

1 **A novel tool to untangle the ecology and fossil preservation knot**
2 **in 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.
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

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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, 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)_{Walcott Quarry}), 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
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(AIE)	1	0,16		0,2	0,15	0,16
P(BIE)	1	0,55	0,66	0	0,35	0,116
P(CIE)	1	0,71	0,85	0,5	0,43	1
P(DIE)	1	0,85	0,66	0	0	0
P(EIA)	0,5	0,12	0	1	0,72	0,25
P(EIB)	0,16	0,74	0,75	0	0,63	0,75
P(EIC)	0,9	0,64	0,75	1	0,31	0,5
P(EID)	0,08	0,3	0,25	0	0	0
Probabilities of internal organ association with a certain mode of life						
P(EIMoL)	1	0,5	0,67	0,17	0,17	0,17

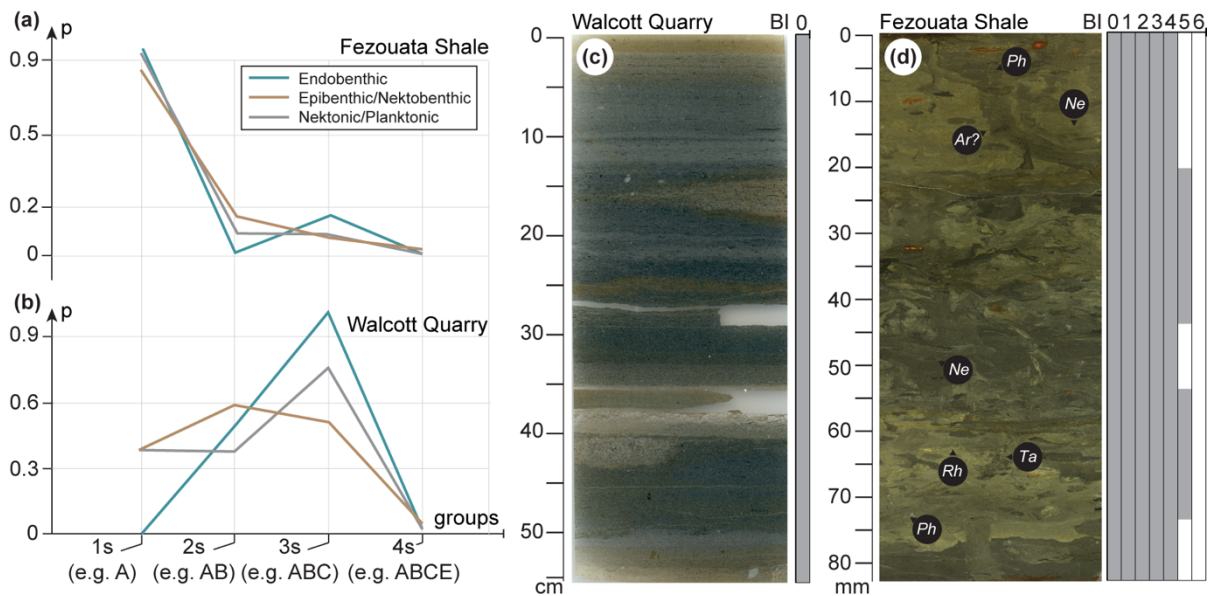
217 internal organs considering that a certain mode of life has been found in also investigated (e.g., P(EIMoL)).

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

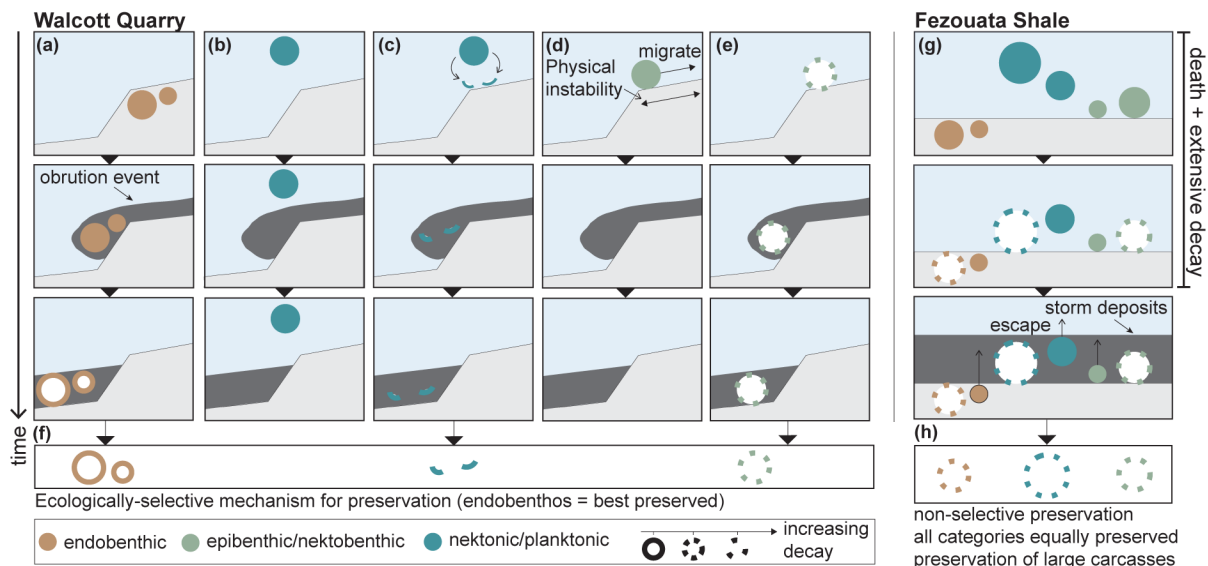
296 less chance of escaping the incoming sediment gravity flow. The rarer preservation of internal
297 organs for the nektonic community in comparison to the endobenthos cannot be solely linked
298 to taxonomic discrepancies between these categories even if the nektonic community had
299 originally more 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



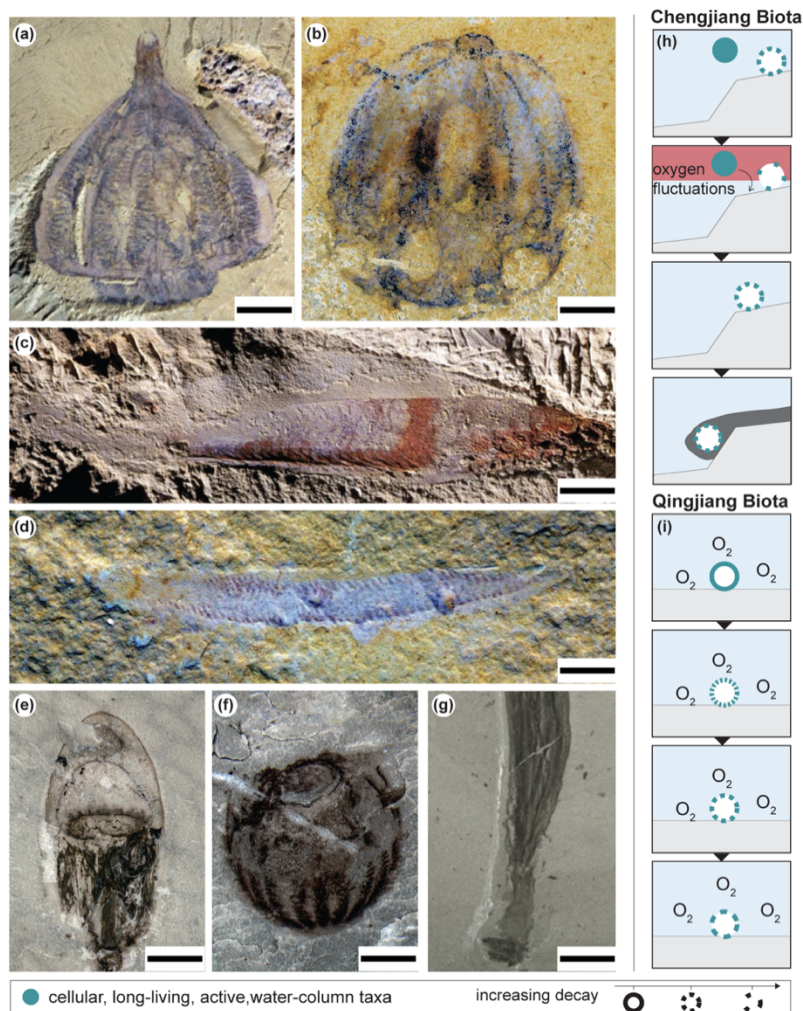
362
 363 **Figure 2.** Taphonomic scenarios in the Walcott Quarry and the Fezouata Shale. Walcott Quarry: endobenthic
 364 taxa are entrained alive and cannot escape the produced mud-rich deposit and are freshly preserved (a).
 365 Nektonic/planktonic taxa living high in the water column can avoid transported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

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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., Antcliffe, 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., Guériau, P., Peris, F.P., Lustrì, 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.