

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

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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. 475Ma).

26 The modelling shows that the mechanism for soft-tissue preservation in the Walcott Quarry is
27 ecologically selective, favoring the endobenthos. This is not found in the Fezouata Shale. Taken
28 in concert with bioturbation data, a new model of comparative preservation is developed based
29 on sedimentary flow dynamics. This suggests that during the Cambrian Explosion and
30 Ordovician Radiation the most exceptional fossils sites must still be calibrated against each
31 other to understand the unfolding evolutionary events and the ecological structuring of ancient
32 animal communities.

33

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

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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, enlightening our
43 understanding of the most significant metazoan diversification in the history of life (Daley et
44 al., 2018; Nanglu et al., 2020). The Fezouata Shale (Early Ordovician, Morocco) offers a unique
45 view of the transition between the Cambrian Explosion and the Ordovician Radiation than was
46 previously known (Van Roy et al., 2010).

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

60 faunal composition of the Ordovician site is markedly different from that of the Walcott Quarry
61 (Van Roy et al., 2015a; Lefebvre et al., 2016, 2019).

62 Assemblage discrepancies between fossil sites are influenced by many factors: ecology,
63 evolution, preservation, and even collection bias (Brasier et al., 2011). This is a broad-scale
64 problem in palaeontology that impacts all time intervals across the whole gamut of evolutionary
65 scenarios from the origin of life to the diversification of hominids (Saleh et al., 2020b). Using
66 abundance data and alpha diversity metrics is the traditional approach for palaeoecological
67 reconstructions (Caron and Jackson, 2008; Saleh et al., 2018; Whitaker and Kimmig, 2020).
68 However, at many sites, these data can be skewed by collection bias caused by government
69 rules, economic value, and scientific interest (Brayard et al., 2011). Even with rarefaction
70 indices (Caron and Jackson, 2008; Nanglu et al., 2020), it is almost impossible to quantify the
71 effect that these biases have on raw taxon abundance data. When trying to understand fossil
72 preservation, a better approach is one based on occurrences rather than abundances as some
73 taxa have tissues that are more likely to be preserved (e.g., mineralized brachiopods) in the
74 fossil record than other taxa (e.g., soft jellyfish), introducing a preservational bias. Moreover,
75 because most taxa have more than one tissue type, it is best to separate the preservation variable
76 by comparing tissue types between fossil sites. Recent probabilistic modelling of genus
77 distributions and combinations of preserved tissue types has shown considerable advantages
78 over traditional approaches (Saleh et al., 2020b). Probability models showed the preservation
79 of anatomical structures in the Walcott Quarry and the Fezouata Shale are significantly different
80 (Saleh et al., 2020b), and the Fezouata Shale did not preserve entirely cellular organisms (e.g.,
81 the body walls of chordates; internal organs such as digestive and nervous tissues) (Saleh et al.,
82 2020b). It is likely the animals were dead and decaying on the seafloor prior to their burial in
83 the Fezouata Shale (Saleh et al., 2021b), and cellular structures in contact with the water column
84 are the fastest to decay (MacGabhann et al., 2020; Saleh et al., 2020b). Herein, this

85 methodology is expanded upon by incorporating data on ecological strategies, to investigate
86 the effect of habitat on fossilization. Consequently, the interplay of taxonomy, preservation,
87 and ecology is analytically approached using the Walcott Quarry and the Fezouata Biota as
88 separate, and then comparable case studies. This quantification allows a separation of
89 ecological and preservation effects helping to form a clearer picture of the dawn of animal life
90 in the early Palaeozoic.

91

92 **2. MATERIAL AND METHODS**

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

104 The number of times each of the different possible tissue type combinations occurred
105 was identified. Tissue types can occur alone without other tissues as A, B, C, D, or E; and in
106 one of ten possible pairs: AB, AC, AD, AE, BC, BD, BE, CD, CE, and DE. There are also 10
107 different possible three-set intersections ABC, ABD, ABE, ACD, ACE, ADE, BCD, BCE,
108 BDE, and CDE. Finally, there are five different possible associations of four-set intersections
109 ABCD, ABCE, ABDE, ACDE, BCDE, and one five-set combination ABCDE, for a total of 31

110 possible combinations. A simple calculation of the number of taxa belonging to each category
 111 introduces a bias in the dataset because each count of a higher-order intersection leads to
 112 multiple counts of lower-order intersections. For example, finding an ABC combination causes
 113 a count of the AB, AC, and BC categories and consequently, one taxon is counted 4 times. This
 114 has to be removed from the data in order to find unique character combinations. This problem
 115 can be solved on a five-set Venn diagram and the unique associations can be obtained (Table
 116 1). Automating the process for a five-fold set problem is challenging and software and
 117 computational programs are generally limited to solving single four-set problems (Chen and
 118 Boutros 2011) or solving the five-set problem indirectly by moving to probability densities of
 119 multiset intersections (Wang et al. 2015). It is worth noting here that two of the characters in
 120 this analysis are biologically mutually exclusive (C and D; an organism cannot be cuticularized
 121 and non-cuticularized) so the problem simplifies somewhat to two intersecting four-fold
 122 problems, as CD and all its subsets are empty. Consequently, the five-way intersection ABCDE
 123 is impossible. Further subsets of C∩D that are also empty are A∩C∩D, B∩C∩D, C∩D∩E,
 124 A∩C∩D∩E, A∩B∩C∩D, and B∩C∩D∩E. Hence, the problem is reduced from 31 to 23
 125 intersections, and the highest intersections that can have a value are A∩B∩C∩E and
 126 A∩B∩D∩E, which can be found directly in the dataset. These values can then be used to
 127 calculate the number of taxa that preserve three tissue types because of the identity:

$$128 \quad X \cap Y = X \cap Y \cap Z' + X \cap Y \cap Z$$

129 With Z' indicating that Z is not included in the count, (X∩Y∩Z' is the intersection of X and Y
 130 only, to the exclusion of Z being associated with them).

$$131 \quad X \cap Y \cap Z' = X \cap Y - X \cap Y \cap Z$$

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

$$134 \quad A \cap B \cap C = A \cap B \cap C \cap E + A \cap B \cap C \cap E'$$

135 Which can be simply rearranged to:

$$136 \quad A \cap B \cap C \cap E' = A \cap B \cap C - A \cap B \cap C \cap E$$

137 In this equation, an unknown exclusive three tissue type association ($A \cap B \cap C \cap E'$) can be
138 calculated from two known quantities which can be recovered directly from the database. It is
139 then trivial to extend this to all the other possible three variable intersections with the corollary
140 that some intersections require the subtraction of both of the four variable intersections if the
141 three-set intersection contains subsets of both of the four variable intersections. For instance:

$$142 \quad A \cap B \cap E \cap C' \cap D' = A \cap B \cap E - (A \cap B \cap C \cap E + A \cap B \cap D \cap E).$$

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

146 A manual approach would be highly prone to error due to the high number of taxa and
147 data entries. Thus, this method has been automated in a single Excel file that contains all of the
148 formulae above such that future analyses need only to construct the data matrix, with data
149 analyses proceeding automatically (Supplementary Material 2). This approach is quicker and
150 more reliable, providing numerous opportunities to cross-check the data: the sum of the values
151 of all 23 subsets; equal number of taxa for all calculations; no empty taxa coding; $C \cap D$
152 intersections remain zero.

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

159 the dataset, was then calculated by adding these probabilities for each mode of life in each biota
160 (Table 1).

161 To examine how exceptional preservation differs between modes of life, further
162 analyses focused on the preservation of soft tissue (E) because all animals have internal tissues
163 and so this category must have been present during the life of the organism (whereas this is not
164 true for all the other categories, for example, it is possible to have no biominerals). The
165 association of soft internal organs (E) with other structures was investigated for all tissue-type
166 categories in the Fezouata shale and the Walcott Quarry. This is achieved by examining
167 conditional probabilities in the subset of A. For example, the probability that a taxon with a
168 biomineral also having preserved internal organs/tissues ($p(E|A)$) is:

$$169 \quad P(E|A) = (A \cap E + A \cap B \cap E + A \cap C \cap E + A \cap D \cap E + A \cap B \cap D \cap E + A \cap B \cap C \cap E) / A$$

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

172 In order to investigate the role of mode of life on fossil preservation the data was then
173 partitioned using mode of life categories. This allows a direct link between exceptional
174 preservation of internal tissues (E) to a specific mode of life category (MoL). Therefore
175 $P(E|MoL)$ is the probability of finding soft internal organs (E) given a certain mode of life is
176 required (Table 1). Then, for the Fezouata Shale and the Walcott Quarry separately, the
177 likelihood of producing the distribution of combinations of soft tissues (E) with a specific mode
178 of life assuming that the endobenthos, for example, has the “true” preservation regime was
179 investigated using a binomial distribution $P(x \geq n) | Bi(n, p)$, with:

180

$$181 \quad P(x) = \binom{n}{x} p^x q^{n-x} = \frac{n!}{(n-x)! x!} p^x q^{n-x}$$

182

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

192 To assess the degree of biogenic reworking, the bioturbation index (BI) was measured
193 (Taylor and Goldring, 1993) for one interval from each site that yielded diverse exceptionally
194 preserved fossils – the phyllopod bed from the Walcott Quarry, and Z-F4m from the Fezouata
195 Shale. BI is equal to zero if bioturbation is absent. BI=1 if the percentage of bioturbation is
196 between 1 and 4% with distinct bedding, few discrete traces and/or escape structures. BI=2 if
197 bioturbation percentage is between 5 and 30% with low trace density and common escape
198 structures. BI=3 if between 31 and 60% of the sediment is bioturbated with a rare overlap of
199 traces. BI=4 if bioturbation is high (61-90%) with a common overlap of traces and primary
200 sedimentary structures are mostly erased. BI=5 is characterized by intense bioturbation (91-
201 99%) and sediment with almost completely disturbed bedding. BI=6 when the sediment is fully
202 bioturbated.

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

	Walcott Quarry			Fezouata Shale		
	Endobenthic	Epibenthic Nektobenthic	Nektonic Planktonic	Endobenthic	Epibenthic Nektobenthic	Nektonic Planktonic
Tissue-type occurrences						
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				
Proportion of each tissue-type						
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
Probabilities of tissue co-occurrences						
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
Probabilities of internal organ association with a certain mode of life						
P(E MoL)	1	0,5	0,67	0,17	0,17	0,17

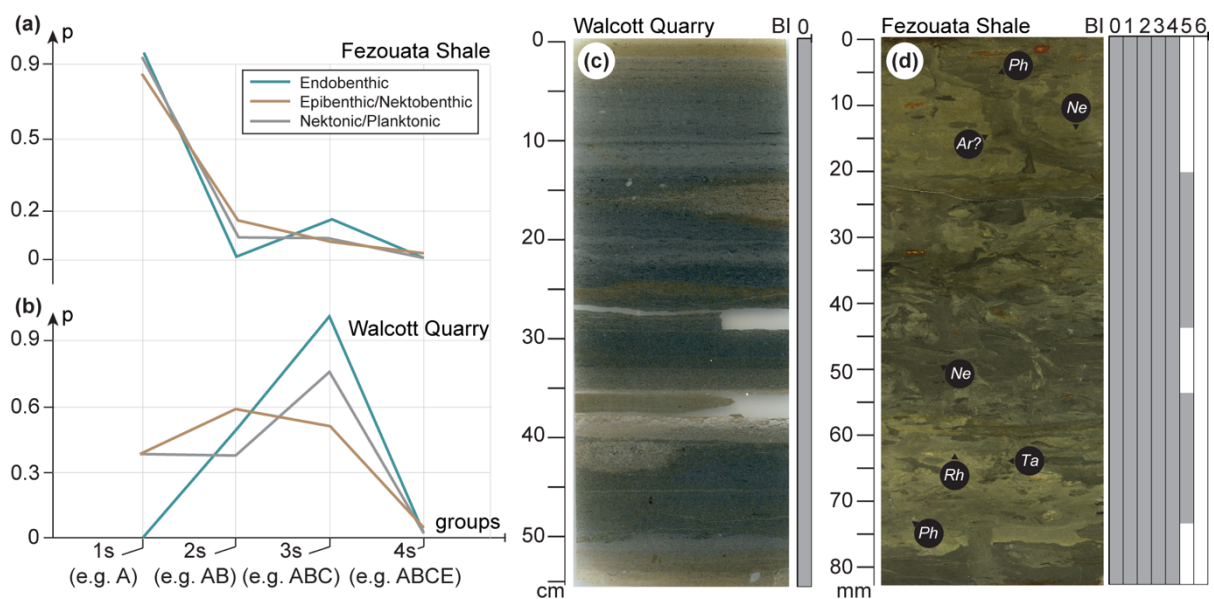
213 3. RESULTS

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

238 Shale (i.e., endobenthic-epibenthic/nektobenthic ($P= 0.56$), endobenthic-nektonic/planktonic
 239 ($P=0.61$), and epibenthic/nektobenthic-nektonic/planktonic ($P=0.61$)).

240 The two units also markedly differ in terms of bioturbation. The Walcott Quarry are
 241 essentially unburrowed (i.e., $BI= 0$) and have pristine preservation of the primary fabric (Fig.
 242 1c). In contrast, the Fezouata Shale is extensively bioturbated (i.e., $BI= 4-5$) with bed
 243 boundaries significantly obliterated and containing *Taenidium* (Ta), *Rhizocorallium* (Rh),
 244 *Phycosiphon* (Ph), *Nereites* (Ne), and *Arenicolites?* (Ar?) (Fig. 1d) among other ichnotaxa. In
 245 the Fezouata Shale discrete trace fossils are overprinted to an undifferentiated burrow mottling,
 246 indicative of a tiering structure and a well-developed mixed layer (Fig. 1d).

247



248

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

256

257 **4. DISCUSSION**

258 **4.1. *Linking ecology to preservation***

259 The absence of biominerals (A) from the nekton/plankton of the Walcott Quarry (Table 1)
260 reflects the original absence from this site, as there is no evidence of nektonic/planktonic taxa
261 with mineralized bodies during the middle Cambrian (Klug et al., 2010). Nektonic/planktonic
262 animals at this time consisted mainly of non-mineralized taxa, such as ctenophores and
263 arthropods (Hou et al., 2004; Vinther et al., 2014; Lerosey-Aubril and Pates, 2018; Whalen and
264 Briggs, 2018; Daley, 2019; Zhao et al., 2019). After accounting for this evolutionary signal, the
265 taphonomic signal still exists for internal tissue and the three mode of life categories (Table 1).

266 In the Walcott Quarry, different mode of life categories preserved contrasted
267 proportions of internal organs (Table 1), even though these organs are equally present in all
268 animals. These difference in preservation between modes of life can be explained by the
269 depositional regime. Classical interpretations suggest organisms were transported from their
270 original habitat to the environment where they were preserved (Piper, 1972; Conway Morris,
271 1986; Gaines, 2014). In this scenario, nektonic, planktonic, epibenthic, and nektobenthic taxa
272 were most likely not affected by obrution events in the same way as the endobenthos. Many
273 endobenthic taxa construct permanent domiciles and are able to vertically adjust their burrows
274 accordingly for both continuous (equilibrium traces) or episodic (escape traces) sedimentation.
275 However, the pristine preservation of the primary fabric in Walcott Quarry shows the thickness
276 of the emplaced sediment was sufficient to prevent the transported endobenthos from escaping,
277 if transported alive (Fig. 2a). Furthermore, even if endobenthic animals were dead and decaying
278 prior to their transport, their decay would have been less than in other animal communities
279 because the body of endobenthic taxa is naturally at least partially buried and has less contact
280 with seawater. Therefore, the preserved endobenthic community in the Walcott Quarry is
281 dominantly formed of organisms that were entrained alive or fresh carcasses explaining the soft

282 tissue preservation (Fig. 2a). In contrast, nektonic taxa that live high in the water column were
283 above the incoming sediment flow (Fig. 2b), and might have been able to escape. This
284 hypothesis can explain the rare occurrence of complete organisms belonging to taxa such as
285 radiodonts in the Walcott Quarry (Daley et al., 2009, 2013). Though radiodonts are diverse in
286 the Burgess Shale, complete carcasses, such as the nektonic predator *Anomalocaris*, are
287 extremely rare, and fossils mainly represent molting products or decomposed carcasses (Daley
288 et al., 2009, 2013, 2014). *Hurdia* is thought to swim close to the seafloor and is ten times more
289 abundant at this locality than *Anomalocaris* (Daley et al., 2009, 2010, 2013, 2014). Molting
290 products and carcasses fall to the seafloor and are passively transported by sediment gravity
291 flows to the preservation site (Fig. 2c), and taxa living low in the water column have less chance
292 of escaping the incoming sediment gravity flow. The rarer preservation of internal organs for
293 the nektonic community in comparison to the endobenthos cannot be solely linked to taxonomic
294 discrepancies between these categories even if the nektonic community had originally more
295 molting animals than the endobenthic one. In our database, the best-preserved fossil for each
296 genus was inventoried (i.e., for a specific genus, even if more than 100 molts have been found,
297 as soon as one specimen shows internal organs, this genus is inventoried as preserving internal
298 organs, such as the case for *Anomalocaris*). Thus, another aspect of the data is that for 33% of
299 nektonic genera ($P(\text{ElMoL})=0.67$; Table 1), no single animal was captured alive or at the same
300 stage of decay as endobenthic taxa in the Walcott Quarry. The absence of complete carcasses
301 of some nektonic taxa and the abundance of their molting products could be a body size effect
302 with a natural weight limit on entrainment in the gravity flows. Further investigation of flow
303 dynamics may help resolve these issues (Bath-Enright et al., 2021).

304 The most intriguing part of our data is that epibenthic animals in the Walcott Quarry
305 show a similar pattern of preservation to nektonic ones (red highlight Table 1). The fact that
306 epibenthic taxa show a lower degree of preservation in comparison to the endobenthos (Table

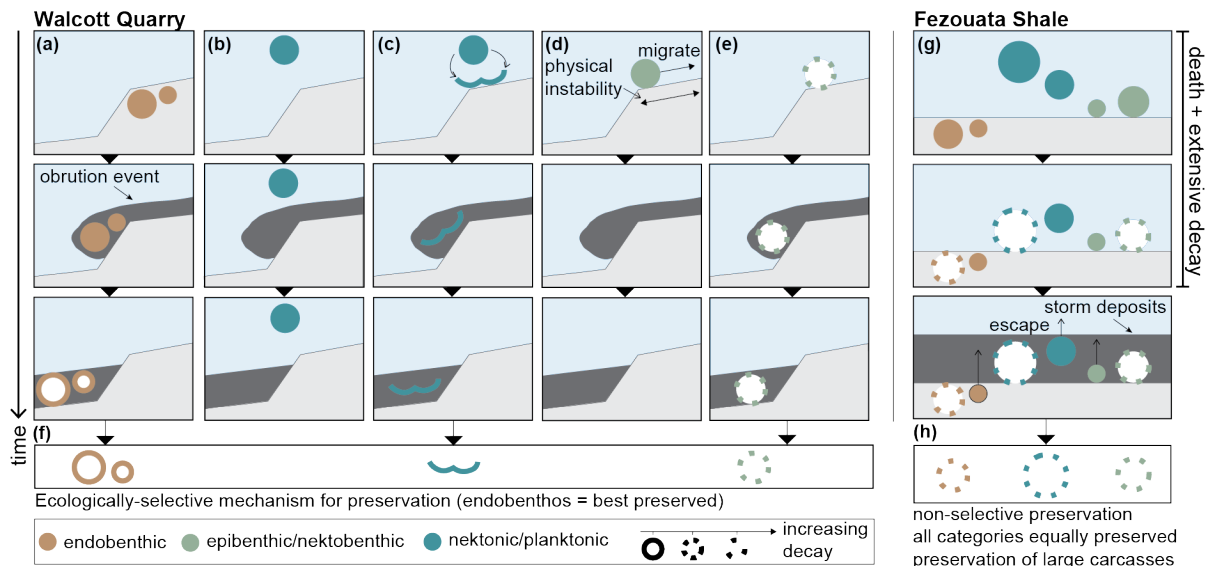
307 1) suggests that some epibenthic taxa were able to either escape (1) burial sediments during
308 transport or (2) before being entombed. The Walcott Quarry deposits were initially interpreted
309 as the products of dilute turbidity currents (Piper, 1972). However, recent studies have shown
310 deposition from pulsating, dense, mud-rich slurry flows, transitional between turbidity and
311 debris flows (Gabbott et al., 2008; Bath-Enright et al., 2021). These currents are extremely fast
312 and involved progressive aggradation rather than en-masse freezing. Mud-rich slurry flows may
313 have been triggered by physical instabilities, such as delta front collapse, storms, or earthquakes
314 (Allison and Brett, 1995; Gabbott et al., 2008). It is most likely that epibenthic taxa were able
315 to sense these instabilities and escape from the environment (Fig. 2d) rather than escaping from
316 fast-moving flows once they are captured. The escape of animals prior to instabilities is well
317 documented (Grant and Halliday, 2010; Grant et al., 2011; Freund and Stolc, 2013) and this
318 behavior may have first evolved during the Cambrian (Kirschvink, 2000; Langenhof and
319 Komdeur, 2018). Escaping the environment prior to the arrival of event sediment has the same
320 implications on preservation as the avoidance of turbulence by nektonic taxa (both lead to the
321 non-preservation of living animals; Fig. 2b, d). In both cases, only decaying carcasses and
322 molting products are preserved (Fig. 2e) explaining the resemblance between epibenthic and
323 nektonic communities and their lower exceptional preservation potential when compared to the
324 endobenthos (Table 1). However, this explanation should not be generalized because if all taxa
325 from the epibenthic community were able to avoid transported sediments, the potential of
326 exceptional preservation would have been much lower in the Walcott Quarry. Currently, at least
327 50% of living epibenthic/nektonic taxa were not able to avoid burial as they show a similar
328 pattern of preservation as the endobenthos ($P(\text{ElMoL}) = 0.5$). Therefore, the mechanism for
329 soft-tissue preservation in the Walcott Quarry is ecologically selective and preserved animal
330 communities in this site exhibit different stages of decay (Fig. 2f). The endobenthic community
331 is the least decayed (Fig. 2f) while the nektonic, nektonic, and epibenthic preservation

332 contain a mix of decaying carcasses and living organisms caught in the flow. Animals that were
333 entrained into the flow alive most likely died either during transport or at the time of deposition
334 because no evidence of escape traces are present in the Walcott Quarry (Fig. 1c) (Allison and
335 Brett, 1995; Mángano et al., 2019). In contrast to most Burgess Shale-type localities, nektonic
336 carapaces from Walcott Quarry do not show associated trace fossils, either due to high
337 frequency of slurry flows or to anoxic bottom conditions (Mángano et al., 2019).

338 The probability models confirm the results of previous sedimentary studies suggesting
339 that the mechanisms of soft part preservation in the Fezouata Shale are not identical to those in
340 the Walcott Quarry (Martin et al., 2016; Vaucher et al., 2016, 2017; Saleh et al., 2020a, 2021a).
341 All mode of life categories in the Fezouata Shale preserved a lower proportion of internal organs
342 than the Walcott Quarry (Table 1). This was previously attributed to the relatively long
343 exposure of carcasses to pre-burial decay in the Fezouata Shale (Saleh et al., 2020a, b) (Fig.
344 2g). This pre-burial decay explains as well the absence of cellular structures in direct contact
345 with seawater (D) from this site (Table 1). However, the major difference between the Walcott
346 Quarry and the Fezouata Shale is that all modes of life in the Ordovician site share a comparable
347 number of structures per taxon and the same proportion of internal tissues (Table 1). This means
348 that burial in the Fezouata Shale is not ecologically selective. In this site, animals were buried
349 *in-situ* during storms and were not transported (Fig. 2g) (Vaucher et al., 2016; Saleh et al.,
350 2021a, b). Furthermore, escaping the effect of this *in-situ* burial in the Fezouata Shale is not
351 limited to the nekton as there are abundant escape trace fossils cross-cutting event deposits
352 (Saleh et al. 2020a). Even infaunal taxa, such as *Wosekella*, were not affected by the distal
353 storms, as they adjusted their position in the sediments and continued to grow after the thin
354 storm deposits (Saleh et al., 2018) (Fig. 2g). Furthermore, because the mechanism for soft-
355 tissue preservation in the Fezouata Shale does not rely on transport, the size of an animal is not
356 significant in defining what can be preserved (Fig. 2k). Large (articulated) carcasses of taxa

357 such as the radiodont *Aegirocassis* can be found in the Fezouata Shale (Van Roy and Briggs,
 358 2011; Gaines et al., 2012; Van Roy et al., 2015b) (Fig. 2h).

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360

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

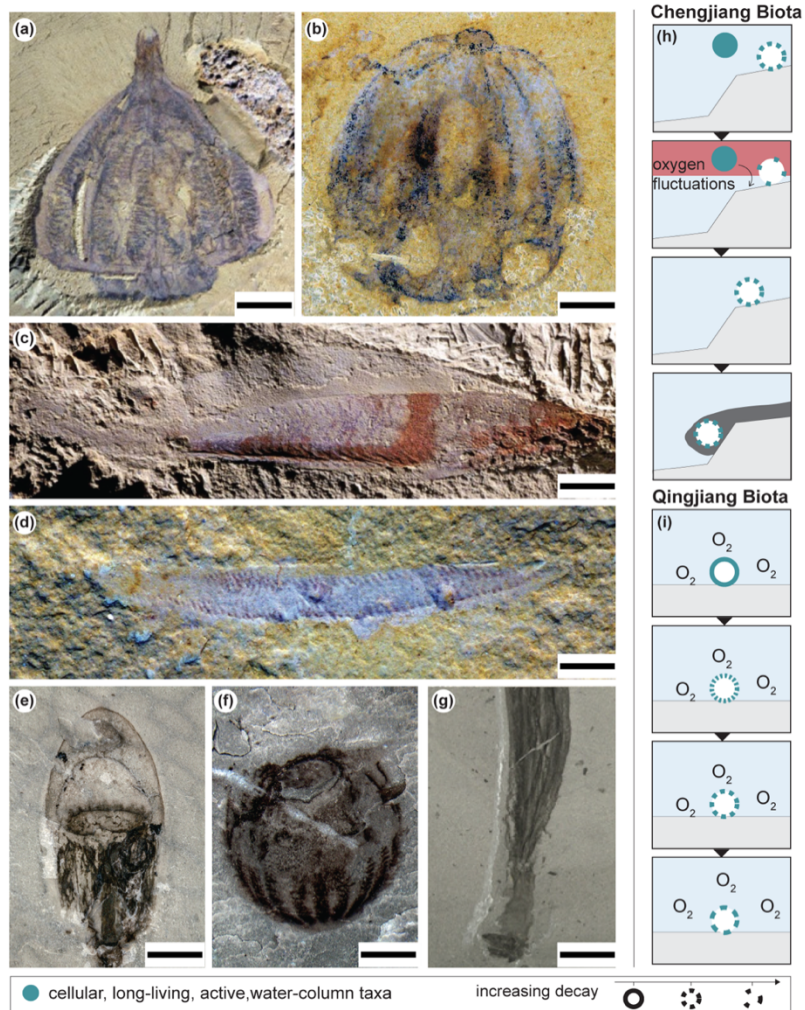
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370 **4.2. Implications in understanding Cambrian ecosystems**

371 The ecologically-selective mechanism of preservation present in the Walcott Quarry is absent
 372 in the Fezouata Shale which might have wider evolutionary implications, particularly when
 373 comparing Cambrian BST deposits. For instance, epibenthic/nektobenthic and
 374 nektonic/planktonic taxa, other than arthropods, such as ctenophores (e.g., *Batofasciculus*,
 375 *Galeactena*, *Gemmactena*, *Maotianoascus*, *Sinoascus*, *Thaumactena*) (Fig. 3a, b) and chordates

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

401 ecosystems owing to their preservation of both hard-to-preserve tissues (i.e., cellular) and
402 ecologies (e.g., nekto-benthic, nektonic). Moreover, even if the Walcott Quarry preserves a
403 lower generic richness of chordates than in the Chengjiang Biota (Fig. 3), one should keep in
404 mind that 57 specimens of *Pikaia* were discovered in the Walcott Quarry (Nanglu et al., 2020),
405 which is non-negligible even though this number is way smaller than the 500 specimens found
406 in the Chengjiang Biota (Hou et al., 2004). The relative abundance of certain chordate genera
407 in the Walcott Quarry can be explained by a specific ecology of these taxa (e.g., swimming
408 closer to the seafloor), that might have been different for other chordates (i.e., swimming higher
409 in the water column). Furthermore, chordates from the Walcott Quarry are limited to only a
410 specific level, within the 55 cm fossiliferous interval. This local abundance of chordates within
411 this level could be explained as well by a timely change in sedimentary flows (e.g., type or
412 frequency) within the Walcott Quarry.



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

5. CONCLUSIONS

427 A new method using data partitioning in a probability model was developed to decode the
428 ecology of ancient ecosystems. By quantifying the role of mode of life in the preservation
429 processes it is possible to reconstruct ecological selectivity in the fossil record. The focus on
430 how flow dynamics interact with different modes of life (i.e., the link between ecology and
431 biostratinomy) complements previous studies focusing on early diagenesis (decay and
432 mineralization). The Walcott Quarry best preserved the endobenthos. Endobenthic animals in
433 the Walcott Quarry were either captured alive and were not able to escape the flow, or consisted
434 of fresh carcasses resulting in their preservation in minute details. Some active organisms living
435 in the water column were able to avoid transport. Meanwhile, some of the carcasses and molts
436 of these taxa delivered to the sea floor are generally preserved. When compared to the Fezouata
437 Shale, the Walcott Quarry preserved a higher proportion of soft tissues and internal organs.
438 However, in the Fezouata Shale, the mechanism for preservation is not ecologically selective
439 as endobenthic, nektobenthic/epibenthic, nektonic/planktonic taxa are equally preserved. Only
440 carcasses were preserved in the Fezouata Shale, and many animals including endobenthic taxa
441 were able to escape if buried alive. When compared to other Cambrian deposits with abundant
442 soft-tissue preservation, such as the Chengjiang and the Qingjiang biotas, the Walcott Quarry
443 is underrepresenting some taxonomic groups such as ctenophores, chordates, and cnidarians.
444 This appears to be a result of preservation rather than evolutionary processes. Consequently,
445 the mechanism and conditions for soft-tissue preservation in the Cambrian are not universal
446 across all BST sites. Subtleties of each unique local setting have a significant effect on the
447 composition of the preserved fossil biota. Finally, it is crucial to emphasize that BST deposits
448 offer a unique opportunity to understand evolutionary events during the Palaeozoic. However,
449 there is no single fossil site that reflects an entirely accurate picture of past ecosystems. Fossil
450 data from numerous localities should be taken in concert and comparatively analyzed, to

451 untangle the preservation, ecology, and evolution knot when studying the origin of complex
452 animal communities.

453

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