 elements preserved in pyritized burrows. The act of burrowing increases organic material in the
255 sediment which drives bacterial sulphate reduction and the sequestration of trace elements.
256 Specifically:

- 257 (i) When an organic rich reservoir is not available, trace elements can be concentrated into
258 burrows which are rich in OM, which promotes pyritization and metal sequestration.

259 Bioturbated sediments across a range of geological ages show anomalous levels of trace
260 elements preserved in pyritized burrows.

261 (ii) The three localities discussed here show an enrichment of Cu, Se, and Pb relative to their
262 host sediments, despite oxidation which might weather and degrade the burrow.

263 (iii) Bioturbated sediments from Hock cliff, Wren's Nest and Southerham Grey Pit are more
264 efficient at sequestering metals when compared with other deposits such as Fe-Mn crusts,
265 which are regarded as rich sources of metals, but accumulate very slowly. Pyritic burrows
266 can sequester Se up to three orders of magnitude faster than Fe-Mn crusts, and Pb and
267 Cu up to two orders of magnitude faster than Fe-Mn crusts.

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431

432 **Fig. 1** Map showing sampling localities of pyritic burrows. **a** – Wren’s Nest, Nodular Beds Member,
433 Silurian. **b** – Hock Cliff, Blue Lias Formation, Jurassic. **c** – Southerham Grey Pit, Zig Zag Chalk Formation,
434 Cretaceous.

435 **Table 1.** Sequestration rates of bioturbated sediments. Average values used in this study and
436 elsewhere; Fe-Mn crusts (Hein et al., 2013, 2003, 1993); Gwna Group sediments (Armstrong et al.,
437 2018); Wren’s Nest formation age and thickness data (Cocks, 2004); Hock Cliff formation age and
438 thickness data Simms et al. (2004); Southerham Grey Pit formation thickness and age data Hopson
439 (2005). Average shale values taken from Hu and Gao (2008) and Stüeken et al. (2015). Hock Cliff and
440 Wren’s Nest burrow sample values obtained by LA-ICP-MS mapping. Host rock values for Hock Cliff &
441 Wren’s Nest were analysed for their bulk trace metal content by inductively coupled plasma-atomic
442 emission spectrometry (ICP-AES) and inductively coupled plasma-mass spectrometry (ICP-MS), at ALS
443 Laboratories, Loughrea, Ireland.

444 **Fig. 2** Elemental content in parts per million (ppm) on the Y axis, sample localities on the X axis.
445 Average shale values (Hu and Gao, 2008; Rudnick and Gao, 2003); Average carbonate values (Frimmel,
446 2009; Shamberger, 1981). Graphs are logarithmic as the average element values are considerably
447 lower than found in pyritic burrows.

448 **Fig. 3** LA-ICP-MS for Fe, Cu, Se and Pb in a pyritic burrow, Hock Cliff. Note the relative enrichments of
449 Cu in the burrow centre, and Se and Pb in the outer burrow wall. Blue colours indicate lower trace
450 element content, and red colours indicate higher trace element content.

451 **Fig. 4** LA-ICP-MS for Fe, Cu, and Pb in a pyritic burrow, Wren’s Nest. Note the relative enrichments of
452 Cu & Pb are more evenly distributed throughout the burrow cross-section. Blue colours indicate lower
453 trace element content, and red colours indicate higher trace element content.

454 **Fig. 5** Summary diagram of pyritic burrow formation and metal enrichment in a marine sedimentary
455 setting, adapted from (Virtasalo et al., 2010). Sulphate-reducing bacteria (SRB).

456 **Fig. 6** A, Pyrite framboids with euhedral overgrowths, Southerham Grey Pit. B, Pyrite framboids, Hock
457 Cliff. C, Euhedral and framboid pyrites weathered to iron oxides but still retain original pyritic
458 morphologies, Southerham Grey Pit.

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