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## **Taphonomy of early life (2.1 Ga) in the francevillian basin (Gabon): Role of organic mineral interactions**

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3 **Taphonomy of early life (2.1 Ga) in the Francevillian Basin (Gabon): Role**  
4 **of organic mineral interactions**

5

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35 **Abstract**

36 The taphonomy of early soft-bodied organisms in Palaeoproterozoic sediments is not yet clearly  
37 understood, even though some locations where these fossils are found present all the conditions for  
38 exceptional fossil preservation. Indeed, the degree of fossil preservation has received attention, but  
39 better knowledge of the environmental conditions and associated taphonomic processes is also essential.  
40 In the Gabonese Francevillian Basin, the discovery of macrofossils (2.1 Ga) of multicellular organisms  
41 in black shales is an outstanding example of this degree of preservation. Indeed, the biological diversity,  
42 as a wide variety of fossil morphologies are observed, is associated with two major taphonomic  
43 processes – moulding (lenticular-shaped forms) or early pyritization, while the fossil host rocks were  
44 not deeply buried and were affected only by weak to moderate diagenesis. However, usually, the  
45 mechanisms of this preservation remain difficult to assess, as the original taphonomic processes are  
46 impacted by diagenesis and still misunderstood. In this way, by closely observing fossil mineralization  
47 in four morphotypes of macrofossils and associated host rocks from mineralogical and textural points  
48 of view, this work aims to provide some keys to a taphonomic comprehension of soft-bodied organism  
49 preservation. After the deposition of dead organisms on the clayey sediment, an illitization process,  
50 which depends on the availability of dissolved K driven by bacterial activity, started from the first stages  
51 of preservation by moulding the lenticular-shaped forms and proceeded in the pores of the other  
52 macrofossils after their pyritization. At the fossil level, the intensity of illitization is controlled by the  
53 mode of preservation and the evolution of the associated permeability. In the nonpyritized lenticular-  
54 shaped specimens, illitization was not achieved, preserving I-S mixed-layer minerals, while in the  
55 pyritized forms, the illitization degree was more extensive. In comparison, I-S mixed-layer minerals are  
56 almost absent in pyritized abiotic concretions. A second process, which occurred later, consists of  
57 general chloritization from fluid circulation. Our detailed results show that each specimen behaved like  
58 a microsystem with its own physico-chemical and mineralogical evolution during  
59 preservation/diagenesis. This finding allows us to propose a conceptual model of the taphonomic  
60 history, describing the fossilization stages for each type of specimen.

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62

## 63 1. Introduction

64 Knowledge of early Precambrian biospheres is primarily based on the study of exceptionally well-  
65 preserved fossilized remains of soft-bodied organisms (Knoll, 1985). Shales appear to be very  
66 favourable host rocks for the preservation of the earliest forms of life (Ngombi-Pemba et al., 2014;  
67 Wilson and Butterfield, 2014), but the mechanisms of this preservation remain difficult to assess, as the  
68 original taphonomic processes are still largely misunderstood and can be impacted by various chemical  
69 and mineralogical transformations.

70 In fact, the preservation of soft bodies involves sufficiently slow biological degradation for the more  
71 resistant organic molecules to be fossilized by imprinting or mineralization (Briggs, 2003). The early  
72 stage of this preservation is mainly controlled by the nature of the sediments and their rate of  
73 accumulation (Briggs and Kear, 1993) in the presence or absence of biological agents (bacteria) together  
74 with the water column chemistry (major elements, dissolved O<sub>2</sub>, etc.) of the depositional environment  
75 (Gaines et al., 2012; Gaines and Droser, 2010). Then, diagenetic processes (e.g., compaction,  
76 cementation, fluid–rock interaction, and potential hypothermal and magmatic activities) can also impact  
77 the quality of fossilization (Muscente et al., 2015). The quality of the conserved fossils, i.e., the degree  
78 of resemblance to the original organisms, is controlled by the intensity of all these predominant factors,  
79 with a direct impact on reconstructing the initial form of soft-bodied organisms and deriving information  
80 on their lifestyles based on the geometric (morphologies, tracks, burrows, etc.) and chemical (organic  
81 molecules, isotopes, etc.) signatures that have been preserved.

82 The Palaeoproterozoic fossil-rich black shales of the Francevillian Basin (Gabon) constitute a  
83 unique case study to fill these gaps. They hold exceptionally fossilized fauna, the oldest ecosystem is  
84 2.1 billion years, they consist of decimetric macrofossils (El Albani et al., 2023, 2014, 2010; Ossa et al.,  
85 2023) of soft-bodied organisms capable of movement (El Albani et al., 2019a), and they are in close  
86 association with photosynthetic microbial mats (Aubineau et al., 2019, 2018; Reynaud et al., 2018).  
87 However, even if this fossiliferous system was not affected by metamorphic conditions – thereby saving  
88 a large amount of taphonomic information (El Albani et al., 2014, 2019a; Gauthier-Lafaye and Weber,  
89 1989; Ngombi-Pemba et al., 2014; Ossa et al., 2013; Weber, 1968a) – the fossilization/preservation  
90 conditions and mechanisms are still unclear. An adapted mineralogical and petrographic study of these  
91 organic matter-/clay-rich rocks should remove these uncertainties.

92 In this way, by closely observing fossil mineralization and host rocks from mineralogical and  
93 textural points of view and by describing organo-mineral interactions, this work aims to provide some  
94 keys to a taphonomic comprehension of soft-bodied organism preservation in Francevillian black shales.  
95 The study strategy involves the following:

96 (i) Remains of both biomineralized and nonmineralized taxa in fossil deposits were discriminated  
97 (Conway Morris, 1986).

98 (ii) Pyritic concretions that have no apparent links with the fossil specimens were observed (El  
99 Albani et al., 2023, 2019b, 2014, 2010; Ossa et al., 2023). This can help us to better understand the  
100 conditions that prevailed during fossilization.

101 (iii) Organo-mineral interactions were characterized. This can serve as indirect evidence for  
102 understanding the taphonomy and biogenicity of the earliest organisms (Lepot, 2020), especially clay  
103 mineral transformation, which can record palaeobiological and palaeoecological variations  
104 (Behrensmeier et al., 2000). In this sense, resolving the role of minerals in the fossilization of soft bodies  
105 is also a key element in understanding any environmental bias in fossil assemblages. Illustrating the  
106 importance of organo-mineral interactions, Burges Shales fossils are certainly preserved primarily as  
107 carbonaceous compressions (Butterfield, 1995), but diagenetic mineralization may have stabilized  
108 organic matter or replicated the morphology (Anderson et al., 2011; Briggs, 2003).

109 Although the mineralogical study of Palaeoproterozoic Francevillian rocks has already been  
110 carried out in part (e.g., Aubineau et al., 2021), a systematic study such as the one presented here is  
111 unprecedented. Clay minerals, specifically illite, mixed-layer minerals (MLMs) and chlorite, have been  
112 documented within or near the fossils but not on a large scale with as many samples as in this study  
113 (more than 40 fossils + host rock samples). In this respect, our approach is resolutely innovative: it  
114 systematically characterizes the mineralogy and textural arrangement of clay minerals and pyrite in the  
115 host rock as well as in the fossils but independently assesses nonpyritized lenticular-shaped specimens,  
116 pyritized lobate forms, string-shaped specimens, and segmented morphologies. The results should allow  
117 us to propose a conceptual model depicting the taphonomy and the mechanisms of mineralization during  
118 fossilization and diagenesis according to the submillimetre-scale physico-chemical conditions.

119

## 120 2. Geological settings

121 The Franceville Basin is filled by a series of unmetamorphosed sedimentary deposits of  
122 Palaeoproterozoic age resting unconformably on an Archean basement (Figs. 1 and 2) (Aubineau et al.,  
123 2021; Bankole et al., 2015; Bros et al., 1992; Gauthier-Lafaye, 1986; Ossa Ossa et al., 2013;  
124 Thiéblemont et al., 2014; Weber, 1968a). The Francevillian siliciclastic fluvial and marine sediments  
125 are subdivided into four major lithostratigraphic formations, FA to FD, from oldest to youngest. The FA  
126 Formation dominantly consists of fluvio-deltaic conglomerates and sandstones (Bankole et al., 2015;  
127 Gauthier-Lafaye and Weber, 1989), while the overlying FB Formation is dominated by heterolithic  
128 marine rocks deposited during a period of tectonic subsidence and basin deepening (Reynaud et al.,  
129 2018). The significant lithological differences and sedimentary structures within this formation resulted  
130 in several lithostratigraphic subdivisions into the FB<sub>1</sub> (including a, b, and c units) and FB<sub>2</sub> (a and b units)  
131 members (Azzily Azzibrouck, 1986; Weber, 1968b). The FC Formation hosts shallow marine  
132 dolostones and cyanobacteria-hosting stromatolitic cherts interbedded with black shale horizons (Lekele  
133 Baghekema et al., 2017; Pr at et al., 2011), while the FD Formation is made of marine black shales with

134 interbedded volcanic tuffs, which were deposited in a transgressive phase (Thiéblemont et al., 2014).  
135 Although large-scale synclinals and anticlinals have been formed in the Francevillian subbasin,  
136 sediments were not deformed, which is marked by the exceptional conditions of preservation of the  
137 entire Francevillian sedimentary stratum.

138 The Francevillian fossil deposits, which belong to the FB<sub>2</sub> Member, are in the Moulendé quarry close  
139 to Franceville town on the northern side of the Mvengué syncline. The latter stretches along an NNW–  
140 SSE axis parallel to the edge of the basin represented by the eastern boundary of the Chaillu Massif (Fig.  
141 1). The tectonic activity with the generation of normal faults predominantly in the centre of the  
142 Francevillian subbasin led to the formation of well-exposed outcrops (Fig. 2); (Gauthier-Lafaye and  
143 Weber, 1989; Mayaga-Mikolo, 1996; Thiéblemont et al., 2009; Weber, 1968b). Sea-level fall that began  
144 during the deposition of the FB<sub>1c</sub> unit and extended during the deposition of the overlying FB<sub>2</sub> Formation  
145 caused contemporary-level to increasingly oxic conditions in the water column with transient oxygen-  
146 deficient bottom waters (Aubineau et al., 2021; Canfield et al., 2013; Ossa Ossa et al., 2018).  
147 Specifically, the FB<sub>2</sub> deposits aged 2092 ± 48 Ma (Ngwal'ghoubou Ikouanga, 2022) are composed of  
148 Poubara sandstones interbedded with thin black shale levels (FB<sub>2a</sub> unit) and 5-m thick black shales with  
149 cm-thick siltstone layers (FB<sub>2b</sub> unit) (Fig. 3). Lithofacies analyses indicated that the black shale deposits  
150 of FB<sub>2b</sub> were emplaced in a calm, low-energy marine environment after a large discharge of sands  
151 (Reynaud et al., 2018). The relatively oxygenated water column, together with the cyanobacterial mats,  
152 may have favoured the development and preservation of complex macroorganisms (Aubineau et al.,  
153 2021, 2018; Canfield et al., 2013; El Albani et al., 2019a; Reynaud et al., 2018).

### 154 3. Materials and Methods

155 The studied specimens were collected from the FB<sub>2b</sub> black shales. Four morphotypes of macrofossils,  
156 including different lobate-shaped, string-shaped, segmented, and lenticular-shaped forms, as well as  
157 microbial mat communities, described as mat-related structures (MRSs), are preserved throughout this  
158 entire rock unit (Aubineau et al., 2018; El Albani et al., 2019b, 2014, 2010). Ten specimens of each  
159 morphology (total of 40) were analysed.

160 The vertical distribution of the fossiliferous content is irregular (Fig. 3). While, the interbedded siltstones  
161 are completely devoid of macrofossils, MRSs have been described inside (Aubineau et al., 2018).  
162 Finally, pyrite concretions (Reynaud et al., 2018) were also found throughout the black shales. They are  
163 aligned in the lower part, are sparse and smaller in the middle part and form almost continuous pyritic  
164 beds in the upper part of the FB<sub>2b</sub> unit. Polished slab sections were made for petrographic  
165 characterization at the macroscale. Microsamples were separated using a Dremel microdrill equipped  
166 with a diamond tip to precisely determine the mineralogical and chemical nature of the specimens.  
167 Specimens of all macrofossil morphological types were analysed: one unmineralized morphological  
168 type (round shape) and three mineralized types (lobed, tubular, and segmented shapes). For each of these

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169 types , the specimen (SP) and the host black shale (BS) have been characterized in detail. Pyritic  
170 concretions (clusters and nodules) present in the host black shales have also been investigated.

### 171 **3.1. Petrographic observations**

172 Petrographic observations of polished thin sections were performed to study the textural relationships,  
173 morphology, mineral assemblages, and chemical composition. Polished thin sections were first  
174 examined by a Nikon ECLIPSE E600 POL optical microscope coupled with a Nikon Digital Sight DS-  
175 U1 camera installed with NIS-Element D software. Selected polished thin sections were carbon-coated  
176 and examined using a JEOL JSM IT500 Scanning Electron Microscope at the University of Poitiers,  
177 France. The scanning electron microscopy (SEM) instrument was equipped with secondary electron  
178 (SE) and backscatter electron (BSE) detectors.

### 179 **3.2. Bulk and clay mineralogy**

180 The bulk and clay mineralogical compositions were obtained by X-ray diffraction (XRD) from randomly  
181 oriented bulk powders and oriented clay preparations, respectively, using conventional procedures  
182 (Brindley and Brown, 1980; Moore and Reynolds, 1997). The X-ray diffractograms were obtained using  
183 a Bruker D8 Advance diffractometer equipped with a copper source ( $\lambda_{\text{CuK}\alpha} = 1.5418 \text{ \AA}$ ). The analytical  
184 conditions were 40 kV and 40 mA; the acquisition parameters were 1 s with a step of  $0.025^\circ 2\theta$  for  
185 angular ranges of  $2-65^\circ 2\theta$  and  $2-30^\circ 2\theta$  for randomly oriented powder and oriented clay samples,  
186 respectively. XRD patterns were deconvoluted in the  $7-10^\circ 2\theta$  range using Fitik software to  
187 semiquantify mixed layer clay minerals (using peak areas).

## 188 **4. Results**

### 189 **4.1. Macroscopic description of studied biotic and abiotic structures.**

190 Here, we report a multiscale description of specimens previously described by El Albani et al. (2023,  
191 2019b, 2014 and 2010).

#### 192 **4.1.1 Lenticular-shaped forms**

193 The lenticular-shaped fossils look like subcircular capsules with a more or less pronounced central bulge  
194 (Fig. 4A-B). They can be found associated with other macrofossils (Fig. 4A), form aggregates  
195 overlapping each other, or are preserved alone (Fig. 4B). The diameters range from 0.3 to 5 cm. The  
196 inner surface comprises a core and a flat collar containing fine radial striations. The length of the collar  
197 represents 25% of the total radius. The observed shape of the lenticular fossils results from epirelief  
198 moulding, i.e., light silty and dark clayey laminae of the host sediments mould the specimens (convexity  
199 of laminae shown in Fig. 4C).

200            **4.1.2. Lobate form**

201    The lobate macrofossils are characterized by a rounded (Fig. 4D) or ovoid (Fig. 4E) inner part and an  
202    outer part composed of a succession of smaller lobes delimited by deep radial striae. The lengths of the  
203    specimens vary from 2 to 4 cm, and their widths vary from 1 to 2 cm. They are almost entirely  
204    mineralized by phenocrystal of euhedral pyrite (2 to 3 mm). The central lobes lack striae and may be  
205    more or less smooth. The lobes are mineralized, consisting of aggregates of euhedral pyrite grains (Fig.  
206    4F). The mineralized specimens locally display a submillimetre-sized border of more “diffuse” pyrite,  
207    particularly at the lobed end - where smaller euhedral pyrite crystals are packed in a clay matrix - which  
208    rapidly fades at the outer edge of the specimen. At the contact zone between the specimens and host  
209    sediments, textural changes in the sediments are visible (Fig. 4F): the host sediment presents alternating  
210    light silty laminae and dark clay laminae that follow the border of the contact zone, suggesting that the  
211    host sediment was not consolidated at the time of fossil mineralization.

212            **4.1.3. String-shaped forms**

213    The string-shaped specimens have a millimetre-scale ovoid diameter and centimetre-scale  
214    elongated body fossils (Fig. 4G, H). The edges are clear (Fig. 4G) but may be bifid (Fig. 4H). They have  
215    been interpreted as multicellular organisms capable of moving vertically or horizontally with respect to  
216    the sediment to reach nutrients (El Albani et al., 2019a). The string-shaped structures are largely  
217    pyritized, but the remaining porosity is filled by a clayey material that is more abundant in the cores of  
218    the fossiliferous structures (Fig. 4I). The host black shale sediments are slightly deformed in the contact  
219    zone with the fossils.

220            **4.1.4. Segmented forms**

221    The segmented specimens, which are pyritized and often associated with pyritized MRSs, appear as  
222    segmented, sinuous cylinders (Fig. 5A). The length of such fossilized structures reaches several  
223    centimetres, while the maximum width is up to 2 cm. The segmented forms may have a homogeneous  
224    shape over the entire length, and a narrowing of a few millimetres has been observed. Pyritization is  
225    likely continuous between segmented fragments. Perpendicular to the elongation, cylindrical fossils  
226    appear completely pyritized, although the core host septaria-type fractures are filled with a dark clayey  
227    matrix (Fig. 5B). Intergranular porosity is strongly reduced at the edges of segmented specimens.

228            **4.1.5. Mat-related structures**

229    Mat-related structures are ubiquitous in both black shale laminae and intercalated siltstone levels.  
230    Numerous mat morphotypes, up to 10, were formed by either mat growth or mat-protected patterns  
231    (Aubineau et al., 2018). The latter resulted from the mat preservation of abiotic structures. One of the

232 most common MRSs in the FB2b unit is the fairy-ring structure (Fig. 5C). In addition, the FB2b MRS  
233 may also be associated with macrofossils.

#### 234 **4.1.6. Pyritized mineral concretions**

235 Mineral concretions consist of aggregates of euhedral pyrite phenocrystals that display specific  
236 morphologies. Concretions may form isolated clusters or discontinuous beds (Fig. 5D-E). The polished  
237 cross-section shows that the pyritization of concretions was intense where the crystal size increases from  
238 the core to the edge (Fig. 5F). Early small euhedral crystals likely served as templates for the later  
239 crystals, which are now observable. A reduction in the intergranular porosity is strongly apparent at the  
240 edges. While the light silty and dark clayey laminae of the host black shales are slightly deformed near  
241 the concretions, a general flexure following the overall structure is lacking. This suggests that the  
242 sediment was partially consolidated when the pyrite crystallized.

### 243 **4.2. Mineralogy**

#### 244 **4.2.1. Host sediments**

245 Based on XRD data and SEM observations, the bulk mineralogy of the host sediments close to each  
246 fossil mainly consists of quartz and clay minerals (Fig. 6A-7A-8A). Carbonates, Do (peak at 2.89 Å –  
247 dolomite, and the peak is sometimes slightly shifted to 2.90 Å – dolomite-Fe-/ankerite), are minor, and  
248 pyrite, Py (peak at 2.71 Å), is in extremely low amounts. The clay fraction (Fig. 6B-7B-8B) is mainly  
249 composed of chlorite, C (characteristic peaks at 14.2 Å and 7.09 Å); illite/mica, I/M (at 10.00 Å); mixed  
250 layers of illite/smectite, MLs and MLi (~ 10.8 Å); and smectite, Sm (16.9 Å), to a lesser extent, which  
251 was identified after ethylene glycol saturation (Fig. 6C-7C-8C). This treatment also causes a slight shift  
252 towards higher 00l spacing and a reduction in the intensity of the ML peak coupled with an appearance  
253 of a shoulder at approximately 9.8 Å.

254 The deconvolution of the XRD patterns for mixed layer ML phases (Fig. 9A, Tab. 1-2) shows a clear  
255 contribution of an illite-rich term in mixed layers (MLi) at 10.3 Å, which may be slightly influenced by  
256 a term richer in illite (illite-like) at 10.1 Å. Assuming that the smectite interlayers are entirely occupied  
257 by divalent cations (Ca, Mg), one can approximate the I/S ratios in both types of ML: MLi (I=94%;  
258 S=6%) and MLs (I=80%; S=20%). In both cases, illite is always the dominant component of these  
259 mixed-layer minerals (Tab. 1).

#### 260 **4.2.2. Lenticular-shaped forms (nonpyritized macrofossils)**

261 The lenticular-shaped forms are mainly filled by quartz (3.34 Å) associated with clay minerals (4.49 Å),  
262 dolomite (2.89 Å), and pyrite to a lesser extent (2.71 Å) (Fig. 6A). The clay fraction consists of chlorite  
263 (14.2 Å and 7.09 Å), illite/mica (10.0 Å), mixed layers of MLi and MLs, and discrete smectites (Fig.

264 6B-6C). The mixed-layer MLs are characterized by a  $d_{001}$  reflection centred at 10.9 Å after glycolation,  
265 which corresponds to ordered MLs with the persistence of some smectite-rich layers (I=82%; S=18%).  
266 Overall, the mineralogical assemblage is identical to the host sediment (Fig. 9B); the illite/smectite ratio  
267 seems to be lower, indicating a lower illite content than in the sediment.

#### 268 **4.2.3. Pyritized fossils**

269 The lobate, string-shaped and segmented specimens are dominantly filled by pyrite (Fig. 7A). Quartz  
270 and clay minerals are identified only after separation of the <2 µm clay fraction. The clay mineral  
271 assemblage, consisting of chlorite, mixed layer MLi and MLs, and illite/mica, is similar to that of the  
272 host black shale sediments (Fig. 7B). Nonetheless, smectite is present in the string-shaped structures  
273 (Fig. 7C). The illite/(MLi) ratio is globally lower than that of the host sediment (Fig. 9B, Tab. 1).  
274 Importantly, the main mineralogical differences between pyritized fossils and their host sediment are  
275 the higher abundance of mixed layers compared to illite/mica combined with the absence of carbonates.

#### 276 **4.2.4. Pyritized concretions**

277 Unsurprisingly, these concretions are made of pyrite with few associated phases (Fig. 8A). Nonetheless,  
278 chlorite, illite, mixed layers of MLi and quartz are observed in the ≤ 2 µm clay fraction (Fig. 8B-8C).  
279 Unlike the sediment and all fossils, low amounts of MLi (10.3-10.4 Å), together with the lack of MLs,  
280 characterize these concretions, as indicated by the high illite/MLi ratio (Fig. 9C, Tabs. 1-2).

### 281 **4.3. Petrography**

#### 282 **4.3.1. Host sediments**

283 Along the stratigraphic sequence of the Moulendé quarry, the host sediments always consist of a clay  
284 matrix, quartz, chlorite, pyrite, and dolomite, as illustrated by XRD data and SEM observations (Fig.  
285 10). The clay phase proportion varies according to the granulometry of the laminae. The clayey facies  
286 (Fig. 10A) correspond to deposits of a densely packed clayey matrix with chlorites, disseminated pyrite  
287 and rounded to subangular quartz grains densely packed. The transitional facies – composed of silty clay  
288 (Fig. 10B) or clayey silt (Fig. 10C and 10D) – is marked by an increase in the grain size of quartz and  
289 chlorite. Compared to the clayey facies, the quartz morphology here is closer to polycrystalline  
290 aggregates. Chlorites display three 2-D morphologies, including lamellar structures, rectangular  
291 platelets, and ovoidal shapes, which can exceed 50 µm in length and diameter (Fig. 10A-10B-10). In all  
292 cases, the particles are composed of poly-lamellar stacks. In addition, the edges of the ovoids show thick  
293 grey halos, probably due to iron depletion from postdepositional alteration and/or recrystallization  
294 processes. The porosity can be filled by intertwined or stacked secondary chlorite lamellae, which  
295 developed at grain contacts with primary phases (quartz, chlorite in platelets) or as coatings (Fig. 10D).  
296 In these facies, pyrite is either disseminated, corresponding to euhedral to subeuhedral crystals, or

297 intergrown with chlorites (Fig. 10C). Although pyrite is a minor phase, its proportion is higher than in  
298 the clayey facies.

#### 299 **4.3.2. Nonpyritized macrofossils: Lenticular-shaped forms**

300 The clay material of the lenticular-shaped forms is mainly filled by illite particles, while quartz grains  
301 are scarce (Fig. 10E). On the other hand, chlorites in flexuous lamellae, oriented parallel to the  
302 stratification, seem to be much more abundant than in the sediments, although chlorite with platelet and  
303 ovoid shapes are present in low amounts. The size (10 to 20  $\mu\text{m}$ ) of the latter is generally smaller than  
304 that of the host sediment. Finally, tiny anhedral, disseminated pyrite grains are observed.

#### 305 **4.3.3. Pyritized fossils**

306 Clayey assemblages identified by XRD fill the intergranular pores between pyrite crystals that preserved  
307 the mineralized macrofossils, while detrital minerals (e.g., quartz, primary chlorite, and dolomite) are  
308 almost absent (Fig. 10F-10G).

309 The lobate, string-shaped, and segmented specimens are essentially composed of illite I/M (Fig. 10F).  
310 Micrometric illite (I/M) is mainly in the form of stacked sheets (Fig. 10) and shows signs of free growth  
311 within the pore spaces. Chlorite has developed as short platelets in the intragranular porosity, probably  
312 at the expense of illite as encompassing relict patches of illitic matrix (Fig. 10F). Inside the porosity,  
313 chlorite lamellae are interbedded with illite as “accordion” structures. Secondary quartz patches are also  
314 observed (Fig. 10G).

#### 315 **4.3.3. Pyritized mineral concretions**

316 Pyrite concretions has allowed the development of strongly interlocking pyrite phenocrystals, reducing  
317 the porosity (Fig. 10H-10I). The clay assemblage that fills the residual porosity of plated concretions  
318 seems to be diagenetic considering their size and shape, and does not contain an illite-rich matrix. In the  
319 nodules, part of the porosity is occupied by the illite. However, chlorite is more abundant than illite (Fig.  
320 10I).

## 321 **5. Discussion**

### 322 ***Processes impacting soft-bodied organism preservation***

323 Studying the degree of conservation of biological bodies is essential for understanding taphonomy.  
324 Moreover, it is of great interest to elucidate the environmental conditions and taphonomic mechanisms  
325 that prevailed during the different stages of preservation (Behrensmeier et al., 2000).

326 The preservation of soft bodies involves sufficiently slow biological degradation for the more resistant  
327 organic molecules to be fossilized by imprinting or mineralization (Briggs, 2003). The early stage of

328 preservation is mainly controlled by the nature of the sediments and their rate of accumulation (Briggs  
329 and Kear, 1993) in the presence or absence of biological agents (bacteria) together with the water column  
330 chemistry (major elements, dissolved O<sub>2</sub>, etc.) of the depositional environment (Gaines et al., 2012;  
331 Gaines and Droser, 2010). Compaction, cementation, fluid–rock interaction, and potential hypothermal  
332 and magmatic activities can also impact the quality of fossilization (Muscente et al., 2015).. Such  
333 parameters have a direct impact on reconstructing the initial form of soft-bodied organisms and deriving  
334 information on their lifestyles based on the geometric (morphologies, tracks, burrows, etc.) and chemical  
335 (organic molecules, isotopes, etc.) signatures that have been preserved.

336

### 337 *Taphonomic information from pyritization*

338 As previously presented, in the FB<sub>2b</sub> formation (El Albani et al., 2010, 2014, 2019, Aubineau et al.  
339 2019), pyritization is not specific to the body fossils but is also associated with abiotic concretions in  
340 the host black shales throughout the stratigraphic sequence. This is expected because the black shale  
341 sediments contained sufficient organic matter and iron to promote pyritization independently of the  
342 carbon origin (Canfield et al., 2013). Petrographic observations of lenticular nonpyritized specimens  
343 indicate that moulding materials are inherited from the host sediments. The similarity of the detrital and  
344 diagenetic clay materials in both the host sediments and lenticular infilling is not observed when  
345 pyritized macrofossils and their associated host sediments are compared.

346 Pyritization of soft bodies related to bacterial sulfate reduction (Gabbott et al., 2004) can occur when  
347 organic biodegradation is relatively rapid (Briggs et al., 1996) and takes place in clay-rich sediments  
348 (Farrell, 2014) under the oxic–anoxic interface (Bernier, 1984). Under these conditions, the formation of  
349 hydrogen sulfide and the occurrence of reactive iron concentration gradients in or around the labile  
350 organic matter of dead organisms (Guan et al., 2017) favour the nucleation of iron sulfide (Allen, 2002)  
351 or iron-rich clays (Petrovich, 2001). Rapid organic matter remineralization produces carbon dioxide (or  
352 methane) and water. The degradation rate is a function of several factors, such as (i) the physico-  
353 chemical properties of the sediments, (ii) the characteristics of the decomposing organic matter, and (iii)  
354 the microbial populations involved (Muscente et al., 2017). In the studied case, the coexistence of  
355 different taphonomic styles in the same sedimentary laminae cannot be explained by variations in criteria  
356 (i) and/or (ii). On the other hand, the speed of degradation can play an important role in favouring  
357 biomineralization. This mechanism depends on the biodegradability of the main molecular compounds  
358 (carbohydrates, lipids, proteins) of the organic matter (e.g., (Stankiewicz et al., 2000), i.e., their ability  
359 to be photodegraded, hydrolysed or incorporated into the biomass by serving as nutrients for  
360 microorganisms (Briggs, 1999). Rapidly decomposing organic matter, known as labile material, is easily  
361 attacked by enzymatic catabolism, and its chemical constituents are easily reused by microbial  
362 metabolism. In contrast, the organic materials that are part of the composition of structural bodies

363 (envelopes, partitions, etc.) can be recalcitrant to decomposition (e.g., Butterfield, 2003; Tegelaar et al.,  
364 1989).

365

366 ***Taphonomic information from clay minerals and their evolution during diagenesis***

367 The Francevillian biota lived in a shallow marine environment where periodically resuspended fine  
368 particles eventually sedimented into fine-grained laminae (Reynaud et al., 2018) in an oxic to suboxic  
369 water column (Aubineau et al., 2021; Canfield et al., 2013). The finely laminated horizons are composed  
370 of quartz and clay minerals associated with low amounts of dolomite and pyrite. The primary clay  
371 mineralogical assemblage of Francevillian sediments evolved differently depending on whether it was  
372 located within the preserved specimens by (i) simple compression casting or by (ii) mineralization  
373 (biogenic or abiotic). The former mechanism can be compared to the Burgess Shale-type preservation  
374 (Butterfield, 1995; Gaines et al., 2005) but without the overprint of metamorphism. Regardless of the  
375 preservation mechanism, all macrofossils are in laminae where clayey microfacies prevail in overall  
376 low-permeability rocks. This suggests a direct relationship between the nature of the original organism,  
377 its taphonomy, and the rock morphological elements that have been preserved.

378 The degree, condition, and mechanism of fossil preservation are strongly controlled by mineral  
379 transformations and/or neo-formations, particularly clay minerals (e.g., (Anderson et al., 2011; Gabbott  
380 et al., 2001; Martin et al., 2004) and associated phases (sulfides, carbonates, etc.). During early  
381 diagenesis, anoxic microenvironments develop in association with organic matter degradation; Fe<sup>2</sup> ions  
382 adsorbed on the preserved biopolymers may favour nucleation of crystals of iron(II)-rich clay minerals  
383 (berthierine or ferroan saponite), which form a coating on the organic remains and/or replace parts of  
384 the organism (Petrovich, 2001). Nevertheless, these minerals associated with both pyritized and  
385 nonpyritized specimens evolve during burial diagenesis, leading to the formation of new phases  
386 inherited from their initial chemical composition. Therefore, the specific study of these minerals is  
387 justified to reveal the conditions and mechanisms of fossil preservation in ancient sediments.

388 At the millimetre to centimetre scale of the fossil microsites and their host sediments, the dominant  
389 mechanism of clay mineral transformation associated with the early stages of preservation of  
390 Francevillian soft-bodied organisms is illitization. This authigenesis is represented first by smectite  
391 *sensu stricto* and then smectite-rich mixed-layer illite/smectite, namely, MLs. Since only a few MLs are  
392 still preserved, extensive illitization occurred. The intensity of this mechanism is primarily controlled  
393 by the potassium availability in the system (Cuadros and Linares, 1996). Considering the absence of K-  
394 feldspars and evidence of K-rich fluids in the study area, the K supply is of paramount importance. Near  
395 the surface, dissolved potassium in the overlying water column was theoretically available (Santiago  
396 Ramos et al., 2018; Sun et al., 2015). However, seawater's sodium concentration and ionic strength are  
397 not very favourable for direct solid-solution exchange and absorption of potassium in the interlayer  
398 spaces of swelling minerals (smectites and illite/smectite mixed layers). Alternatively, potassium may

399 have been supplied by the degradation of MRSs that naturally fixed K for cellular machinery (Aubineau  
400 et al., 2019). The latter mechanism, in the marine environment, has long been known to regulate  
401 microorganism growth and cellular osmotic pressure (Rhoads and Epstein, 2003) and to collaborate in  
402 many metabolic reactions, such as protein synthesis and enzyme activation (Stautz et al., 2021). Thus,  
403 a similar mechanism of K concentration can be argued for bacteria that degrade the organic matter of  
404 dead organisms, which is the most plausible explanation. In this case, heterotrophic microbial respiration  
405 degrading the organic matter would have promoted K release and concentration in the interstitial pore  
406 waters of the unconsolidated sediments. This K increase would have favoured the conversion of swelling  
407 smectite into MLs in the early stages of burial and, ultimately, illite, which would correspond to induced  
408 biogenic mineralization. Despite the presence of K in the marine system, in both cases, the end of  
409 bacterial activity stopped K accumulation in the preserving microsystem and thus reduced the illitization  
410 mechanism.

411 Illitization is a general mineral transformation that affects both the host sediments and the studied  
412 specimens. This mechanism involves the transformation of MLs into MLi as transitional phases and  
413 then into illite. Nevertheless, the degree of this transformation is variable regarding the proportion of  
414 illite–MLi–MLs phases. When the K content was sufficient, the MLi could be completely transformed  
415 into illite-like and/or illite phases. However, here, all samples have remaining MLs and/or MLi. In the  
416 case of the nonpyritized fossils, illitization was not achieved, as testified by the preservation of  
417 illite/smectite mixed layers (MLs) and the lower illite/MLi ratio. The same occurred in the pyritized  
418 specimens, but illitization was more intense, i.e., a higher illite/MLi ratio, except for segmented forms.  
419 For other forms, the host sediments present higher illite/MLi ratios than fossils, while the pyrite  
420 concretions show MLi that is very enriched in K and a higher illite/MLi ratio. These heterogeneous  
421 results highlight that each fossil represents a microsystem whose location, nature and rate of degradation  
422 influence the availability of potassium, controlling the intensity of illitization.

423 The illitization mechanism was followed by chloritization, as shown by the development of secondary  
424 chlorites from the microcrystalline illitic matrices and/or recrystallized MLi in “accordion-like”  
425 structures. The presence of many chlorite shapes is due to the mixing of primary and secondary phases  
426 (Fig. 10). In the fossils, ovoids and laths are observed in low amounts on the outer rims associated with  
427 reduced porosity and are absent in the central part. Conversely, “accordion-like” structures and radial  
428 shapes are much more abundant in the central parts of the pyritized specimens but absent in the  
429 nonpyritized circular forms.

430 In host sediments and fossils, chlorite shapes indicate different origins. Ovoid forms are clearly detrital.  
431 The other shapes are probably secondary products from direct precipitation (fibroradial) or from  
432 transformation of a precursor (accordion-like shapes). In the latter case and in the illitic clay matrix,  
433 chloritization seems to be developed at the expense of the smectitic part of the clay phases and  
434 encapsulates residual S–MLs–MLi. Under these conditions, both transformation and

435 dissolution/precipitation mechanisms are probably involved. In contrast, in the concretions,  
436 chloritization results from direct precipitation in a free pore space, leading to the development of  
437 chlorite-dolomite paragenesis in the intergranular porosity. Regardless of the study area, chloritization  
438 occurred after the early phase of illitization and during burial diagenesis, benefiting from fluid  
439 circulation that supplied the necessary Fe and Mg.

440

#### 441 *Towards a taphonomic conceptual model*

442 Our results allow us to summarize the taphonomic history by a conceptual model (Fig. 11), describing  
443 the fossilization stages of each type of specimen within a microsystem.

444 After their death, the specimens are deposited on clayey sediment that is mainly composed of quartz,  
445 clay minerals, small amounts of dolomites and pyrite. The specimens are quickly buried within specific  
446 microenvironments, where all of the fossilization mechanisms take place. In this way, lenticular  
447 specimens undergo nonpyritized fossilization, while the lobed, segmented and tubular forms are  
448 pyritized.

449 After decomposition of the organism's body, lenticular forms are trapped in a sediment that is still loose  
450 but coherent enough to maintain the mould. The voids left by decomposition are progressively filled by  
451 particles via size sorting, favouring a high concentration of fine material within the specimen.

452 The mode of fossilization of the pyritized forms is approximately identical. After their deposition, the  
453 specimens are degraded progressively by sulfate-reducing bacteria during burial activity. The  
454 conservation of the specimens is conditioned by the speed of degradation of the internal structures and  
455 favoured by the bacterial activity. Early pyritization permits 3D preservation of each specimen.

456 After this early stage of fossilization, a secondary diagenetic overprint participates in the stabilization  
457 of the specimens. This is represented by the illitization of the smectitic phases. This illitization is  
458 controlled by the availability of K and the permeability of each microsystem. Due to the high  
459 concentration of finer materials, nonpyrite specimens present microsystems in which exchanges with  
460 the outside are more reduced compared to pyrite specimens and concretions. The intensity of the  
461 illitization reaction increases progressively from the nonpyritic forms to the abiotic concretions through  
462 the pyritic specimens. These microsystems are later subjected to generalized chloritization, reflecting  
463 the circulation of fluids rich in Fe and Mg. Abiotic pyrite concretions are formed during late diagenesis.

464 As summarized here, our data provide robust evidence that clay minerals, such as smectite, illite,  
465 illite/smectite mixed layers, and chlorite, can be used as indicators for the physico-chemical changes  
466 that occur at the local scale during the preservation of soft-bodied organisms.

467 **6. Conclusion**

468 The 2.1 Ga Francevillian fossils preserved in black shales show two early preservation modes  
469 corresponding to moulding/compression and pyritization. In the pore spaces of the sediments and fossils,  
470 the mechanisms of clay transformation associated with the evolution of the system are successively  
471 illitization and chloritization. The intensity of these processes and the habit of the authigenic clay  
472 minerals depend on the degree of porosity and key element availability, such as K. Thus, the intensity  
473 of illitization at the early stage differs between the sediment, pyritized and nonpyritized fossils and pyrite  
474 concretions of the same age. The potassium availability may have been controlled by the microbial  
475 activity of bacterial mats everywhere in the black shale levels, leading to the biodegradation of organic  
476 matter from soft bodies. In this scheme, each fossil represents a microsystem. At a late stage,  
477 chloritization begins, and its intensity is determined by the contents of soluble iron and magnesium from  
478 fluid circulation.

479 In the same depositional setting, we observe heterogeneous clay mineralogical assemblages, depending  
480 on the presence or absence of organic matter remains. We also observe contrasting clay mineralogy by  
481 comparing biotic and abiotic pyritized specimens. In fact, preservation (moulding and pyritization)  
482 occurred within microsites, whose properties significantly impacted the clay mineral reactions, which  
483 cemented the pore spaces and thus contributed to the final fossilization. Fossil microsites must be  
484 considered microsystems that have undergone physical and chemical changes that are different from  
485 those of their immediate surrounding environment, which is similar to additional indirect evidence of  
486 the existence of biological remains encapsulated in the sediment. These data could represent a diagnostic  
487 tool for detecting traces of life in rocks from the early Earth.

488

489

490 **Author Contributions:** A.E.A. designed the research. A.E.A., J.N.I., C.F and F.B. wrote the  
491 manuscript. A.E.A, J.N.I, O.B., A.T and C.L. did the field work. J.N.I., C.F., A.M., A.A.E., A.R. and  
492 A.E.A. prepared the samples and performed XRD analyses and models. L.R., A.C.W. Performed Re/Os  
493 datations.

494

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510 **Table 1** – Ratios of areas of  $d_{001}$  reflections of illite/mica and illite/smectite mixed-layers  
511 rich in illite, measured from diffractogram patterns of air-dried oriented preparations.

Host sediment and specimen associated		Illite (10.0 Å) (cts. °2 $\theta$ )	MLi ( $\approx$ 10.5 Å) (cts. °2 $\theta$ )	Major peak area
				Ratio Aillite/AMLi
Circular (R)	max.	469	3774	0.12
	min.	215	3654	0.06
Lobated (L)	max.	658	2719	0.24
	min.	118	1100	0.11
Segmented (S)	max.	1540	3664	0.42
	min.	41	2303	0.02
Tubular (T)	max.	1475	1432	1.03
	min.	578	2706	0.21
Concretions (Co)	max.	119	42	2.85
	min.	427	1603	0.27

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514 **Table 2** – Semi-quantitative overview of the mineralogy of the clay phases based on XRD analysis  
515 and deconvolution of diffractograms. Empty circles: traces.

		Smectite s.s.	MLs	MLi and Illite like	Illite s.s. Mica
Host rock		○	○	●●	●●●
Lenticular fossil	<i>non pyritized</i>	●●	●●●	●●●●	○
Lobate fossil	<i>pyritized</i>	●	●●	●●●	●
Segmented fossil	<i>pyritized</i>	●	●●	●●●●	○

Tubular fossil	<i>pyritized</i>	•	••	••	•
Concretions	<i>pyrite</i>		•	•	••

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519 **Figure 1** – Geological map of the Françoise Basin (Gabon).  
520 **Figure 2** – Geological section showing the structure and the lithostratigraphic sequence of the  
521 Françoise deposits on the northern edge of Mvengué syncline.  
522 **Figure 3** – Lithostratigraphy of the studied section (Moulendé quarry).  
523 **Figure 4** – Photographs showing the spatial relations between: **A**) pyritized lobate (pl) and non-  
524 pyritized lenticular shaped specimens. Arrows represent at top left a lenticular-shaped specimen and  
525 pyritized specimen at the right side. **B**) top view and **C**) cross section of unpyritized lenticular-shaped  
526 specimen. Arrows represent a sharp limit between a lenticular-shaped specimen and host-sediment.  
527 **D**) pyritized round lobated shapes, **E**) pyritized oval lobated shape, **F**) cross-section of a pyritized  
528 lobated shape. Arrows represent a sharp limit between the pyritized specimen and host-sediment with  
529 the evidence of pre-compaction. **G**) simple tubular shape, **H**) bifid tubular shape, **I**) cross-section of  
530 tubular shape. Abbreviations: (SP) specimen, (BS) black shale. Scale 1 cm.  
531 **Figure 5** – Photographs showing: **A**) pyritized segmented shape in contact with the bacterial mat  
532 (arrow), **B**) cross-section of segmented shape. Arrow represent the sharp and pre-compactional limit  
533 between specimen and host-sediment. **C**) Fairy ring structure type of bacterial mat (Aubineau et al  
534 2018), **D**) plated coarse pyrite concretion, **E**) top view and **F**) cross-section of nodular pyrite  
535 concretion. Arrow represent the contact between coarse pyrite crystals cross-cutting the host-sediment.  
536 Abbreviations: (SP) specimen, (BS) black shale host. Scale 1 cm.  
537 **Figure 6** – **A**) Powder diffractograms showing bulk mineral composition of the host sediments and  
538 non pyritized macro-fossils (circulars), **B**) Diffractograms of oriented air-dry preparations **C**)  
539 Diffractograms of oriented preparations after ethylene glycol solvation. Minerals: (C) Chlorite, (Do)  
540 Dolomite, (I/M) illite and/or Mica, (MLi) Mixed-layer illite-rich, (MLs) Mixed-layers smectite-rich,  
541 (Py) Pyrite, (Q) Quartz.  
542 **Figure 7** – **A**) Powder diffractograms showing the bulk mineral composition of the host sediments and  
543 pyritized macro-fossils (lobates, tubulars and segmenteds), **B**) Diffractograms of oriented air-dry  
544 preparations **C**) Diffractograms of oriented preparations after ethylene glycol solvation. Minerals: (C)  
545 Chlorite, (Do) Dolomite, (I/M) illite and/or Mica, (MLi) Mixed-layer illite-rich, (MLs) Mixed-layers  
546 smectite-rich, (Py) Pyrite, (Q) Quartz, (Sm) Smectite.  
547 **Figure 8**– **A**) Powder diffractograms showing the bulk mineral composition of the host sediments and  
548 concretion, **B**) Diffractograms of oriented air-dry preparations and **C**) Diffractograms of oriented  
549 preparations after ethylene glycol solvation. Minerals: (C) Chlorite, (Do) Dolomite, (I/M) illite and/or  
550 Mica, (MLi) Mixed-layer illite-rich, (MLs) Mixed-layers smectite-rich, (Py) Pyrite, (Q) Quartz, (Sm)  
551 Smectite.  
552 **Figure 9** – Examples of diffractograms deconvolution obtained with air-dried oriented preparation of:  
553 **(A)** host sediment, **(B)** macrofossil samples, and **(C)** concretion. Distribution of clay minerals

554 proportions in quaternary plot with illite (I), Chlorite (C), Mixed-layers smectite-rich (MLs) and  
555 illite-rich (Mli) end-members. Minerals: (C) Chlorite, (I) Illite and (MLi) Mixed-layers illite-rich  
556 and/or illite-like, (MLs) Mixed-layers smectite-rich.

557 **Figure 10** – Micrographs in backscattered electron (BSE) of the host sediments (**A, B, C, D**), non-  
558 pyritized macrofossils (**E**), infilling of intergranular porosity of pyritized macrofossils (**F, G**), and  
559 infillings of intergranular porosity of plated (**H**) and nodular (**I**) pyrite concretions. Abbreviations: (C)  
560 Chlorite, (Do) Dolomite, (IM) Illite/Mica, (MA) Undifferentiated Clay Matrix, (Py) pyrite, (Q) Quartz.

561 **Figure 11** – Conceptual model illustrating the taphonomy and mechanisms of mineralization during  
562 burial diagenesis.

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565 **Figure 1:**

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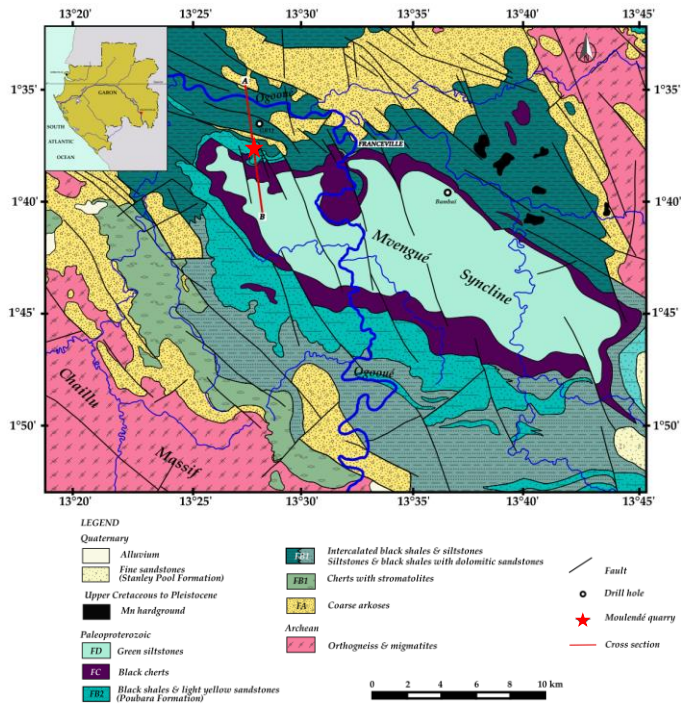
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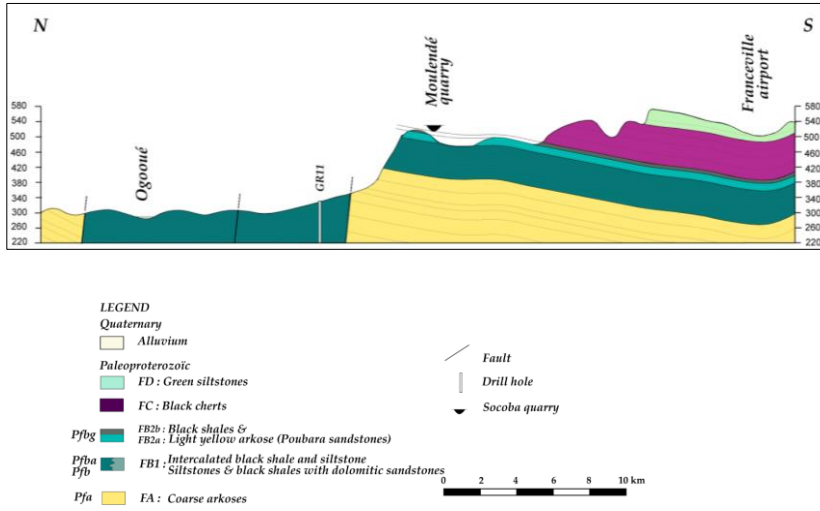
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582 **Figure 2**

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584 **Figure 3**

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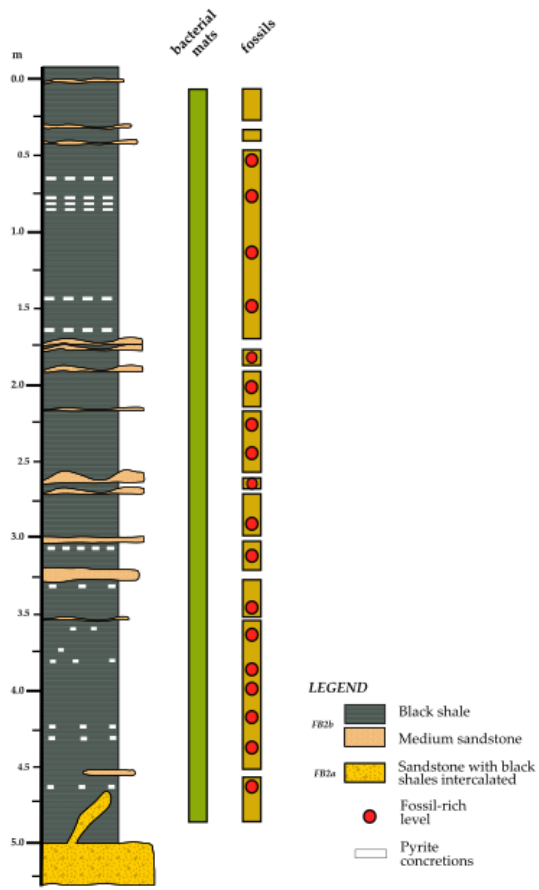
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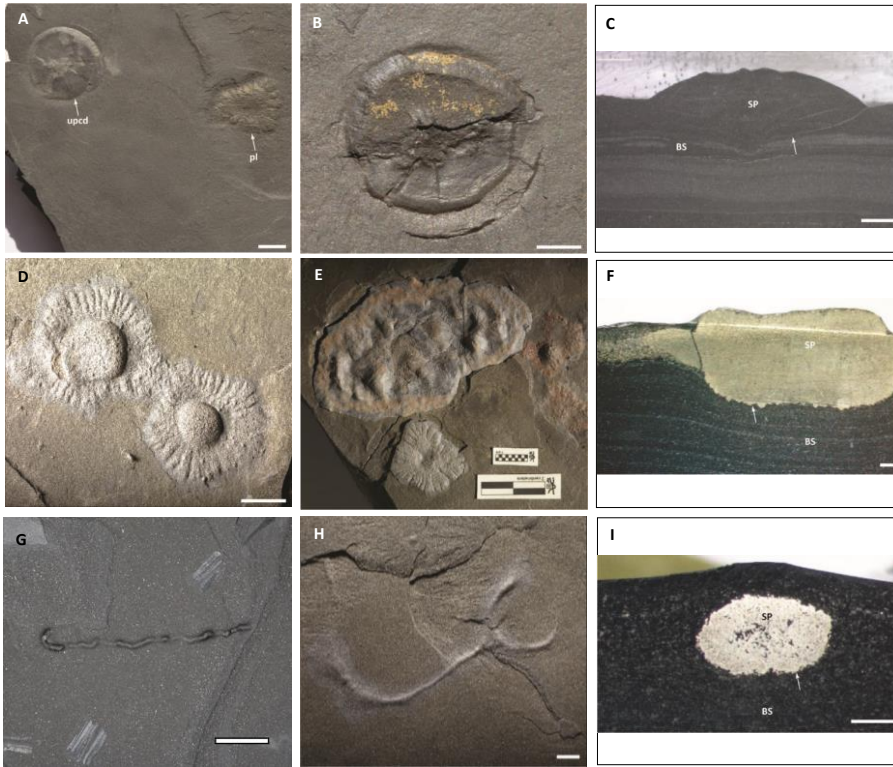
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613 **Figure 4**



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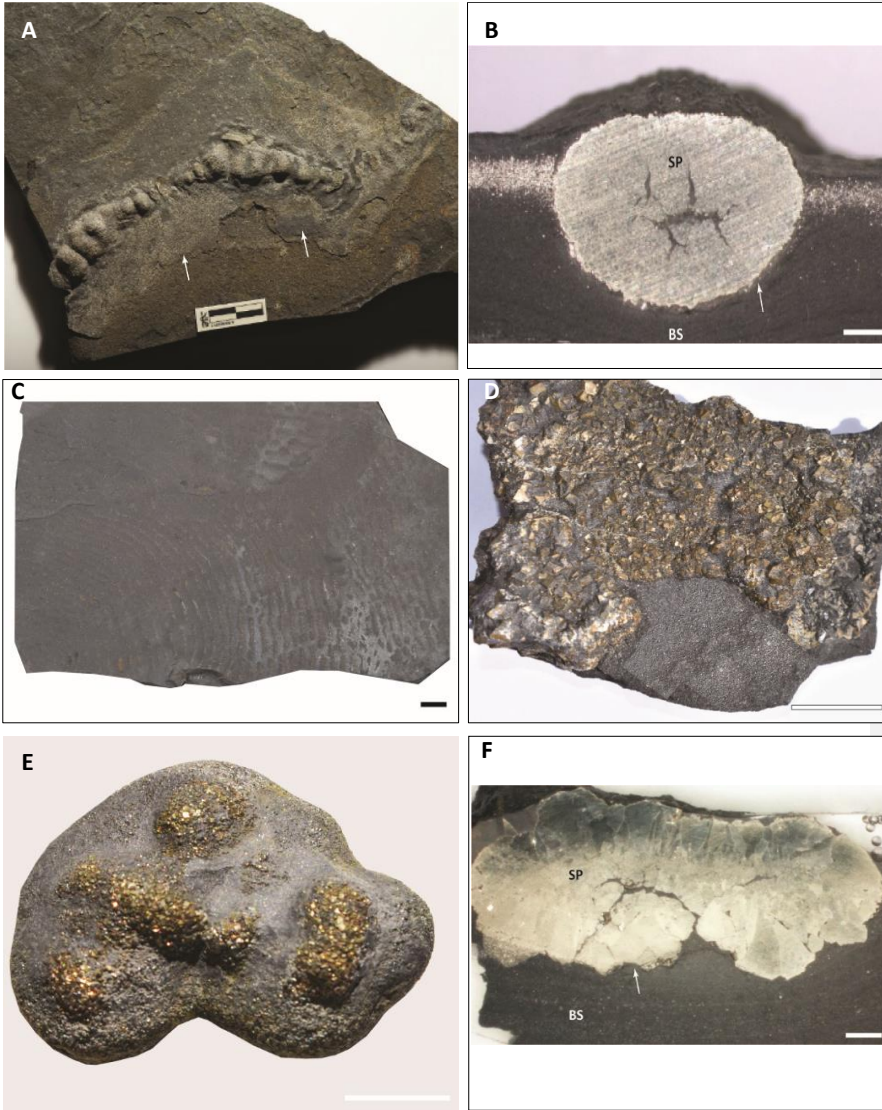
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626 **Figure 5**



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632 **Figure 6:**

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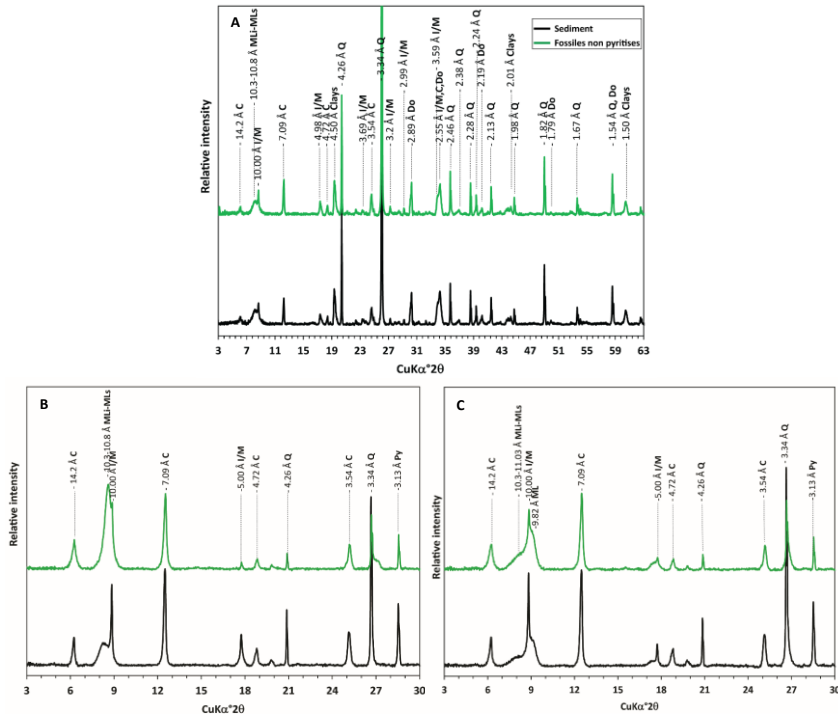
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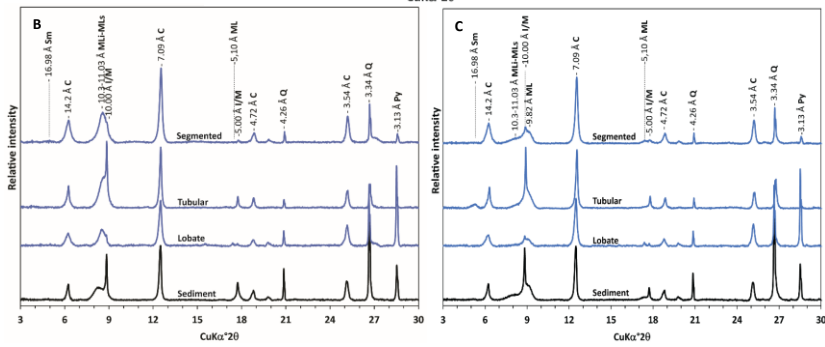
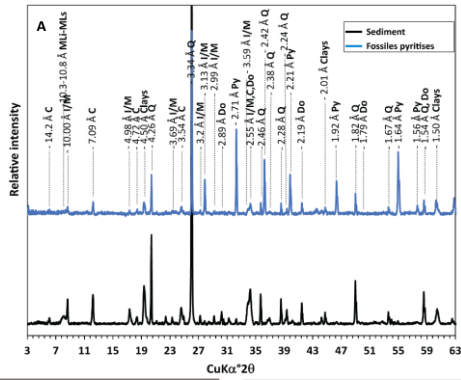
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642 **Figure 7:**

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654 **Figure 8:**

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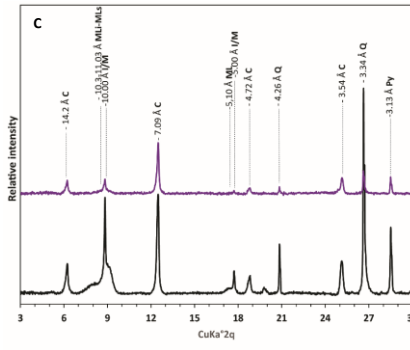
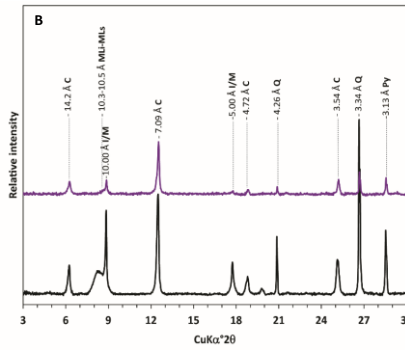
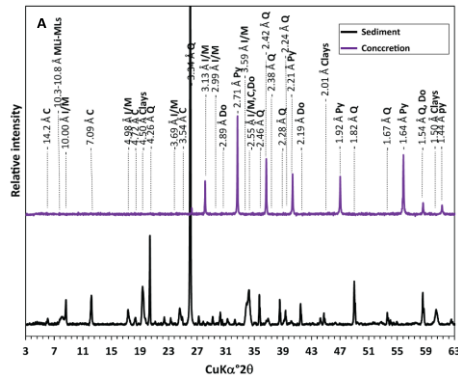
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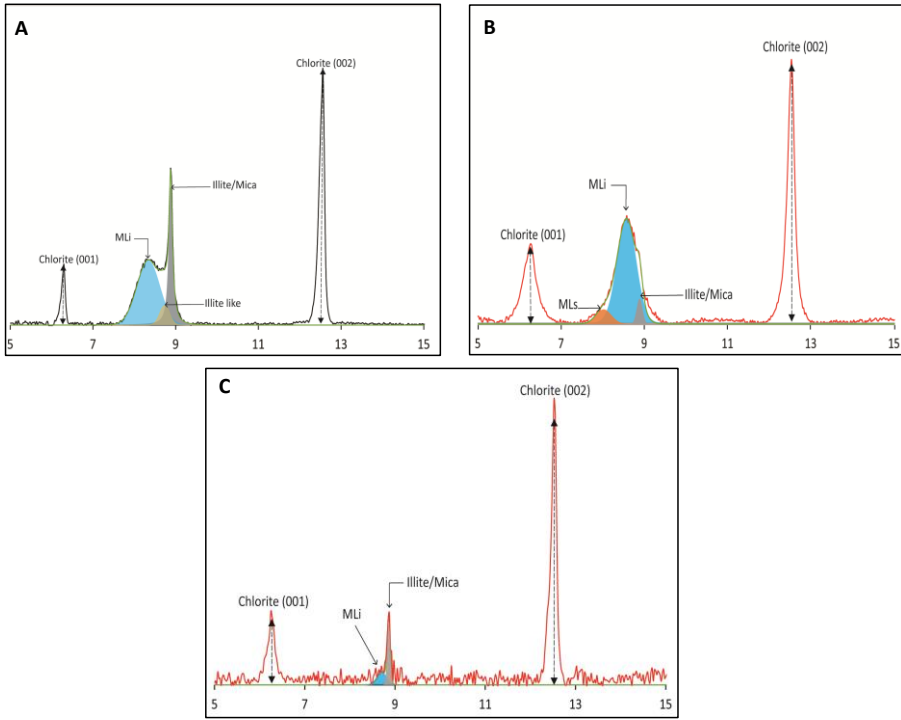
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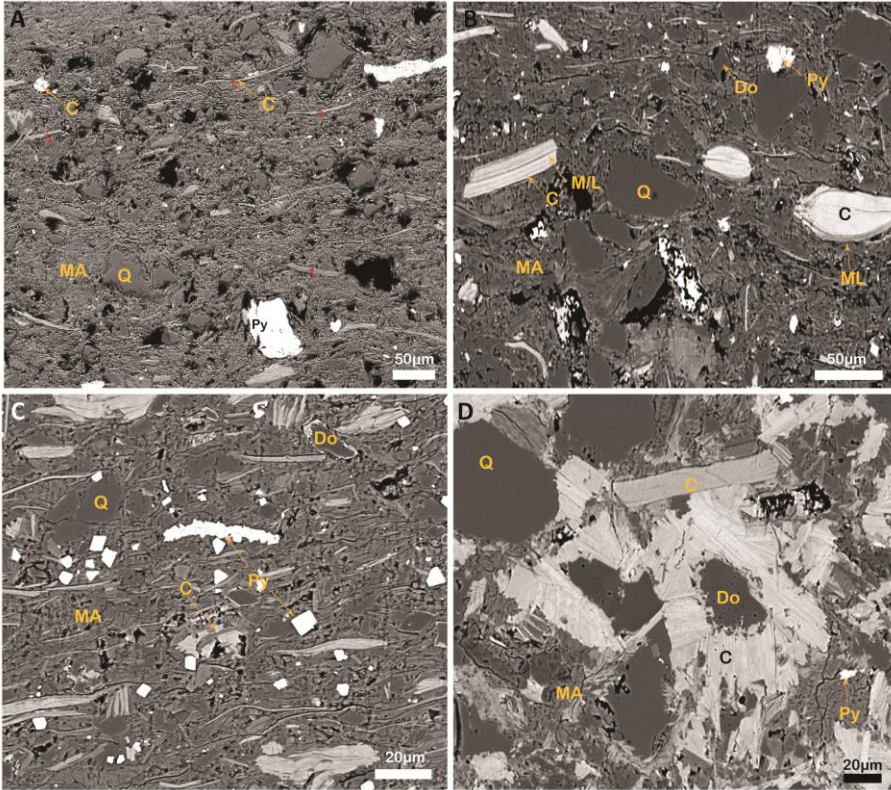
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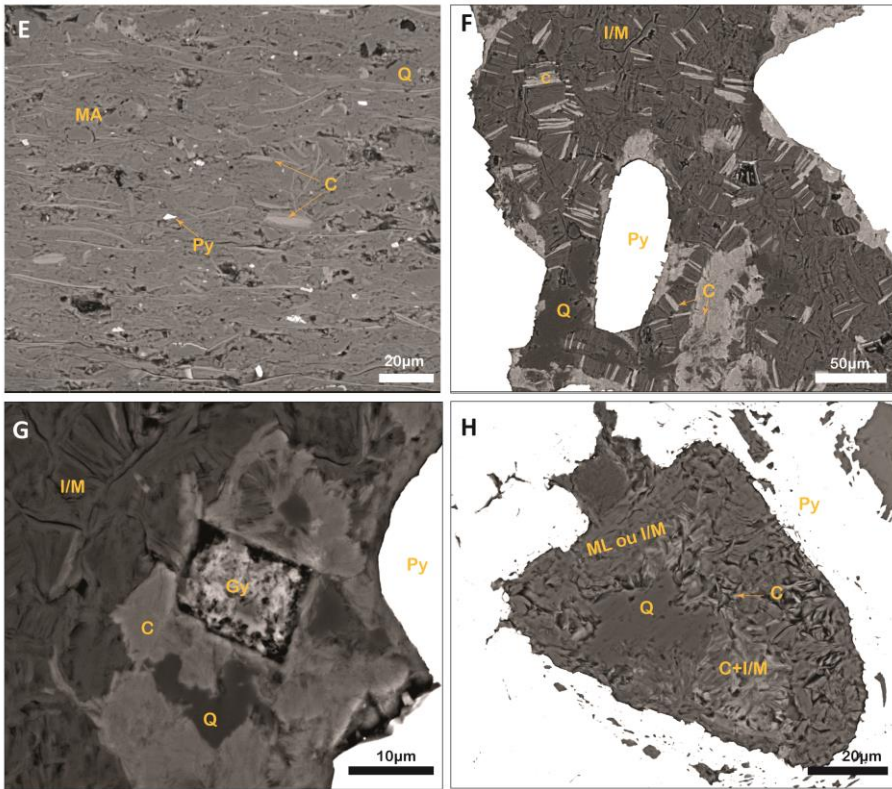
669 **Figure 10:**

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672 **Figure 11 (Suite)**



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675 **Figure 11 (suite)**

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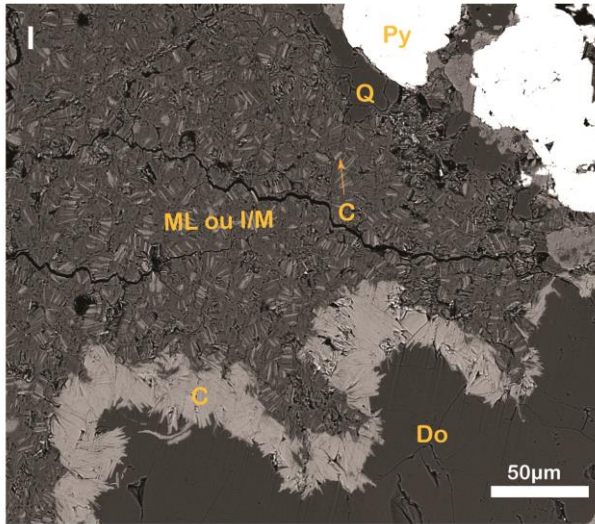
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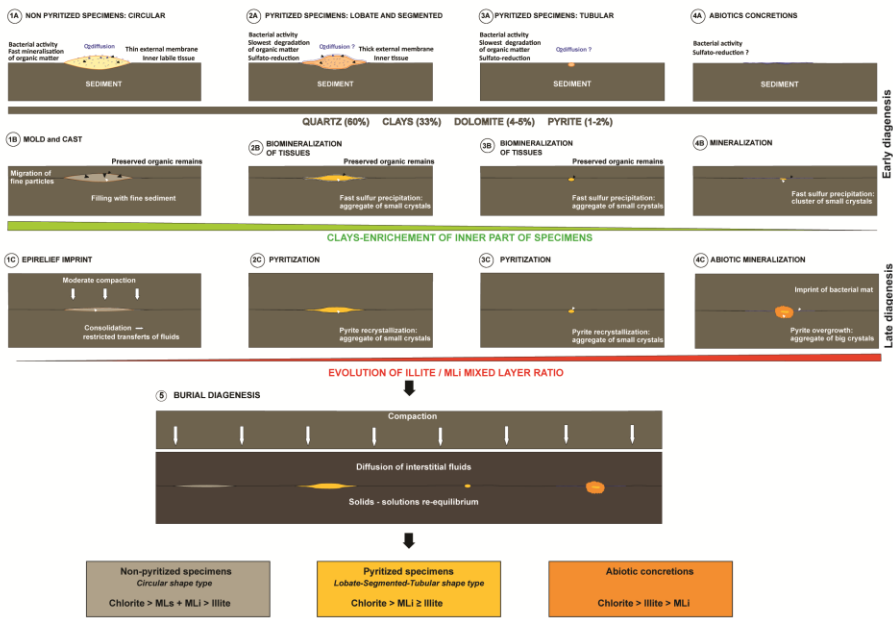
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698 **Figure 12**

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702 **References**

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