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## Biogenic iron preserves structures during fossilization: A hypothesis

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1 Title: **Biogenic iron preserves structures during fossilization: A hypothesis**

2

3 Subtitle: Iron from decaying tissues may stabilize their morphology in the fossil record

4

5

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18 **Summary**

19 In this study, we hypothesize that iron from labile biological tissues, liberated during decay,  
20 may have played a role in inhibiting loss of anatomical information during fossilization of  
21 extinct organisms. Most tissues in the animal kingdom contain iron in different forms. The  
22 most widely distributed iron-bearing molecule in modern taxa is ferritin, a globular protein  
23 that contains iron crystallites in the form of ferrihydrite minerals. Iron concentrations in  
24 ferritin are particularly high and ferrihydrites are extremely reactive. When organisms are  
25 decaying on the sea floor under anoxic environmental conditions, ferrihydrites may initialize  
26 the selective pyritization (replication in  $\text{FeS}_2$ ) of some tissues. This model explains why some  
27 decay-prone tissues are preserved, while other more resistant structures decayed and are  
28 absent in many fossils. It also implies that structures described as brains in Cambrian  
29 arthropods are not fossilization artifacts but instead a source of information on the anatomical  
30 evolution at the dawn of complex animal life.

31

32 **Keywords:** exceptional fossil preservation, nervous systems, Burgess Shale, Fezouata Shale,  
33 Chengjiang Biota, taphonomy, mineralization

## 34 **1. Introduction**

35 Inspecting the fossil record is crucial to understanding the biology of past life on earth.  
36 Exceptionally preserved biotas, preserving soft-bodied metazoans (e.g. sponges; early  
37 chordates) and their labile anatomies (e.g. digestive tracts, muscles, and nervous systems)  
38 constitute a unique window on ancient ecosystems<sup>[1-3]</sup>. For instance, the Burgess Shale  
39 deposit in Canada yielded a considerable number of fossils shedding lights on spectacular  
40 Cambrian taxa preserved in high fidelity<sup>[4-10]</sup>. Exceptionally preserved soft parts in fossils  
41 from the Fezouata Shale (Ordovician, Morocco) were decisive in ending long-standing  
42 debates on the systematic affinities of various enigmatic taxa (e.g. machaeridians,  
43 stylophorans)<sup>[11-13]</sup>. The Chengjiang Biota (Cambrian, China) has also yielded a considerable  
44 amount of soft arthropod taxa with complex nervous systems<sup>[14-16]</sup>. In most cases, nervous  
45 tissues from the Chengjiang Biota are pyritized (i.e. preserved in FeS<sub>2</sub>) or show the  
46 association of pyrite and organic matter<sup>[14-17]</sup>. Pyritized tissues are frequently preserved alone  
47 in the fossils, while other tissues or organs (except the cuticle or body walls) are completely  
48 absent<sup>[17]</sup>. Experimental taphonomic studies investigating how biological tissues decay under  
49 various, controlled laboratory conditions questioned the validity of these paleontological  
50 discoveries by showing that nervous systems have little to no chance of preservation because  
51 they are observed to be rapidly lost under experimental conditions<sup>[18-20]</sup>. These experimental  
52 results have consequently given rise to contrasting conceptual frameworks in the paleontology  
53 and evolutionary biology communities<sup>[21-23]</sup>. Although vital to constrain preservation<sup>[23]</sup>,  
54 experimental decay data should be interpreted carefully and not projected directly onto  
55 enigmatic features in the geological record because fossils are not simply rotten carcasses and  
56 decay resistance is an imperfect indicator of fossilization potential<sup>[24]</sup>. Currently, there is no  
57 model accounting for the preservation of a specific labile tissue in a specimen where other  
58 more resistant tissues are completely absent. We investigate preservation patterns in such  
59 problematic structures and compare it to the patterns of pyritization in non-altered sediments,  
60 and propose an explanation for the contrast observed between the fossil record and modern  
61 decay experiments.

62

## 63 **2. Enigmatic structures are preserved in pyrite and organic matter**

64 Anatomical structures described as brains in fossils from the Chengjiang Biota were  
65 investigated using X-ray fluorescence mapping, which revealed the presence of carbon and  
66 iron<sup>[17]</sup> (Fig. 1a-d). Electron microscopy shows that iron occurs either as small euhedral  
67 crystals (around 2 microns in size) or as framboids (around 10 microns in size)<sup>[17]</sup> (Fig. 1e-h).  
68 Pyrite crystal morphology indicates that pyritization occurred very early during the  
69 fossilization process, shortly after the death of the organism<sup>[25,26]</sup>. Carbon in these fossils is  
70 preserved as compressed dark films<sup>[17]</sup> (Fig. 1i, j). Chengjiang fossils broken through the  
71 middle show pyrite overlaying carbonaceous films on both parts<sup>[17]</sup>, pointing to a centrifugal  
72 pattern of pyritization (Fig. 1k). Centrifugal pyritization, similar to patterns of tissue  
73 preservation in the Chengjiang Biota, is also present in fresh core sediments (Fig. 2a) from  
74 levels with exceptional preservation within the Fezouata Shale, where Raman spectroscopy  
75 identified large pyrite clusters surrounded by organic matter (Fig. 2b-d).

76 FeS<sub>2</sub> precipitation in sediments requires decaying organic material, and iron that is usually  
77 provided by surrounding sediments in addition to sulfates SO<sub>4</sub><sup>-</sup> from sea waters<sup>[27,28]</sup>. Under  
78 sulfate-reducing conditions, bacteria transform organic matter and sulfates into HS<sup>-</sup> and then  
79 to hydrogen sulfides H<sub>2</sub>S, which react with Fe in a series of reactions to form pyrite<sup>[26-28]</sup>. If  
80 the sediment surrounding dead animals is poor in organic matter, as was the case in the  
81 Fezouata Shale<sup>[29]</sup>, sulfate reduction is limited to decaying carcasses<sup>[29]</sup>. Within a decaying  
82 carcass, anatomical features can react differently to decay<sup>[30]</sup>. Easily degradable structures  
83 (e.g. tissues and organs formed of cells)<sup>[3]</sup> constitute a hotspot for H<sub>2</sub>S production, whereas

84 more resistant structures (e.g. biomineralized parts), do not produce enough H<sub>2</sub>S, and thus do  
85 not pyritize<sup>[31]</sup>. Furthermore, decay discrepancies exist even between different fast decaying  
86 cellular structures. Some cellular structures are solely degraded by external bacterial  
87 communities, while others degrade under the activity of their internal microbial biota and  
88 enzymes as well<sup>[30,32]</sup>. If decay by external bacteria is dominant and iron is available,  
89 pyritization starts at the outer part of the organic material where both H<sub>2</sub>S and Fe are present,  
90 leading to a centripetal pattern of preservation (Fig. 3a). This pattern is observed in the fossil  
91 record<sup>[27]</sup> and does not refute occurrences of centrifugal pyritization, because some tissues  
92 decay under the activity of their internal bacteria and enzymes. If such internal decay is  
93 dominant and iron is present, more H<sub>2</sub>S is produced internally, leading to the centrifugal  
94 pattern of preservation (Fig. 3b). It is likely that preserved structures in the Chengjiang Biota  
95 and the Fezouata Shale decayed under the activity of their internal microbial biotas and  
96 enzymes in the presence of iron. The proposed model based on H<sub>2</sub>S limitation and production  
97 patterns<sup>[25,27,31]</sup> can explain (1) the centrifugal pyritization of nervous systems in Cambrian  
98 arthropods and (2) the association of this anatomy to non-pyritized cuticular body walls that  
99 did not produce enough H<sub>2</sub>S for their pyritization<sup>[25,31]</sup>. However, it fails to explain the  
100 selective pyritization of a specific cellular structure (i.e. nervous system) while other internal  
101 structures (e.g. digestive and vascular systems) decayed, producing H<sub>2</sub>S, but did not pyritize.  
102 Thus, it is crucial to investigate patterns of iron distribution in the sediment surrounding  
103 decaying carcasses.

104

### 105 **3. Abiotic iron is not fast enough to preserve labile tissues**

106 The most classical and widely accepted sources of iron for pyritization are abiotic<sup>[28,33]</sup>. In the  
107 Fezouata Shale, iron oxides found in sediments (e.g. hematite  $\alpha$ -Fe<sub>2</sub>O<sub>3</sub>; Fig. 2b-d) constitute  
108 only a small fraction of the rock (i.e. <1%)<sup>[26]</sup>. However, in a comparable way to numerous  
109 Cambrian sites with exceptional fossil preservation, iron-rich silicates such as  
110 berthierine/chamosite are dominant (i.e. between 5 and 15% of the total rock  
111 composition)<sup>[26,34]</sup>. Berthierine/chamosite results from the transformation of a primary clay  
112 mineral (e.g. glauconite, odinite, kaolinite, or other similar precursor minerals)<sup>[35]</sup> under  
113 anoxic conditions and high iron concentrations<sup>[26]</sup>. Thus, iron in this mineralogical phase  
114 gives an estimate of the quantity of iron in the environment<sup>[26,34,35]</sup>. The formation of  
115 berthierine/chamosite in the Fezouata Shale required at least  $\sim 8 \cdot 10^{-5}$  M (defined here the M  
116 notation) of iron (see supplementary material). These concentrations are high and are slightly  
117 less than the ones in modern anoxic sediments at  $10^{-4}$  M and are enough to pyritize at the site  
118 of decay<sup>[27]</sup>. Thus, in theory and in terms of concentrations, abiotic iron is not a limiting  
119 parameter in levels with exceptional preservation in the Fezouata Shale<sup>[26]</sup> in a similar way to  
120 sites with exceptional fossil preservation from the Cambrian<sup>[34,36]</sup>. However, there must have  
121 been other parameters controlling the availability of this iron during soft tissues degradation  
122 and inhibiting pyrite from replicating all internal systems. Laboratory experiments have  
123 shown that most anatomical structures in soft animals decay very fast within hours or days  
124 after death<sup>[18,20,37]</sup>. For instance, nervous tissues decayed under 11 days for chordates and  
125 under 4 days for ecdysozoans<sup>[18,20]</sup>. On the contrary, most iron-rich phases in contact with H<sub>2</sub>S  
126 require longer times to deliver their iron (Table 1)<sup>[38]</sup>. This timing exceeds the timing of  
127 biological tissue decay, especially for labile anatomies such as the brain<sup>[18,20,32,37]</sup>. Thus,  
128 another source of available iron must exist in order to selectively pyritize a tissue/organ  
129 shortly after the death of the organism.

130

### 131 **4. Biogenic iron is available during decay**

132 If abiotic iron is not enough to start the pyritization process investigation on biogenic iron  
133 source should take place. In analyzed samples (i.e. thin sections) from the Fezouata Shale,

134 maghemite (i.e.  $\gamma$ -Fe<sub>2</sub>O<sub>3</sub> structurally similar to magnetite) is associated with pyrite (Fig. 2b-d).  
135 Two widely recognized mechanisms for maghemite formation exist<sup>[39,40]</sup>. In the first  
136 mechanism, lepidocrocite, a fibrous iron oxide-hydroxide, transforms partially to maghemite  
137 at temperatures around 200°C and completely at temperatures higher than 570°C<sup>[39]</sup>.  
138 Maghemite can also result from buried ferrihydrites at temperatures between 100 and 300°  
139 C<sup>[40]</sup>. Sediments from the Fezouata Shale were cooked at temperatures between 100 and  
140 200°C<sup>[26,41]</sup>. These temperatures and the absence of lepidocrocite in the analyzed samples but  
141 also from tens of other intervals in the Fezouata Shale<sup>[26]</sup> indicate that maghemite in these  
142 samples originates most probably from ferrihydrites. Ferrihydrite is a mineral with a wide  
143 biological distribution that can explain why maghemite is only found in association with  
144 pyritized organic matter and not in the sediment.

145 In all animals, ferritin is a metalloprotein that stores an excess of iron in the form of a hydrous  
146 ferric oxide-phosphate mineral [FeO(OH)]<sub>8</sub> [FeO(H<sub>2</sub>PO<sub>4</sub>)] similar in structure to the mineral  
147 ferrihydrite<sup>[42,43]</sup>. Ferritin-ferrihydrites are found in nervous systems, muscles and sensory  
148 organs such as the eyes<sup>[44-46]</sup>. Ferritin is capable of storing as many as 4,500 iron atoms in its  
149 core (i.e. concentration equivalent to 0.25M)<sup>[46]</sup>. Increased accumulations of ferritin-  
150 ferrihydrites were evidenced in marine invertebrates after their exposure to dysoxic/anoxic  
151 conditions<sup>[47]</sup> comparable to the environments in which animals from the Chengjiang Biota  
152 and the Fezouata Shale were preserved<sup>[48,49]</sup>. In experimental studies, it was shown that under  
153 bacterial sulfate reducing (BSR) conditions and when sulfates are present, ferrihydrites  
154 release high quantities (~ 87%) of reactive Fe<sup>[50]</sup> (i.e. 0.22M). This iron delivery is 40%  
155 higher than the yield from the same quantity of hematite<sup>[50]</sup>. Furthermore, ferrihydrite is the  
156 fastest to deliver reactive iron (Table 1), with a half-life under BSR conditions of only 2.8  
157 hours<sup>[38]</sup>. Ferrihydrite is also a solid phase meaning that it does not migrate<sup>[51]</sup>. Thus, 0.11M  
158 of iron becomes available *in-situ* within a couple of hours of the start of decay. These  
159 concentrations are well above those in modern anoxic sediments<sup>[27]</sup>, and are definitely enough  
160 to initiate pyritization at the site of decay.

161

## 162 **5. Biogenic iron explains the selective pyritization of soft anatomies**

163 Ferrihydrite in biological tissues constitutes a local source that rapidly provides high  
164 quantities of reactive Fe<sup>[38]</sup> that can initialize the process of pyritization. In this sense, shortly  
165 after the death of an organism, decay of the most labile tissue starts producing H<sub>2</sub>S. If this  
166 tissue contains ferrihydrites, it produces as well a considerable amount of reactive iron (Fig.  
167 4). The produced H<sub>2</sub>S and Fe react to form pyrite nuclei (Fig. 4) that further growth from H<sub>2</sub>S  
168 and Fe availability as decay occurs (Fig. 4). The extensive activity of decay leads also to the  
169 degradation of more resistant tissues (Fig. 4). However, if these less labile tissues are iron  
170 poor, they produce only H<sub>2</sub>S without iron (Fig. 4). Thus, the replication of such tissue in  
171 pyrite is not initiated, leading to a loss of the original morphology or even the complete  
172 disappearance of the tissue/organ (Fig. 4). When abiotic iron becomes available, it can play a  
173 role in pyrite growth in tissues that previously provided biogenic iron (Fig. 4). This  
174 hypothesis shows how biogenic iron stabilizes the morphology of decay-prone anatomical  
175 structures, before the less reactive iron phases become available.

176

## 177 **6. Hypothesis testing requires a multidisciplinary approach**

178 Although fossil mineralization is common in the geological record<sup>[53-58]</sup>, little work has been  
179 done to investigate the role of tissue chemistry during the mineralization process. Recently, it  
180 was suggested that the recurrent association of a particular mineralogical phase  
181 fluorapatite, Fe-sulfides (pyrite, pyrrhotite)

182 with a specific tissue in La Voulte-sur-Rhône (Jurassic, France), ( precise the nature of the  
183 mineralogical phase ? the type of tissue? And/or organism? Age and context sedim) can be  
184 due to differences in the original biochemical signal of the organic matter<sup>[52]</sup>.

185 crustacean fossils preserved within carbonate-rich concretions from the Jurassic Konservat-  
186 Lagerstätte of La Voulte-sur-Rhône (Ardèche, France)

187 However, much work remains to be done to precise the fate and behavior of biogenic iron  
188 during the taphonomic processes, and fully enlighten the black box of pyritization.

189

190 In order to test the hypothesis and determine the precise roles played by biogenic iron and  
191 iron from sediments, several lines of investigation should be undertaken combining  
192 geochemical, biological and experimental taphonomy approaches.

193

194

195 It would be ideal to start testing the hypothesis on nonweathered fossils. However, to our  
196 knowledge, no pyritized fossils from completely fresh sediments are discovered yet. Until  
197 then, yielding investigations on fresh pyrite, not particularly associated with any fossil can  
198 also be helpful because pyrite formation requires organic matter, and different organic  
199 materials reflect different original biochemical compositions.

200 >> these sentences are not clear for me...

201

202 Iron isotopic investigations on pyrite crystals from both the sediments and the pyritized fossils  
203 would help to decipher the multiple iron-sources and their role in pyritization. If these  
204 isotopic investigations were made at the nanoscale, they can inform on the source and  
205 chronology of iron delivery from the initiation of pyrite precipitation to the subsequent pyrite  
206 crystals growth.

207

208 What about sulfur isotopes?

209 Do you think minor elements (bio-related?) would be of interest?

210

211 Biological approaches are also very helpful in testing this biogenic iron hypothesis, for  
212 example by making a comparison between iron concentrations in different modern animal  
213 groups and those measured in pyritized tissues found in the fossil record. An even more  
214 detailed approach would be to quantify iron in different kinds of tissues within the same  
215 group. For instance, according to this hypothesis, if a specific group shows a higher  
216 concentration of iron in a specific tissue, we would expect to find this particular structure  
217 pyritized more often than the others in the geological record.

218 All these quantitative data will also help calibrate the new proposed model and understand its  
219 feasibility in natural environments. Most importantly, future decay experiments should focus  
220 not only on the general environmental conditions that lead to exceptional preservation, but  
221 also on the chemical signature surrounding each tissue during its degradation independently  
222 from the physical ability of this tissue to resist decay. These decay experiments should be  
223 done in the presence of different sediment compositions and under different bacterial  
224 communities to see if decaying carcasses act variously under different environmental  
225 conditions. Once iron sources, iron quantities in biological tissues, decay behavior, in addition  
226 to favorable sedimentological phases are discovered, pyrite precipitation from biological  
227 tissues could be replicated in laboratory aquariums.

228

229

230

231 Further isotopic investigations along this lines of the data presented here should be  
232 undertaken on pyrite crystals should to determine iron sources at different stages of the  
233 mineralization process. Additionally, the possible role of a biogenic iron source in other  
234 exceptionally preserved biotas could be explored in this context<sup>[40]</sup>. For example, at the  
235 Burgess Shale (Cambrian, Canada), nervous systems are preserved as carbonaceous  
236 compressions without any pyrite<sup>[41,42]</sup> since overall conditions were favorable for  
237 phosphatization<sup>[43]</sup>. Nevertheless, berthierine, an iron-rich mineral known to slow down  
238 decay<sup>[44]</sup>, is found in all levels with exceptional preservation. Future studies should investigate  
239 if this iron-rich mineral, also reported in hundreds of other intervals with exceptional  
240 preservation around the world<sup>[26]</sup>, is preferentially associated to specific labile soft parts.  
241 Biological approaches for hypothesis testing including quantitative iron-analysis of modern  
242 tissues and animals using mass spectrometry to help calibrate the new proposed model.  
243 Finally, future decay experiments should focus not only on the general environmental  
244 conditions that lead to exceptional preservation, but also on the chemical signature  
245 surrounding each tissue during its degradation independently from the physical ability of this  
246 tissue to resist decay.

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249  
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251

## 252 7. Conclusions and outlook

253 The present biogenic iron hypothesis helps us understand the sole presence of the most-labile  
254 tissues in some specimens where other more decay-resistant soft parts are absent. It also  
255 shows that pyritization starts very early during decay, preserving in high fidelity tissues that  
256 are originally iron-rich, resolving the morphological accuracy of Cambrian arthropod brains.  
257 Furthermore, it indicates that both decay experiments and paleontological descriptions are  
258 complementary, not incompatible. It opens new avenues of research by highlighting the  
259 importance of tissue chemistry during the fossilization process especially in the case of  
260 nervous tissues that are preserved in carbonaceous compressions without any pyrite<sup>[59-61]</sup>.

261

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274

## 275 Conflict of interest

276 None

277

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374

### 375 **Figure captions**

376 **Figure 1.** Preservation of Cambrian brains in *Fuxanhuia protensa* from the Chengjiang Biota.

377 a) YKLP 15006 shows dark brown areas interpreted as nervous tissues under direct

378 illumination. b) Carbon distribution in the studied specimen. c) Iron distribution. d) Merged

379 iron and carbon signals show an almost perfect superposition between these two elements.

380 White arrows indicate the rare places where both elements do not co-occur. e-h) Iron is

381 preserved in small euhedral and framboidal pyrite. i, j) Minerals overlay dark compressed  
382 carbonaceous material. The distribution of carbonaceous films under pyrite minerals in both  
383 part and counter-part suggest a centrifugal pattern of pyritization (k).

384 **Figure 2.** Pyritization in the Fezouata Shale. Pyrite crystals marked by white arrows in fresh  
385 core deposits (a) showing a centrifugal pattern of pyritization (b, c). Colored points in (b) and  
386 (c) correspond to the spectra shown in (d). Iron oxide phase identification is based on Raman  
387 peak indexation in natural samples<sup>[62]</sup>.

388

389 Label each peak with the value of the Raman shift in  $\text{cm}^{-1}$ , it is easier for the reader to  
390 compare data.

391

392 For the hematite and maghemite, do you have signal in the 1000- 1600  $\text{cm}^{-1}$  range for  
393 comparasion with the other spectra??

394

395

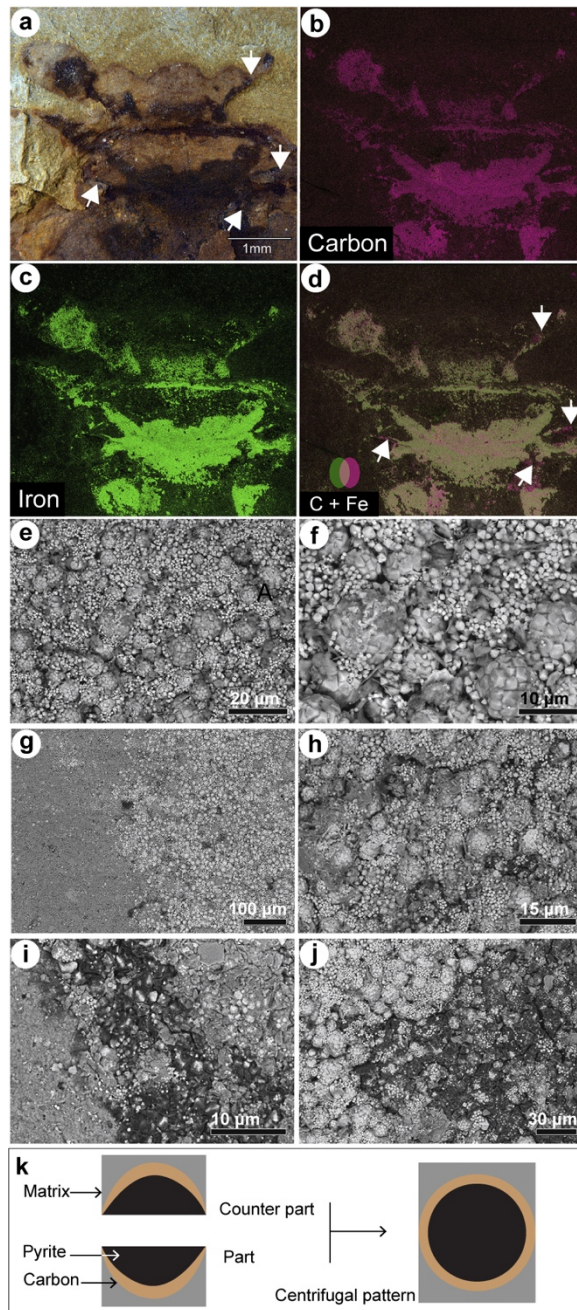
396 **Figure 3.** Patterns of soft tissue decay. a) Soft parts decaying under the activity of external  
397 bacteria lead to a centripetal pyritization. b) Soft parts decaying under their own bacterial  
398 community and enzymes contribute in a centrifugal pyritization.

399 **Figure 4.** Hypothesis for labile tissue preservation and resistant tissue loss.

400

<b>Iron phase</b>	<b>Half-life</b>
Goethite	11.5 days
Hematite	31 days
Magnetite	105 years
Reactive silicates	230 years
Sheet silicates	84000 years
Augite, amphibole	>84000 years

401 Table 1. Half-lives of iron phases under permissive conditions for pyrite precipitation.  
402 (references ?) – what do you mean for “reactive” silicates?



**Figure 1**

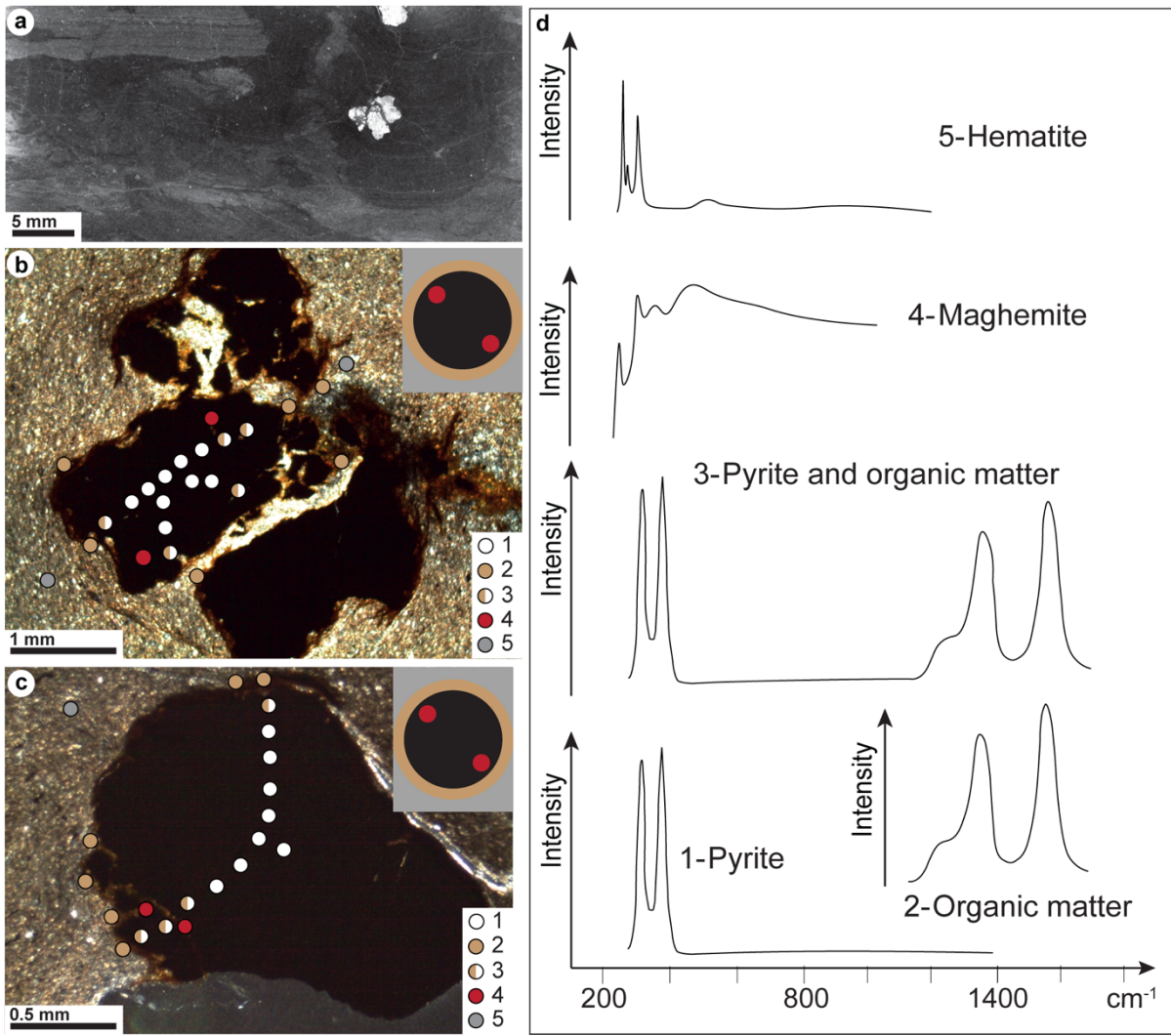
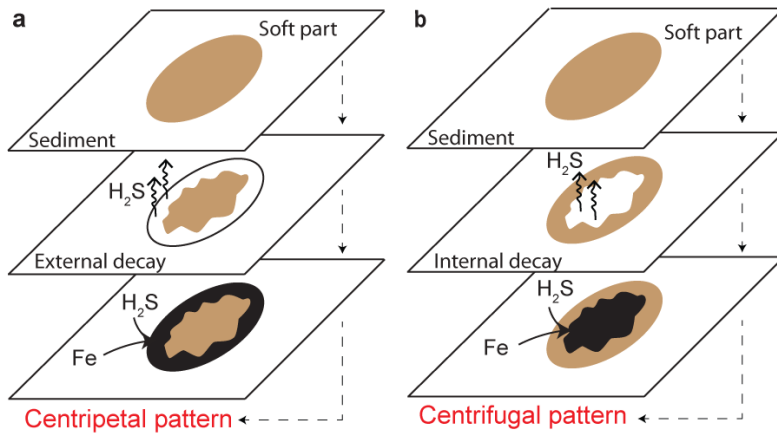
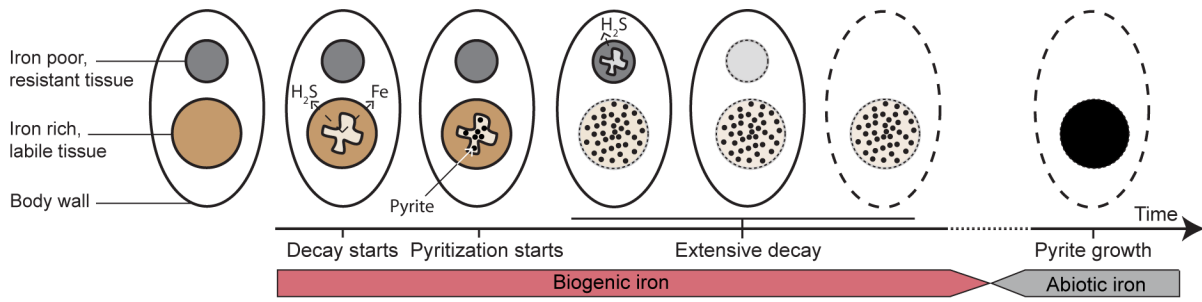


Figure 2



**Figure 3**



**Figure 4**