



**HAL**  
open science

## **A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas**

Farid Saleh, Orla Bath-Enright, Allison C Daley, Bertrand Lefebvre, Bernard Pittet, Antoine Vite, Xiaoya Ma, M Gabriela Mángano, Luis A Buatois, Jonathan B Antcliffe

### ► To cite this version:

Farid Saleh, Orla Bath-Enright, Allison C Daley, Bertrand Lefebvre, Bernard Pittet, et al.. A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas. *Earth and Planetary Science Letters*, 2021, 569, pp.117061. 10.1016/j.epsl.2021.117061 . hal-03433555

**HAL Id: hal-03433555**

**<https://hal.science/hal-03433555>**

Submitted on 17 Nov 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **A novel tool to untangle the ecology and fossil preservation knot**  
2 **in exceptionally preserved biotas**

3 Farid Saleh<sup>1,2\*</sup>, Orla Bath-Enright<sup>3</sup>, Allison C. Daley<sup>3</sup>, Bertrand Lefebvre<sup>4</sup>, Bernard Pittet<sup>4</sup>,  
4 Antoine Vite<sup>4</sup>, Xiaoya Ma<sup>1,2,3</sup>, M. Gabriela Mángano<sup>6</sup>, Luis A. Buatois<sup>6</sup>, and Jonathan B.  
5 Antcliffe<sup>3</sup>

6 <sup>1</sup>*Yunnan Key Laboratory for Palaeobiology, Institute of Palaeontology, Yunnan University,*  
7 *Kunming, China*

8 <sup>2</sup>*MEC International Joint Laboratory for Palaeobiology and Palaeoenvironment, Institute of*  
9 *Palaeontology, Yunnan University, Kunming, China*

10 <sup>3</sup>*Institute of Earth Sciences, University of Lausanne, Géopolis, CH-1015 Lausanne,*  
11 *Switzerland*

12 <sup>4</sup>*Université de Lyon, Université Claude Bernard Lyon1, École Normale Supérieure de Lyon,*  
13 *CNRS, UMR5276, LGL-TPE, Villeurbanne, France*

14 <sup>5</sup>*Centre for Ecology and Conservation, University of Exeter, Penryn, UK*

15 <sup>6</sup>*Department of Geological Sciences, University of Saskatchewan, Saskatoon SK S7N 5E2,*  
16 *Canada*

17

18 **Abstract**

19 Understanding the functioning of extinct ecosystems is a complicated knot of ecological,  
20 evolutionary, and preservational strands that must be untangled. For instance, anatomical and  
21 behavioral differences can profoundly alter fossilization pathways. This is particularly true in  
22 exceptionally preserved soft-bodied biotas that record the earliest phases of animal evolution  
23 during the Cambrian Explosion and the Ordovician Radiation. Herein, a novel method of data  
24 partitioning based on probabilistic modelling is developed to examine these processes for the  
25 Walcott Quarry, Burgess Shale, Canada (510Ma), and the Fezouata Shale, Morocco (c.  
26 475Ma). The modelling shows that the mechanism for soft-tissue preservation in the Walcott  
27 Quarry is ecologically selective, favoring the endobenthos. This is not found in the Fezouata  
28 Shale. Taken in concert with bioturbation data, a new model of comparative preservation is  
29 developed based on sedimentary flow dynamics. This suggests that during the Cambrian

30 Explosion and Ordovician Radiation the most exceptional fossils sites must still be calibrated  
31 against each other to understand the unfolding evolutionary events and the ecological  
32 structuring of ancient animal communities.

33

34 Keywords: ecology, evolution, soft-tissue preservation, taphonomy

35 Corresponding author (\*): Farid Saleh (farid.nassim.saleh@gmail.com)

## 36 1. INTRODUCTION

37 Early animal communities from the Cambrian and the Ordovician are some of the most  
38 complete in the fossil record, with exceptional fossilization of soft tissues giving a  
39 comprehensive view of faunal diversity during the Cambrian Explosion and the Ordovician  
40 Radiation. The Walcott Quarry (Miaolingian, Wuliuan, Cambrian, Burgess Shale, Canada)  
41 bears a diverse assemblage of soft-bodied animals preserved in minute details (Nanglu et al.,  
42 2020). More than 100 genera have been described from the Walcott Quarry, helping to  
43 resolve the enigma of metazoan origins in the Cambrian (Daley et al., 2018; Nanglu et al.,  
44 2020). The Fezouata Shale offers a more complete view of the transition between the  
45 Cambrian Explosion and the Ordovician Radiation than was previously known (Van Roy et  
46 al., 2010).

47 The Walcott Quarry and the Fezouata Shale share the same Burgess Shale-type (BST)  
48 mode of preservation defined by carbonaceous compressions (Gaines et al., 2008; Saleh et al.,  
49 2020a). Accessory authigenic mineralization (i.e., pyritization, phosphatization) may occur  
50 but this remains secondary to carbonaceous compressions (Gaines et al., 2008; Gaines, 2014;  
51 Saleh et al., 2019, 2020b-c). Preservation was aided by rapid sediment influx (Gaines, 2014).  
52 Clay minerals may have facilitated the exceptional preservation of soft tissues by slowing  
53 down bacterial decay (McMahon et al., 2016; Anderson et al., 2018, 2020; Saleh et al., 2019).  
54 The general conditions for BST preservation are broadly shared between the Fezouata Shale  
55 and the Walcott Quarry (Saleh et al., 2020a); yet important abiotic and biological differences  
56 exist. For instance, the Fezouata Shale is a wave-dominated shallow-marine polar  
57 environment (70-100m), whereas the Walcott Quarry is deposited at the bottom of an  
58 escarpment in a tropical sea (Martin et al., 2016; Vaucher et al., 2016, 2017; Saleh et al.,  
59 2021a). While the Fezouata Biota shares some taxa with Cambrian ecosystems (e.g.,  
60 marrellomorphs, radiodonts, and lobopodians), the general faunal composition of the  
61 Ordovician site is markedly different from that of the Walcott Quarry (Van Roy et al., 2015a;  
62 Lefebvre et al., 2016, 2019).

63 Assemblage discrepancies between fossil sites are influenced by many factors: ecology,  
64 evolution, preservation, and even collection bias (Brasier et al., 2011). This is a broad-scale

65 problem in palaeontology that impacts all time intervals across the whole gamut of  
66 evolutionary scenarios from the origin of life to the diversification of hominids (Saleh et al.,  
67 2020b). Using abundance data and alpha diversity metrics is the traditional approach for  
68 palaeoecological reconstructions (Caron and Jackson, 2008; Saleh et al., 2018; Whitaker and  
69 Kimmig, 2020). However, at many sites, these data can be skewed by collection bias caused  
70 by government rules, economic value, and scientific interest (Brayard et al., 2011). Even with  
71 rarefaction indices (Caron and Jackson, 2008; Nanglu et al., 2020), it is almost impossible to  
72 quantify the effect that these biases have on raw taxon abundance data. When trying to  
73 understand fossil preservation, a better approach is one based on occurrences rather than  
74 abundances as some taxa have tissues that are more likely to be preserved (e.g., mineralized  
75 brachiopods) in the fossil record than other taxa (e.g., soft jellyfish), introducing a  
76 preservational bias. Moreover, because most taxa have more than one tissue type, it is best to  
77 separate the preservation variable by comparing tissue types between fossil sites. Recent  
78 probabilistic modelling of genus distributions and combinations of preserved tissue types has  
79 shown considerable advantages over traditional approaches (Saleh et al., 2020b). Probability  
80 models showed the preservation of anatomical structures in the Walcott Quarry and the  
81 Fezouata Shale are significantly different (Saleh et al., 2020b), and the Fezouata Shale did not  
82 preserve entirely cellular organisms (e.g., the body walls of chordates; internal organs such as  
83 digestive and nervous tissues) (Saleh et al., 2020b). It is likely the animals were dead and  
84 decaying on the seafloor prior to their burial in the Fezouata Shale (Saleh et al., 2021b), and  
85 cellular structures in contact with the water column are the fastest to decay (MacGabhann et  
86 al., 2020; Saleh et al., 2020b). Herein, this methodology is expanded upon by incorporating  
87 data on ecological strategies, to investigate the effect of habitat on fossilization.  
88 Consequently, the interplay of taxonomy, preservation, and ecology is analytically  
89 approached using the Walcott Quarry and the Fezouata Biota as separate, and then  
90 comparable case studies. This quantification allows a separation of ecological and  
91 preservation effects helping to form a clearer picture of the dawn of animal life in the early  
92 Palaeozoic.

93

## 94 2. MATERIAL AND METHODS

95 The data matrices for the generic composition and biological tissue occurrences [i.e.,  
96 biominerals (A) such as brachiopod shells, sclerites (B) such as the headshield of some  
97 arthropods, cuticle formed of polysaccharides (C) such as the body walls of priapulids,  
98 cellular body walls (D) as in cambroernids, and internal organs (E) such as digestive and  
99 nervous systems] in the Walcott Quarry and the Fezouata Shale were taken from a previously  
100 published database (Saleh et al., 2020b) based on the collections of the University of Lyon  
101 (France), the University of Marrakech (Morocco), and the University of Lausanne  
102 (Switzerland), the Royal Ontario Museum (Canada), and the Peabody Museum (USA). Taxa  
103 were separated between mode of life categories (i.e., endobenthic, nektobenthic/epibenthic,  
104 planktonic/nektonic) based on the literature (Caron and Jackson, 2008; O'Brien and Caron,  
105 2015; Nanglu et al., 2020) and our own experience. Raw data is provided in the  
106 Supplementary Material 1.

107         The number of times each of the different possible tissue type combinations occurred  
108 was identified. Tissue types can occur alone without other tissues as A, B, C, D, or E; and in  
109 one of ten possible pairs: AB, AC, AD, AE, BC, BD, BE, CD, CE, and DE. There are also 10  
110 different possible three-set intersections ABC, ABD, ABE, ACD, ACE, ADE, BCD, BCE,  
111 BDE, and CDE. Finally, there are five different possible associations of four-set intersections  
112 ABCD, ABCE, ABDE, ACDE, BCDE, and one five-set combination ABCDE, for a total of  
113 31 possible combinations. A simple calculation of the number of taxa belonging to each  
114 category introduces a bias in the dataset because each count of a higher-order intersection  
115 leads to multiple counts of lower-order intersections. For example, finding an ABC  
116 combination causes a count of the AB, AC, and BC categories and consequently, one taxon is  
117 counted 4 times. This has to be removed from the data in order to find unique character  
118 combinations. This problem can be solved on a five-set Venn diagram and the unique  
119 associations can be obtained (Table 1). Automating the process for a five-fold set problem is  
120 challenging and software and computational programs are generally limited to solving single

121 four-set problems (Chen and Boutros 2011) or solving the five-set problem indirectly by  
 122 moving to probability densities of multiset intersections (Wang et al. 2015). It is worth noting  
 123 here that two of the characters in this analysis are biologically mutually exclusive (C and D;  
 124 an organism cannot be cuticularized and non-cuticularized) so the problem simplifies  
 125 somewhat to two intersecting four-fold problems, as CD and all its subsets are empty.  
 126 Consequently, the five-way intersection ABCDE is impossible. Further subsets of C∩D that  
 127 are also empty are A∩C∩D, B∩C∩D, C∩D∩E, A∩C∩D∩E, A∩B∩C∩D, and B∩C∩D∩E.  
 128 Hence, the problem is reduced from 31 to 23 intersections and the highest intersections that  
 129 can have a value are A∩B∩C∩E and A∩B∩D∩E and these can be found directly in the  
 130 dataset. These values can then be used to calculate the number of taxa that preserve three  
 131 tissue types because of the identity:

$$132 \quad X \cap Y = X \cap Y \cap Z' + X \cap Y \cap Z$$

133 With Z' being everything but Z (X∩Y∩Z' is the association of X and Y with any other tissue  
 134 type except Z). The equation can be rearranged as:

$$135 \quad X \cap Y \cap Z' = X \cap Y - X \cap Y \cap Z$$

136 Thus, knowing a value for A∩B∩C∩E and for instance A∩B∩C we can calculate the desired  
 137 value of A∩B∩C∩E'. Using the identity:

$$138 \quad A \cap B \cap C = A \cap B \cap C \cap E + A \cap B \cap C \cap E'$$

139 Which can be simply rearranged to:

$$140 \quad A \cap B \cap C \cap E' = A \cap B \cap C - A \cap B \cap C \cap E$$

141 In this equation, an unknown exclusive three tissue type association (A∩B∩C∩E') can be  
 142 calculated from two known quantities which can be recovered directly from the database. It is  
 143 then trivial to extend this to all the other possible three variable intersections with the  
 144 corollary that some intersections require the subtraction of both of the four variable

145 intersections if the three-set intersection contains subsets of both of the four variable  
146 intersections. For instance:

$$147 \quad A \cap B \cap E \cap C' \cap D' = A \cap B \cap E - (A \cap B \cap C \cap E + A \cap B \cap D \cap E).$$

148 Once the unique associations of three variables are known they can be used, following similar  
149 logic, to calculate all the unique two-variable intersections (e.g.,  $A \cap B \cap C' \cap D' \cap E'$ ) and  
150 finally, the one variable intersections (e.g.,  $A \cap B' \cap C' \cap D' \cap E'$ ).

151 A manual approach would be highly prone to error due to the high number of taxa and  
152 data entries. Thus, this method has been automated in a single Excel file that contains all of  
153 the formulae above such that future analyses need only to construct the data matrix, with data  
154 analyses proceeding automatically. This approach is quicker and more reliable, providing  
155 numerous opportunities to cross-check the data: the sum of the values of all 23 subsets; equal  
156 number of taxa for all calculations; no empty taxa coding;  $C \cap D$  intersections remain zero.

157 The data is then analyzed as a discrete probability distribution. The total number of  
158 genera having just one character (i.e., A, or B, or C, or D, or E) was plotted against the  
159 number of genera that have pairs (e.g., AB), threes (e.g., ABC), or fours (e.g., ABCE) for all  
160 modes of life in the Walcott Quarry and the Fezouata Shale (Fig. 1a, b). The probability of  
161 occurrences  $P(A)$ ,  $P(B)$ ,  $P(C)$ ,  $P(D)$ , and  $P(E)$  was calculated (Table 1) by taking the set value  
162 for “A” and dividing by  $n$  to obtain  $P(A)$ . The average number of tissue types per genus, as  
163 derived from the dataset, was then calculated by adding these probabilities for each mode of  
164 life in each biota (Table 1).

165 To examine how exceptional preservation differs between modes of life, further  
166 analyses focused on the preservation of soft tissue (E) because all animals have internal  
167 tissues and so this category must have been present during the life of the organism (whereas  
168 this is not true for all the other categories, for example, it is possible to have no biominerals).  
169 The association of soft internal organs (E) with other structures was investigated for all tissue-  
170 type categories in the Fezouata shale and the Walcott Quarry. This is achieved by examining



171 conditional probabilities in the subset of A. For example, the probability that a taxon with a  
172 biomineral also having preserved internal organs/tissues ( $p(E|A)$ ).

$$173 \quad P(E|A) = (A \cap E + A \cap B \cap E + A \cap C \cap E + A \cap D \cap E + A \cap B \cap D \cap E + A \cap B \cap C \cap E) / A$$

174 The reverse conditional approach of finding A given that E has occurred  $p(A|E)$  was  
175 also calculated, following a similar logic (automated in the Supplementary Material 2).

176 In order to investigate the role of mode of life on fossil preservation the data was then  
177 partitioned using mode of life categories. This allows a direct link between exceptional  
178 preservation of internal tissues (E) to a specific mode of life category (MoL). Therefore  
179  $P(E|MoL)$  is the probability of finding soft internal organs (E) given a certain mode of life is  
180 required (Table 1). Then, for the Fezouata Shale and the Walcott Quarry separately, the  
181 likelihood of producing the distribution of combinations of soft tissues (E) with a specific  
182 mode of life assuming that the endobenthos, for example, has the “true” preservation regime  
183 was investigated using a binomial distribution  $P(x \geq n) | Bi(n, p)$ , with:

184

$$P(x) = \binom{n}{x} p^x q^{n-x} = \frac{n!}{(n-x)! x!} p^x q^{n-x}$$

185

186 In the Walcott Quarry,  $p=P(E|endobenthic)$ ,  $q=1-p$ ,  $n$  is the number of  
187 epibenthic/nektobenthic genera preserving an internal organ (E), and  $x$  is the total number of  
188 taxa that could potentially preserve E which is, in this case, the total number of  
189 epibenthic/nektobenthic genera in the Walcott Quarry (because they all possessed internal  
190 organs during life). All calculated probabilities are summed and the probability  $P(x \geq n) | Bi(n,$   
191  $p)$ , of producing the value of  $P(E|nektobenthic)$  considering that internal organ preservation in  
192 the endobenthic community  $P(E|endobenthic)$  is the “true” distribution is then obtained,  
193 giving the critical interval of the distribution. This was then also performed for  
194 nektonic/planktonic taxa, and then repeated entirely for the Fezouata Shale.

195 To provide environmental context, the bioturbation index (BI) was measured (Taylor  
196 and Goldring, 1993) for one interval from each site that yielded diverse exceptionally  
197 preserved fossils – the phyllopod bed from the Walcott Quarry, and Z-F4m from the Fezouata

198 Shale. BI is equal to zero if bioturbation is absent. BI=1 if the percentage of bioturbation is  
199 between 1 and 4% with distinct bedding, few discrete traces and/or escape structures (Taylor  
200 and Goldring, 1993). BI=2 if bioturbation percentage is between 5 and 30% with low trace  
201 density and common escape structures (Taylor and Goldring, 1993). BI=3 if between 31 and  
202 60% of the sediment is bioturbated with a rare overlap of traces (Taylor and Goldring, 1993).  
203 BI=4 if bioturbation is high (61-90%) with a common overlap of traces and primary  
204 sedimentary structures are mostly erased (Taylor and Goldring, 1993). BI=5 is characterized  
205 by intense bioturbation (91-99%) (Taylor and Goldring, 1993) and sediment with almost  
206 completely disturbed bedding. BI=6 when the sediment is fully bioturbated (Taylor and  
207 Goldring, 1993).

208 **Table 1.** Summary statistics for the Walcott Quarry and the Fezouata Shale. A = biominerals, B = sclerites, C =  
 209 cuticle, D = cellular body walls, and E = internal organs. Numbers of genera belonging to each category (e.g., A,  
 210 AB, ABE) for each mode of life in all exceptionally preserved biotas are summarized. The proportion of each  
 211 type of tissue in all categories (e.g., P(A), P(C)) are calculated. The sum of these probabilities shows the number  
 212 of tissues per taxon. Probabilities of finding internal tissue in association with other structures (e.g., P(AIE);  
 213 P(EIB)) are calculated as well. For each site and for a certain probability (e.g., P(EIB)<sub>Walcott Quarry</sub>), comparable numbers  
 214 between modes of life are highlighted in red. Note that for the Walcott Quarry, the obtained numbers for the  
 215 epibenthic/nektobenthic and the nektonic/planktonic communities are more similar to each other than to the  
 216 endobenthos. There is no clear pattern between modes of life in the Fezouata Shale. The probability of finding

	Walcott Quarry			Fezouata Shale		
	Endobenthic	Epibenthic Nektobenthic	Nektonic Planktonic	Endobenthic	Epibenthic Nektobenthic	Nektonic Planktonic
<b>Tissue-type occurrences</b>						
N	12	77	12	6	131	24
A		14		4	82	5
B		5	2		18	15
C				1	2	
D			1			
E						
AB		6			3	
AC		2				
AD		1			1	
AE		1			8	1
BC		7	1		7	
BD		1				
BE		2			2	1
CE	3	1				
DE	1	9	2			
ABC		2				
ABE					5	
ACE	6	2		1		
BCE	2	20	6		4	2
BDE		2				
ABCE		1			3	
ABDE		1				
<b>Proportion of each tissue-type</b>						
P(A)	0,5	0,38	0	0,83	0,77	0,25
P(B)	0,17	0,61	0,75	0	0,3	0,75
P(C)	0,92	0,45	0,58	0,33	0,12	0,08
P(D)	0,08	0,18	0,25	0	0	0
P(E)	1	0,5	0,67	0,17	0,17	0,17
N(tissue/taxon)	2,66	2,14	2,25	1,33	1,36	1,25
<b>Probabilities of tissue co-occurrences</b>						
P(A E)	1	0,16		0,2	0,15	0,16
P(B E)	1	0,55	0,66	0	0,35	0,116
P(C E)	1	0,71	0,85	0,5	0,43	1
P(D E)	1	0,85	0,66	0	0	0
P(E A)	0,5	0,12	0	1	0,72	0,25
P(E B)	0,16	0,74	0,75	0	0,63	0,75
P(E C)	0,9	0,64	0,75	1	0,31	0,5
P(E D)	0,08	0,3	0,25	0	0	0
<b>Probabilities of internal organ association with a certain mode of life</b>						
P(E MoL)	1	0,5	0,67	0,17	0,17	0,17

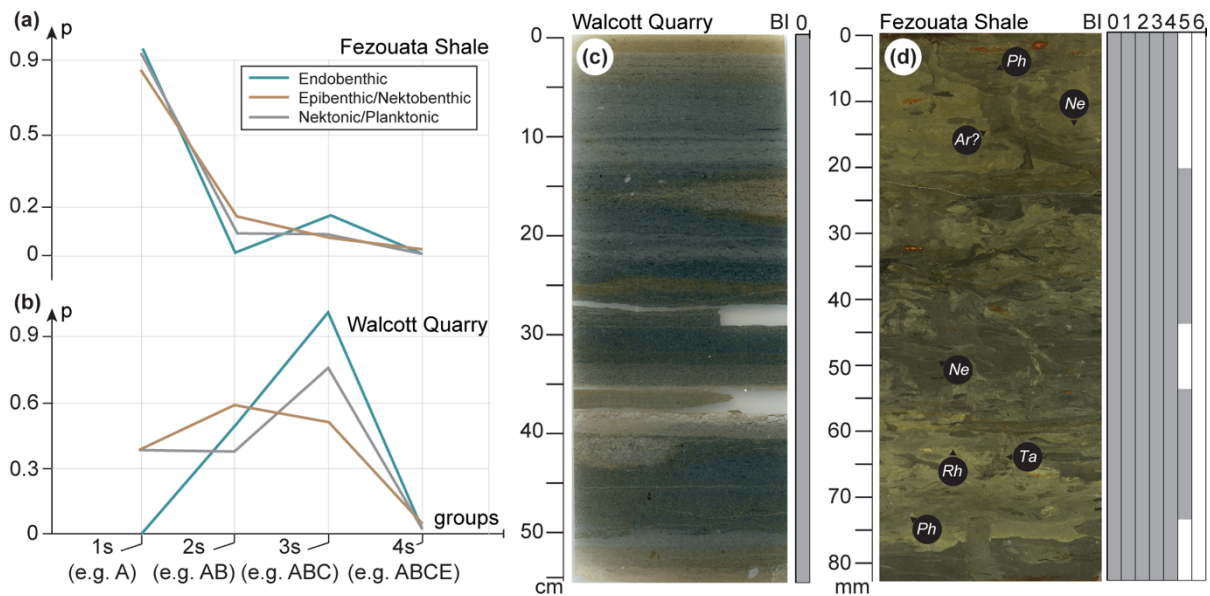
217 internal organs considering that a certain mode of life has been found in also investigated (e.g., P(E|MoL)).

### 218 3. RESULTS

219 In general, most tissue types exist in all mode of life categories (Table 1). However, a few  
220 exceptions exist. In the Fezouata Shale, cellular structures in direct contact with seawater (D)  
221 are not found in any of the animal groups (Table 1), and sclerotized structures (B) are absent  
222 from the endobenthic community (Table 1). Biominerals (A) are not present in the nektonic  
223 community of the Walcott Quarry (Table 1). In the Fezouata Shale all mode of life categories  
224 show comparable patterns of preservation (Fig. 1a) with a similar number of tissues per taxon  
225 (Table 1). The endobenthic, epibenthic/nekto-benthic, and nektonic/planktonic communities  
226 preserved 1.33, 1.36, and 1.25 tissue per taxon respectively (Table 1). In the Walcott Quarry,  
227 there are generally more tissues preserved per taxon than in the Fezouata Shale, and these  
228 values show more variation between the three modes of life (Fig. 1b). Endobenthic taxa in the  
229 Walcott quarry preserve the highest number of tissues per taxon (i.e., 2.66 tissues per taxon,  
230 with the epibenthic/nekto-benthic and the nektonic/planktonic communities 2.14 and 2.25  
231 tissues per taxon respectively) (Table 1). In the Walcott Quarry, internal tissue associations  
232 (E) with other biological structures (A, B, C, and D) are more similar between  
233 nektonic/planktonic and epibenthic/nekto-benthic communities than to endobenthic taxa (red  
234 highlight in table 1). The entire endobenthic community preserved internal organs while it  
235 was only a half for epibenthic/nekto-benthic, and a third for nektonic/planktonic taxa (Table  
236 1). The endobenthic community is significantly different from both the  
237 epibenthic/nekto-benthic (i.e.,  $P = 9.19 \times 10^{-55}$ ) and the nektonic/planktonic (i.e.,  $P = 4.56 \times 10^{-6}$ )  
238 communities. The latter two habitats are not statistically significantly different from each  
239 other (i.e.,  $P = 0.19$ ). In the Fezouata Shale, less than one-fifth of all animal communities  
240 preserved internal organs (Table 1, P(E|MoL)). There is no clear pattern of similarity between  
241 the three mode of life communities in terms of internal tissue associations with other  
242 biological structures (Table 1). Moreover, there are no significant differences in tissue  
243 associations between the three mode of life categories in the Fezouata Shale (i.e.,  
244 endobenthic-epibenthic/nekto-benthic ( $P = 0.56$ ), endobenthic-nektonic/planktonic ( $P = 0.61$ ),  
245 and epibenthic/nekto-benthic-nektonic/planktonic ( $P = 0.61$ )).

246 The two units also markedly differ in terms of bioturbation, with the Walcott Quarry  
 247 being essentially unburrowed (i.e., BI= 0) (Fig. 1c), whereas the Fezouata Shale is extensively  
 248 bioturbated (i.e., BI= 4-5) (Fig. 1d) containing *Taenidium* (Ta), *Rhizocorallium* (Rh),  
 249 *Phycosiphon* (Ph), *Nereites* (Ne), and *Arenicolites?* (Ar?) (Fig. 1d). In the Fezouata Shale  
 250 discrete trace fossils are overprinted to an undifferentiated burrow mottling, indicative of a  
 251 tiering structure and a well-developed mixed layer (Fig. 1d).

252



253

254 **Figure 1.** Differences in proportions of genera (Y-axis) between single (e.g., A, B, C), paired (e.g., AB, BC,  
 255 CE), triple (e.g., ABC, ACE) and quadruple (e.g., ABCE) character categories (marked as 1s, 2s, 3s, and 4s on  
 256 the X-axis) and modes of life in the Fezouata Shale (a), and the Walcott Quarry (b). Bioturbation index (BI) for  
 257 the undisturbed Walcott Quarry sediments (c) and the heavily bioturbated Fezouata Shale (d) which containing  
 258 *Taenidium* (Ta), *Rhizocorallium* (Rh), *Phycosiphon* (Ph), *Nereites* (Ne), and *Arenicolites?* (Ar?).

259

## 260 4. DISCUSSION

### 261 4.1. Linking ecology to preservation

262 The absence of biominerals (A) from the nekton/plankton of the Walcott Quarry (Table 1)  
 263 reflects the original absence from this site, as there is no evidence of nektonic/planktonic taxa  
 264 with mineralized bodies during the Middle Cambrian (Klug et al., 2010). Nektonic/planktonic  
 265 animals at this time consisted mainly of non-mineralized taxa, such as ctenophores and  
 266 arthropods (Hou et al., 2004; Vinther et al., 2014; Lerosey-Aubril and Pates, 2018; Whalen

267 and Briggs, 2018; Daley, 2019; Zhao et al., 2019). After accounting for this evolutionary  
268 signal, the taphonomic signal still exists for internal tissue and the three mode of life  
269 categories (Table 1).

270 In the Walcott Quarry, different mode of life categories preserved contrasted  
271 proportions of internal organs (Table 1), even though these organs are equally present in all  
272 animals. These difference in preservation between habitats can be explained by the  
273 depositional regime. Classical interpretations suggest organisms were transported from their  
274 habitat to the environment where they were preserved (Conway Morris, 1986; Gaines, 2014).  
275 In this scenario, nektonic, planktonic, epibenthic, and nektobenthic taxa were not affected by  
276 obrution events in the same way as the endobenthos. Many endobenthic taxa construct  
277 permanent domiciles and are able to vertically adjust their burrows accordingly for both  
278 continuous (equilibrium traces) or episodic (escape traces) sedimentation. However, the  
279 pristine preservation of the primary fabric in Walcott Quarry shows the thickness of the  
280 emplaced sediment was sufficient to prevent the transported endobenthos from escaping (Fig.  
281 2a). Furthermore, even if endobenthic animals were dead and decaying prior to their transport,  
282 their decay would have been less than in other animal communities because the body of  
283 endobenthic taxa is naturally at least partially buried and has less contact with seawater.  
284 Therefore, the preserved endobenthic community in the Walcott Quarry is dominantly formed  
285 of organisms that were entrained alive and/or fresh carcasses explaining the soft tissue  
286 preservation (Fig. 2a). In contrast, nektonic taxa that live high in the water column were  
287 above the incoming sediment flow (Fig. 2b), and might have been able to escape. This  
288 hypothesis can explain the rare occurrence of complete organisms belonging to taxa such as  
289 radiodonts in the Walcott Quarry (Daley et al., 2009, 2013). Though radiodonts are diverse in  
290 the Burgess Shale, complete carcasses such as the nektonic predator, *Anomalocaris*, are  
291 extremely rare, and fossils mainly represent molting products or decomposed carcasses  
292 (Daley et al., 2009, 2013, 2014). *Hurdia* is thought to swim close to the seafloor and is ten  
293 times more abundant at this locality than *Anomalocaris* (Daley et al., 2009, 2010, 2013,  
294 2014). Molting products and carcasses fall to the seafloor and are passively transported by  
295 event deposits to the preservation site (Fig. 2c), and taxa living low in the water column have

296 less chance of escaping the incoming sediment gravity flow. The rarer preservation of internal  
297 organs for the nektonic community in comparison to the endobenthos cannot be solely linked  
298 to taxonomic discrepancies between these categories even if the nektonic community had  
299 originally more molting animals than the endobenthic one. In our database, the best-preserved  
300 fossil for each genus was inventoried (i.e., for a specific genus, even if more than 100 molts  
301 have been found, as soon as one specimen shows internal organs, this genus is inventoried as  
302 preserving internal organs, such as the case for *Anomalocaris*). Thus, another aspect of the  
303 data is that for 33% of nektonic genera ( $P(\text{ElMoL})= 0.67$ ; Table 1), no single animal was  
304 captured alive or at the same stage of decay as endobenthic taxa in the Walcott Quarry. The  
305 absence of complete carcasses of some nektonic taxa and the abundance of their molting  
306 products could be a body size effect with a natural weight limit on entrainment in the gravity  
307 flows. Further investigation of flow dynamics may help resolve these issues.

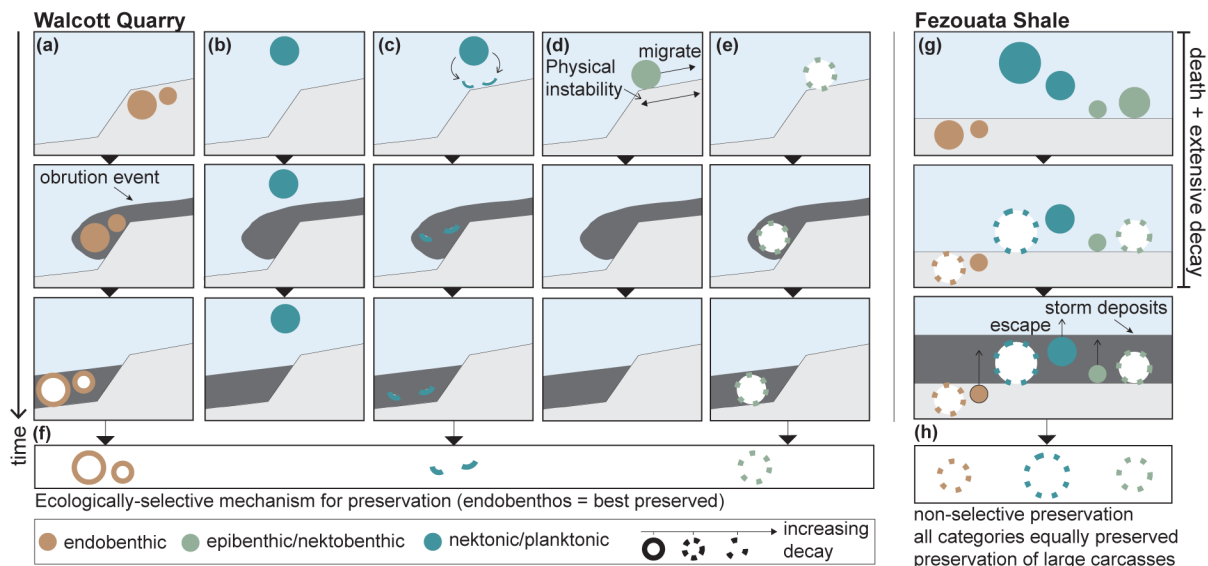
308         The most intriguing part of our data is that epibenthic animals in the Walcott Quarry  
309 show a similar pattern of preservation to nektonic ones (red highlight Table 1). The fact that  
310 epibenthic taxa show a lower degree of preservation in comparison to the endobenthos (Table  
311 1) suggests that some epibenthic taxa were able to either escape (1) burial sediments during  
312 transport or (2) before being entombed. The Walcott Quarry deposits were initially interpreted  
313 as the products of dilute turbidity currents (Piper, 1972). However, recent studies have shown  
314 deposition from pulsating, dense, mud-rich slurry flows, transitional between turbidity and  
315 debris flows (Gabbott et al., 2008). These currents are extremely fast and involved  
316 progressive aggradation rather than en-masse freezing. Mud-rich slurry flows may have been  
317 triggered by physical instabilities, such as delta front collapse, storms, or earthquakes (Allison  
318 and Brett, 1995; Gabbott et al., 2008). It is most likely that epibenthic taxa were able to sense  
319 these instabilities and escape from the environment (Fig. 2d) rather than escaping from fast-  
320 moving flows once they are captured. The escape of animals prior to instabilities is well  
321 documented (Grant and Halliday, 2010; Grant et al., 2011; Freund and Stolc, 2013) and this  
322 behavior may have first evolved during the Cambrian (Kirschvink, 2000; Langenhof and  
323 Komdeur, 2018). Escaping the environment prior to the arrival of event deposits has the same  
324 implications on preservation as the avoidance of turbulences by nektonic taxa (both lead to

325 the non-preservation of living animals; Fig. 2b, d). In both cases, only decaying carcasses and  
326 molting products are preserved (Fig. 2e) explaining the resemblance between epibenthic and  
327 nektonic communities and their lower exceptional preservation potential when compared to  
328 the endobenthos (Table 1). However, this explanation should not be generalized because if all  
329 taxa from the epibenthic community were able to avoid transported sediments, the potential of  
330 exceptional preservation would have been much lower in the Walcott Quarry. Currently, at  
331 least 50% of living epibenthic/nektobenthic taxa were not able to avoid burial as they show a  
332 similar pattern of preservation as the endobenthos ( $P(\text{ElMoL}) = 0.5$ ). Therefore, the  
333 mechanism for soft-tissue preservation in the Walcott Quarry is ecologically selective and  
334 preserved animal communities in this site exhibit different stages of decay (Fig. 2f). The  
335 endobenthic community is the least decayed (Fig. 2f) while the nektonic, nektobenthic, and  
336 epibenthic preservation contain a mix of decaying carcasses and living organisms caught in  
337 the flow. Animals that were entrained into the flow alive died either during transport or at the  
338 time of deposition because no evidence of escape traces are present in the Walcott Quarry  
339 (Fig. 1c) (Allison and Brett, 1995; Mángano et al., 2019).

340 The probability models confirm the results of previous sedimentary studies suggesting  
341 that the mechanism of soft part preservation in the Fezouata Shale are not identical to those in  
342 the Walcott Quarry (Martin et al., 2016; Vaucher et al., 2016, 2017; Saleh et al., 2020a,  
343 2021a). All mode of life categories in the Fezouata Shale preserved a lower proportion of  
344 internal organs than the Walcott Quarry (Table 1). This was previously attributed to the  
345 relatively long exposure of carcasses to pre-burial decay in the Fezouata Shale (Saleh et al.,  
346 2020a, b) (Fig. 2g). This pre-burial decay explains as well the absence of cellular structures in  
347 direct contact with seawater (D) from this site (Table 1). However, the major difference  
348 between the Walcott Quarry and the Fezouata Shale is that all modes of life in the Ordovician  
349 site share a comparable number of structures per taxon and the same proportion of internal  
350 tissues (Table 1). This means that burial in the Fezouata Shale is not ecologically selective. In  
351 this site, animals were buried *in-situ* during storms and were not transported (Fig. 2g) (Saleh  
352 et al., 2021a, b). Furthermore, escaping the effect of this *in-situ* burial in the Fezouata Shale is  
353 not limited to the nekton as there are abundant escape trace fossils cross-cutting event



354 deposits (Saleh et al. 2020a). Even infaunal taxa, such as *Wosekella*, were not affected by the  
 355 distal storms, as they adjusted their position in the sediments and continued to grow after the  
 356 thin storm deposits (Saleh et al., 2018) (Fig. 2g). Furthermore, because the mechanism for  
 357 soft-tissue preservation in the Fezouata Shale does not rely on transport, the size of an animal  
 358 is not significant in defining what can be preserved (Fig. 2k). Large (articulated) carcasses of  
 359 taxa such as the radiodont *Aegirocassis* can be found in the Fezouata Shale (Van Roy and  
 360 Briggs, 2011; Gaines et al., 2012; Van Roy et al., 2015b) (Fig. 2h).  
 361



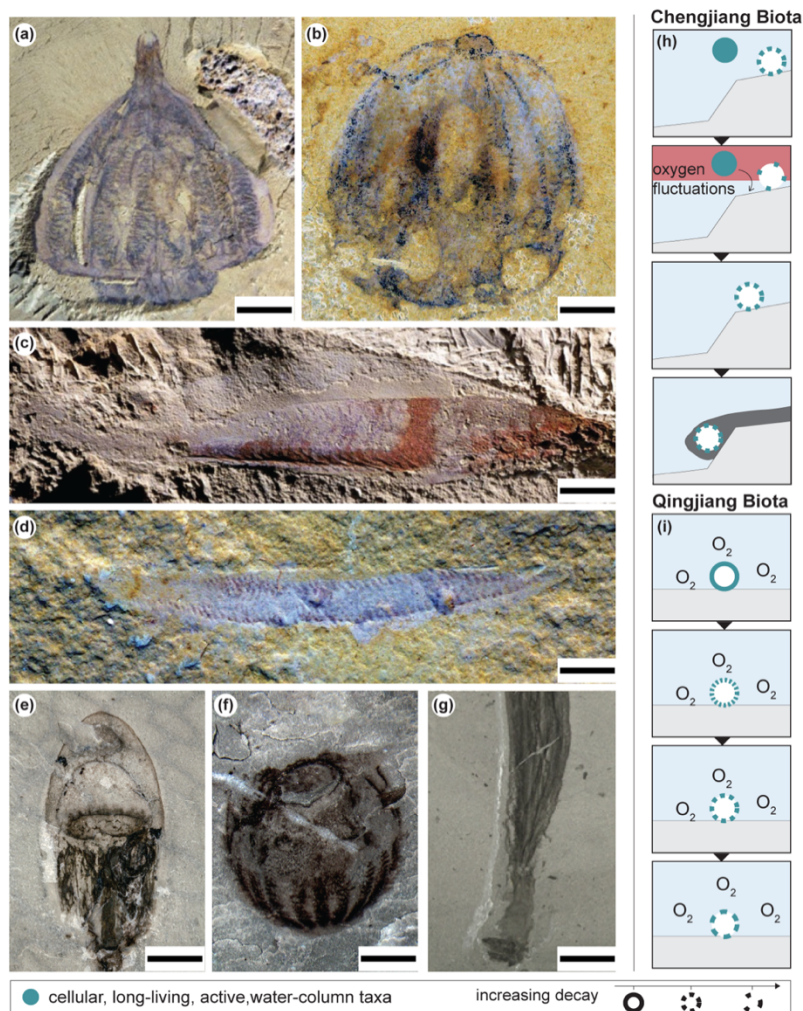
362 **Figure 2.** Taphonomic scenarios in the Walcott Quarry and the Fezouata Shale. Walcott Quarry: endobenthic  
 363 taxa are entrained alive and cannot escape the produced mud-rich deposit and are freshly preserved (a).  
 364 Nektonic/planktonic taxa living high in the water column can avoid transported sediments (b). Molting products  
 365 fall passively to the seafloor, might get transported (c). Some epibenthic/nekto-benthic animals might have been  
 366 able to sense physical disturbances and escape the environment prior to the arrival of burial material (d).  
 367 Carcasses of these taxa are preserved (e). The preservation of the endobenthos is higher than other animal  
 368 communities (f). Fezouata Shale: carcasses decay on the seafloor (g). When storms cause sediment influx, most  
 369 living animals escape resulting in the preservation of non-fresh carcasses for all mode of life categories (h).  
 370  
 371

#### 372 4.2. Implications in understanding Cambrian ecosystems

373 The ecologically-selective mechanism of preservation present in the Walcott Quarry is absent  
 374 in the Fezouata Shale which might have wider evolutionary implications, particularly when  
 375 comparing Cambrian BST deposits. For instance, epibenthic/nekto-benthic and

376 nektonic/planktonic taxa, other than arthropods, such as ctenophores (e.g., *Batofasciculus*,  
377 *Galeactena*, *Gemmactena*, *Maotianoascus*, *Sinoascus*, *Thaumactena*) (Fig. 3a, b) and  
378 chordates (e.g., *Cathaymyrus*, *Haikouichthys*, *Myllokunmingia*, *Zhongjianichthys*,  
379 *Zhongxiniscus*) (Fig. 3c, d) belonging to the D category (i.e., cellular body walls), are  
380 regularly reported from the Chengjiang Biota (Cambrian Stage 3, China) (Shu et al., 1996,  
381 1999; Hou et al., 2004; Zhao et al., 2019; Saleh et al., 2020b), while they are much rarer in the  
382 Walcott Quarry (i.e., 4 genera only) (Nanglu et al., 2020; Saleh et al., 2020b). Furthermore,  
383 the Cambrian Stage 3 Qingjiang Biota (China) is apparently dominated by ctenophores and  
384 medusoid cnidarians (Fig. 3e, f) (Fu et al., 2019). In the Walcott Quarry, cnidarians remain  
385 scarce and are mainly represented by polypoid forms (e.g., *Mackenzia*) (Conway Morris,  
386 1993) (Fig. 3g). These discrepancies probably result from the ecologically-selective  
387 preservation bias for the Walcott Quarry. Preservation potential for ctenophores, chordates,  
388 and medusoids is low in the Walcott Quarry as: (1) Organisms may avoid transported  
389 sediments (Fig. 2b, d); (2) The preserved nektonic/planktonic community consists partially of  
390 carcasses and molting products (Fig. 2c, e); (3) Cellular structures in direct contact with  
391 seawater are among the fastest to decay (MacGabhann et al., 2019; Saleh et al., 2020b); and  
392 (4) Some of these organisms have a long lifespan (Petralia et al., 2017) and do not molt in a  
393 similar way to ecdysozoans. The preservation of a diverse ctenophore and chordate  
394 assemblage in the Chengjiang Biota and their absence from the Walcott Quarry remains  
395 poorly understood. A mechanism is required that would allow the death and fall of  
396 nektonic/planktonic taxa from the water column to the sea floor increasing the chance for a  
397 fresh carcass to be captured by the flow (e.g., oxygen fluctuations in the water column;  
398 Hammarlund et al., 2017; Qi et al., 2018) (Fig. 3h). Moreover, anoxia may increase the rate of  
399 decay for some cnidarian tissues (Hancy and Antcliffe, 2020). In this sense, preserved  
400 cnidarians in the Qingjiang Biota might be correlated with more oxygen availability than in  
401 the Walcott Quarry (Hancy and Antcliffe, 2020) (Fig. 3i). Geochemical and sedimentological  
402 data is not yet available to evaluate these hypotheses for the Qingjiang Biota. Yet the  
403 Chengjiang and Qingjiang Biotas are particularly important in completing our understanding  
404 of Palaeozoic ecosystems owing to their preservation of both hard-to-preserve tissues (i.e.,

405 cellular) and ecologies (e.g., nektonic, nektonic). Moreover, even if the Walcott Quarry  
 406 preserves a lower generic richness of chordates than in the Chengjiang Biota (Fig. 3), one  
 407 should keep in mind that 57 specimens of *Pikaia* were discovered in the Walcott Quarry  
 408 (Nanglu et al., 2020), while less than 10 specimens are known for each chordate genus in the  
 409 Chengjiang Biota. Such numbers do not question the robustness of the probability model  
 410 presented in this study. On the contrary, the probability model gives a new and  
 411 complementary perspective. The abundance of certain chordate genera in the Walcott Quarry  
 412 can be explained by a specific ecology of these taxa (e.g., swimming closer to the seafloor),  
 413 that might have been different for other chordates (i.e., swimming higher in the water  
 414 column). Furthermore, Chordates from the Walcott Quarry are limited to only a specific level,  
 415 within the 55 cm fossiliferous interval. This local abundance of chordates could be explained  
 416 as well by a timely change in sedimentary flows within the Walcott Quarry.



417

418 **Figure 3.** Ecological and preservational discrepancies between Cambrian Burgess Shale-type deposits.  
419 Ctenophores from the Chengjiang Biota: (a) *Galeactena hemispherica* (YKLP13810, 5mm scale-bar) (Ou et al.,  
420 2015), and (b) *Maotianoascus octonarius* (RCCBYU10217; 1.5mm scale-bar) (Ou et al., 2015). Chordates from  
421 the Chengjiang Biota: (c) *Myllokunmingia fengjiaoa* (RCCBYU-10200a; 1mm scale-bar) (Caron et al., 2010),  
422 and (d) *Zhongxiniscus intermedius* (YIGSHef64682; 1mm scale-bar) (Huilin et al., 2010). (e) Medusoid  
423 cnidarian (3mm scale-bar) and (f) ctenophore (4mm scale-bar) from the Qingjiang Biota (Fu et al., 2019). (g)  
424 Polypoid cnidarian from Walcott Quarry (*Mackenzia costalis*; ROM61115; 12mm scale-bar) (Conway Morris,  
425 1993). The preservation of a diverse ctenophore, chordate, and medusoid assemblage might have been facilitated  
426 by regular oxygen fluctuations (Hammarlund et al., 2017; Qi et al., 2018) augmenting the chances of capturing a  
427 fresh carcass in the Chengjiang Biota (h) and by oxygen availability reducing the decay rate of some cnidarians  
428 in the Qingjiang Biota (i) (Hancy and Antcliffe, 2020).

429

## 430 5. CONCLUSIONS

431 A new method using data partitioning in a probability model was developed to decode the  
432 ecology of ancient ecosystems. By quantifying the role of mode of life in the preservation  
433 processes it is possible to reconstruct ecological selectivity in the fossil record. The focus on  
434 how sedimentary flows interact with different modes of life categories (biostratinomy)  
435 complements previous studies focusing on early diagenesis (decay and mineralization). The  
436 Walcott Quarry best preserved the endobenthos. Endobenthic animals in the Walcott Quarry  
437 were captured alive and were not able to escape the flow resulting in their preservation in  
438 minute details. Some active organisms living in the water column were able to avoid  
439 transported sediments, and decaying carcasses and molting products of these taxa are  
440 generally preserved. When compared to the Fezouata Shale, the Walcott Quarry preserved a  
441 higher proportion of soft tissues and internal organs. However, in the Fezouata Shale, the  
442 mechanism for preservation is not ecologically selective as endobenthic,  
443 nektobenthic/epibenthic, nektonic/planktonic taxa are equally preserved. Only carcasses were  
444 preserved in the Fezouata Shale, and many animals including endobenthic taxa were able to  
445 escape if buried alive. When compared to other Cambrian deposits with abundant soft-tissue  
446 preservation, such as the Chengjiang and the Qingjiang biotas, the Walcott Quarry is  
447 underrepresenting some taxonomic groups such as ctenophores, chordates, and cnidarians.  
448 This appears to be a result of preservation rather than evolutionary processes. Consequently,

449 the mechanism and conditions for soft-tissue preservation in the Cambrian are not universal  
450 across all BST sites. Subtleties of each unique local setting have a significant effect on the  
451 composition of the preserved fossil biota. Finally, it is crucial to emphasize that BST deposits  
452 offer a unique opportunity to understand evolutionary events during the Palaeozoic. However,  
453 there is no single fossil site that reflects an entirely accurate picture of past ecosystems. Fossil  
454 data from numerous localities should be taken in concert and comparatively analyzed, to  
455 untangle the preservation, ecology, and evolution knot when studying the origin of complex  
456 animal communities.

457

## 458 **ACKNOWLEDGEMENTS**

459 This paper is supported by grant no. 2020M683388 from the Chinese Postdoctoral Science  
460 Foundation awarded to FS and by grant no. 205321\_179084 from the Swiss National Science  
461 Foundation, awarded to ACD as principal investigator. Research by MGM and LAB was  
462 supported by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants  
463 311727–20 and 422931-20, respectively. This paper is a contribution of the IGCP653, and  
464 735 programs.

465

## 466 **REFERENCES**

- 467 Allison, P. A., Brett, C. E., 1995. In situ benthos and paleo-oxygenation in the Middle  
468 Cambrian Burgess Shale, British Columbia, Canada. *Geology* 23, 1079–1082.
- 469 Anderson, R. P., Tosca, N. J., Gaines, R. R., Mongiardino Koch, N., Briggs, D. E. G., 2018.  
470 A mineralogical signature for Burgess Shale–type fossilization. *Geology* 46, 347–350.
- 471 Anderson, R. P., Tosca, N.J., Cinque, G., Frogley, M.D., Lekkas, I., Akey, A., Hughes, G.M.,  
472 Bergmann, K.D., Knoll, A.H., Briggs, D.E.G., 2020. Aluminosilicate haloes preserve  
473 complex life approximately 800 million years ago. *Interface Focus* 10, 20200011.
- 474 Block, S. M. Biophysical aspects of sensory transduction. in *Sensory Transduction* (eds.  
475 Corey, D. P. & Roper, S. D.) 424 (Rockefeller University Press, 1992).
- 476 Brasier, M. D., Antcliffe, J. B., Callow, R. H. T. Evolutionary Trends in Remarkable Fossil  
477 Preservation Across the Ediacaran–Cambrian Transition and the Impact of Metazoan

478 Mixing. in 519–567 (Springer, Dordrecht, 2011). doi:10.1007/978-90-481-8643-3\_15.

479 Brayard, A., Nützel, A., Kaim, A., Escarguel, G., Hautmann, M., Stephen, D.A., Bylund,  
480 K.G., Jenks, J., Bucher, H., 2011. Gastropod evidence against the Early Triassic  
481 Lilliput effect: Reply. *Geology* 39, e233–e233.

482 Caron, J. B., Jackson, D. A., 2008. Paleoecology of the Greater Phyllopod Bed community,  
483 Burgess Shale. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 258, 222–256.

484 Caron, J.B., Conway Morris, S., Shu, D., 2010. Tentaculate fossils from the Cambrian of  
485 Canada (British Columbia) and China (Yunnan) interpreted as Primitive  
486 Deuterostomes. *PLoS One* 5, e9586.

487 Conway Morris, S., 1986. The community structure of the Middle Cambrian phyllopod bed  
488 (Burgess Shale). *Palaeontology* 29, 423–467.

489 Conway Morris, S., 1993. Ediacaran-like fossils in Cambrian Burgess Shale-type faunas of  
490 North America. *Palaeontology* 36, 593–635.

491 Daley, A. C., Budd, G. E., Caron, J. B., Edgecombe, G. D., Collins, D., 2009. The Burgess  
492 Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution.  
493 *Science*. 323, 1597–1600.

494 Daley, A. C., Budd, G. E., 2010. New anomalocaridid appendages from the Burgess Shale,  
495 Canada. *Palaeontology*, 53 (4), 721–738.

496 Daley, A. C., Budd, G. E., Caron, J. B., 2013. Morphology and systematics of the  
497 anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and  
498 Utah. *J. Syst. Palaeontol.* 11, 743–787.

499 Daley, A. C., Edgecombe, G. D., 2014. Morphology of *Anomalocaris canadensis* from the  
500 Burgess Shale. *J. Paleontol.* 88, 68–91.

501 Daley, A. C., Antcliffe, J. B., Drage, H. B., Pates, S., 2018. Early fossil record of  
502 Euarthropoda and the Cambrian Explosion. *Proc. Natl. Acad. Sci.* 115, 5323–5331.

503 Daley, A., 2019. A treasure trove of Cambrian fossils. *Science*. 363, 1284–1285.

504 Freund, F., Stolc, V., 2013. Nature of Pre-Earthquake Phenomena and their Effects on Living  
505 Organisms. *Animals* 3, 513–531.

506 Fu, D., Tong, G., Dai, T., Liu, W., Yang, Y., Zhang, Y., Cui, L., Li, L., Yun, H., Wu, Y., Sun,

507 A., Liu, C., Pei, W., Gaines, R. R., Zhang, X., 2019. The Qingjiang Biota—a Burgess  
508 Shale-type fossil Lagerstätte from the early Cambrian of South China. *Science* 363,  
509 1338–1342.

510 Gabbott, S. E., Zalasiewicz, J., Collins, D., 2008. Sedimentation of the Phyllopod bed within  
511 the Cambrian Burgess Shale Formation of British Columbia. *J. Geol. Soc. London.*  
512 165, 307–318.

513 Gaines, R. R., Briggs, D. E. G., Yuanlong, Z., 2008. Cambrian Burgess Shale-type deposits  
514 share a common mode of fossilization. *Geology* 36, 755-758.

515 Gaines, R. R., Briggs, D. E. G., Orr, P. J., Van Roy, P., 2012. Preservation of giant  
516 anomalocaridids in silica-chlorite concretions from the Early Ordovician of Morocco.  
517 *Palaios* 27, 317–325.

518 Gaines, R. R., 2014. Burgess Shale-type Preservation and its Distribution in Space and Time.  
519 *Paleontol. Soc. Pap.* 20, 123–146.

520 Grant, R. A., Halliday, T., 2010. Predicting the unpredictable; evidence of pre-seismic  
521 anticipatory behaviour in the common toad. *J. Zool.* 281, 263-271.

522 Grant, R. A., Halliday, T., Balderer, W.P., Leuenberger, F., Newcomer, M., Cyr, G., Freund,  
523 F.T., 2011. Ground Water Chemistry Changes before Major Earthquakes and Possible  
524 Effects on Animals. *Int. J. Environ. Res. Public Health* 8, 1936–1956.

525 Hammarlund, E. U., Gaines, R.R., Prokopenko, M.G., Qi, C., Hou, X.G., Canfield, D.E., 2017.  
526 Early Cambrian oxygen minimum zone-like conditions at Chengjiang. *Earth Planet.*  
527 *Sci. Lett.* 475, 160–168.

528 Hancy, A. D., Antcliffe, J. B., 2020. Anoxia can increase the rate of decay for cnidarian  
529 tissue: Using *Actinia equina* to understand the early fossil record. *Geobiology* 18(2),  
530 167-184.

531 Hou, X., Aldridge, R., Aldridge, R.J., Bergstrom, J., Siveter, D.J., Siveter, D., Feng, X.H.,  
532 The Cambrian fossils of Chengjiang, China: the flowering of early animal life.  
533 (Blackwell, 2004).

534 Huilin, L., Shixue, H., Liangzhong, C., 2010. New Early Cambrian Chordates from Haikou,  
535 Kunming. *Acta Geol. Sin. - English Ed.* 75, 345–348.

536 Kirschvink, J. L., 2000. Earthquake Prediction by Animals: Evolution and Sensory  
537 Perception. *Bulletin of the Seismological Society of America* 90, 312-323.

538 Klug, C., Kröger, B., Kiessling, W., Mullins, G. L., Servais, T., Fryda, J., Korn, D., Turner,  
539 S., 2010. The Devonian nekton revolution. *Lethaia* 43, 465–477.

540 Langenhof, M. R., Komdeur, J., 2018. Why and how the early-life environment affects  
541 development of coping behaviours. *Behav. Ecol. Sociobiol.* 72, 1–32.

542 Lefebvre, B., Allaire, N., Guensburg, T.E., Hunter, A.W., Kouraïss, K., Martin, E.L., Nardin,  
543 E., Noailles, F., Pittet, B., Sumrall, C.D., Zamora, S., 2016, Palaeoecological aspects  
544 of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas,  
545 Morocco. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 460, 97–121.

546 Lefebvre, B., Guensburg, T.E., Martin, E.L., Mooi, R., Nardin, E., Nohejlová, M., Saleh, F.,  
547 Kouraïss, K., El Hariri, K. and David, B., 2019. Exceptionally preserved soft parts in  
548 fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within  
549 basal deuterostomes. *Geobios* 52, 27-36.

550 Lerosey-Aubril, R., Pates, S., 2018. New suspension-feeding radiodont suggests evolution of  
551 microplanktivory in Cambrian macronekton. *Nat. Commun.* 9, 1–9.

552 MacGabhann, B. A., Schiffbauer, J.D., Hagadorn, J.W., Van Roy, P., Lynch, E.P., Morrison,  
553 L. and Murray, J., 2019. Resolution of the earliest metazoan record: Differential  
554 taphonomy of Ediacaran and Paleozoic fossil molds and casts. *Palaeogeogr.*  
555 *Palaeoclimatol. Palaeoecol.* 513, 146–165.

556 Mángano, M. G., Hawkes, C. D., Caron, J.-B., 2019. Trace fossils associated with Burgess  
557 Shale non-biom mineralized carapaces: bringing taphonomic and ecological controls into  
558 focus. *Royal Society Open Science* 6(1), 172074.

559 Martin, E. L. O., Pittet, B., Gutiérrez-Marco, J.C., Vannier, J., El Hariri, K., Lerosey-Aubril,  
560 R., Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T.R., Van Roy, P., Vaucher,  
561 R., Lefebvre, B., 2016. The Lower Ordovician Fezouata Konservat-Lagerstätte from  
562 Morocco: age, environment and evolutionary perspectives. *Gondwana Research*, 34,  
563 pp.274-283. 2016. The Lower Ordovician Fezouata Konservat-Lagerstätte from  
564 Morocco: Age, environment and evolutionary perspectives. *Gondwana Res.* 34, 274–



565 283.

566 McMahon, S., Anderson, R. P., Saupe, E. E., Briggs, D. E. G., 2016. Experimental evidence  
567 that clay inhibits bacterial decomposers: Implications for preservation of organic  
568 fossils. *Geology* 44, 867–870.

569 Nanglu, K., Caron, J., Gaines, R., 2020. The Burgess Shale paleocommunity with new  
570 insights from Marble Canyon, British Columbia. *Paleobiology* 46, 58–81.

571 O'Brien, L. J., Caron, J. B., 2015. Paleocommunity analysis of the Burgess Shale Tulip Beds,  
572 Mount Stephen, British Columbia: Comparison with the Walcott Quarry and  
573 implications for community variation in the Burgess Shale. *Paleobiology* 42, 27–53.

574 Ou, Q., Xiao, S., Han, J., Sun, G., Zhang, F., Zhang, Z., Shu, D., 2015. A vanished history of  
575 skeletonization in Cambrian comb jellies. *Sci. Adv.* 1, e1500092.

576 Petralia, R. S., Mattson, M. P., Yao, P. J., 2014. Aging and longevity in the simplest animals  
577 and the quest for immortality. *Aging Res. Rev.* 16, 66–82.

578 Piper, D. J. W., 1972. Sediments of the Middle Cambrian Burgess Shale, Canada. *Lethaia* 5,  
579 169–175.

580 Qi, C., Gabbott, S.E., Ma, X., Xie, L., Deng, W., Jin, C., Hou, X.G., 2018. Influence of redox  
581 conditions on animal distribution and soft-bodied fossil preservation of the Lower  
582 Cambrian Chengjiang Biota. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 507, 180–187.

583 Saleh, F., Candela, Y., Harper, D.A., Polechová, M., Lefebvre, B. and Pittet, B., 2018. Storm-  
584 induced community dynamics in the Fezouata Biota (Lower Ordovician, Morocco).  
585 *Palaios* 33, 535–541.

586 Saleh, F., Pittet, B., Perrillat, J., Lefebvre, B., 2019. Orbital control on exceptional fossil  
587 preservation. *Geology* 47, 1–5.

588 Saleh, F., Pittet, B., Sansjofre, P., Guériau, P., Lalonde, S., Perrillat, J.P., Vidal, M., Lucas,  
589 V., El Hariri, K., Kouraiss, K., Lefebvre, B., 2020a. Taphonomic pathway of  
590 exceptionally preserved fossils in the Lower Ordovician of Morocco. *Geobios* 60, 99-  
591 115.

592 Saleh, F., Antcliff, J.B., Lefebvre, B., Pittet, B., Laibl, L., Peris, F.P., Lustrì, L., Guériau, P.,  
593 Daley, A.C., 2020b. Taphonomic bias in exceptionally preserved biotas. *Earth Planet.*

594 Sci. Lett. 529, 115873.

595 Saleh, F., Daley, A. C., Lefebvre, B., Pittet, B., Perrillat, J. P., 2020c. Biogenic iron preserves  
596 structures during fossilization: A hypothesis. *BioEssays* 42, 1900243.

597 Saleh, F., Vaucher, R., Antcliffe, J.B., Daley, A.C., El Hariri, K., Kouraiss, K., Lefebvre, B.,  
598 Martin, E.L., Perrillat, J.P., Sansjofre, P., Vidal, M., 2021a. Insights into soft-part  
599 preservation from the Early Ordovician Fezouata Biota. *Earth-Science Reviews* 213,  
600 103464.

601 Saleh, F., Vidal, M., Laibl, L., Sansjofre, P., Guérliau, P., Peris, F.P., Lustri, L., Lucas, V.,  
602 Lefebvre, B., Pittet, B., El Hariri, K., Daley, A. C., 2021b. Large trilobites in a stress-  
603 free Early Ordovician environment. *Geol. Mag.* 158(2), 261-270.

604 Shu, D. G., Conway Morris, S., Zhang, X. L., 1996. A *Pikaia*-like chordate from the lower  
605 Cambrian of China. *Nature* 384, 157–158.

606 Shu, D. G., Luo, H.L., Morris, S.C., Zhang, X.L., Hu, S.X., Chen, L., Han, J.I.A.N., Zhu, M.,  
607 Li, Y., Chen, L.Z., 1999. Lower Cambrian vertebrates from south China. *Nature* 402,  
608 42–46.

609 Taylor, A. M., Goldring, R., 1993. Description and analysis of bioturbation and ichnofabric. *J.*  
610 *Geol. Soc. London.* 150, 141–148.

611 Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., El Hariri, K.,  
612 Briggs, D.E.G., 2010. Ordovician faunas of Burgess Shale type. *Nature* 465, 215–218.

613 Van Roy, P., Briggs, D. E. G., 2011. A giant Ordovician anomalocaridid. *Nature* 473, 510–  
614 513.

615 Van Roy, P., Briggs, D. E. G., Gaines, R. R., 2015a. The Fezouata fossils of Morocco; an  
616 extraordinary record of marine life in the Early Ordovician. *J. Geol. Soc. London.* 172,  
617 541–549.

618 Van Roy, P., Daley, A. C., Briggs, D. E. G., 2015b. Anomalocaridid trunk limb homology  
619 revealed by a giant filter-feeder with paired flaps. *Nature* 522, 77–80.

620 Vaucher, R., Martin, E. L. O., Hormière, H. Pittet, B., 2016. A genetic link between  
621 Konzentrat- and Konservat-Lagerstätten in the Fezouata Shale (Lower Ordovician,  
622 Morocco). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 460, 24–34.

- 623 Vaucher, R., Pittet, B., Hormière, H., Martin, E. L. O., Lefebvre, B., 2017. A wave-  
624 dominated, tide-modulated model for the Lower Ordovician of the Anti-Atlas,  
625 Morocco. *Sedimentology* 64, 777–807.
- 626 Vinther, J., Stein, M., Longrich, N. R., Harper, D. A. T., 2014. A suspension-feeding  
627 anomalocarid from the Early Cambrian. *Nature* 507, 496–499.
- 628 Whalen, C. D., Briggs, D. E. G., 2018. The Palaeozoic colonization of the water column and  
629 the rise of global nekton. *Proc. R. Soc. B Biol. Sci.* 285, 20180883.
- 630 Whitaker, A. F., Kimmig, J., 2020. Anthropologically introduced biases in natural history  
631 collections, with a case study on the invertebrate paleontology collections from the  
632 middle Cambrian Spence Shale Lagerstätte. *Palaeontologia Electronica* 23(3), a58.
- 633 Zhao, Y., Vinther, J., Parry, L.A., Wei, F., Green, E., Pisani, D., Hou, X., Edgecombe, G.D.,  
634 Cong, P., 2019. Cambrian sessile, suspension feeding stem-group ctenophores and  
635 evolution of the comb jelly body plan. *Curr. Biol.* 29, 1112–1125.