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

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Abstract

Understanding the functioning of extinct ecosystems is a complicated knot of ecological, evolutionary, and preservational strands that must be untangled. For instance, anatomical and behavioral differences can profoundly alter fossilization pathways. This is particularly true in exceptionally preserved soft-bodied biotas that record the earliest phases of animal evolution during the Cambrian Explosion and the Ordovician Radiation. Herein, a novel method of data partitioning based on probabilistic modelling is developed to examine these processes for the Walcott Quarry, Burgess Shale, Canada (510Ma), and the Fezouata Shale, Morocco (c. 475Ma). The modelling shows that the mechanism for soft-tissue preservation in the Walcott Quarry is ecologically selective, favoring the endobenthos. This is not found in the Fezouata Shale. Taken in concert with bioturbation data, a new model of comparative preservation is 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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1. INTRODUCTION

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

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

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

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

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

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

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

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

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

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

Which can be simply rearranged to:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

To provide environmental context, the bioturbation index (BI) was measured (Taylor and Goldring, 1993) for one interval from each site that yielded diverse exceptionally 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).

Table 1. Summary statistics for the Walcott Quarry and the Fezouata Shale. A = biominerals, B = sclerites, C = cuticle, D = cellular body walls, and E = internal organs. Numbers of genera belonging to each category (e.g., A, AB, ABE) for each mode of life in all exceptionally preserved biotas are summarized. The proportion of each type of tissue in all categories (e.g., P(A), P(C)) are calculated. The sum of these probabilities shows the number of tissues per taxon. Probabilities of finding internal tissue in association with other structures (e.g., P(A|E); P(E|B)) are calculated as well. For each site and for a certain probability (e.g., $P(E|B)_{\text{Walcott Quarry}}$), comparable numbers between modes of life are highlighted in red. Note that for the Walcott Quarry, the obtained numbers for the epibenthic/nektobenthic and the nektonic/planktonic communities are more similar to each other than to the 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(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

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

3. RESULTS

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

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

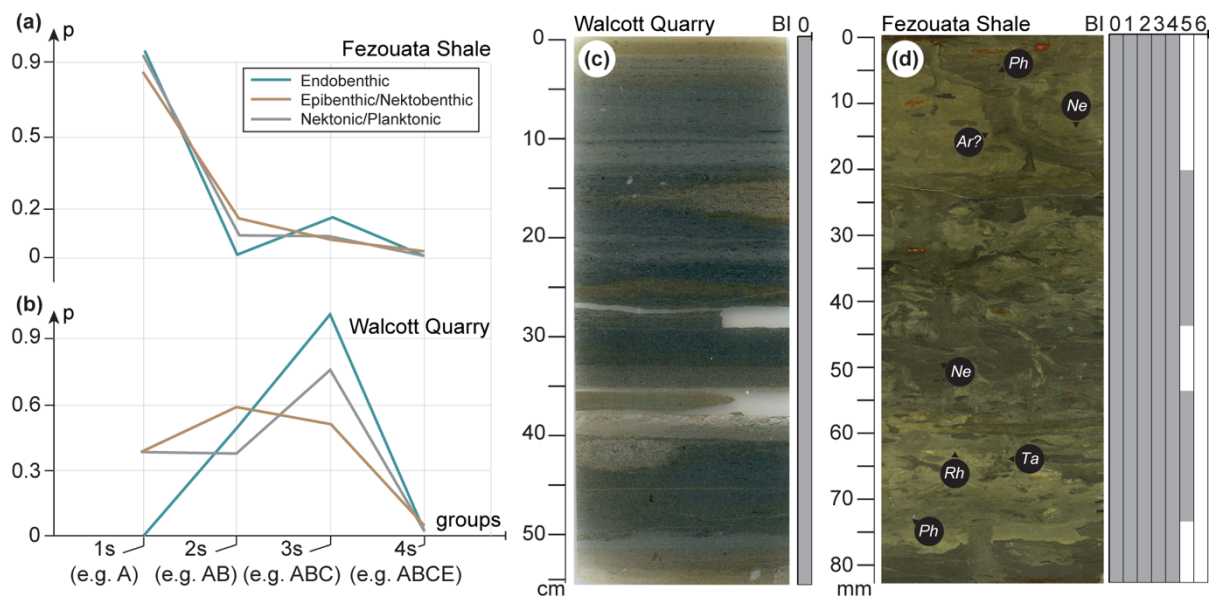


Figure 1. Differences in proportions of genera (Y-axis) between single (e.g., A, B, C), paired (e.g., AB, BC, CE), triple (e.g., ABC, ACE) and quadruple (e.g., ABCE) character categories (marked as 1s, 2s, 3s, and 4s on the X-axis) and modes of life in the Fezouata Shale (a), and the Walcott Quarry (b).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

4. DISCUSSION

4.1. Linking ecology to preservation

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

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

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

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

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

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

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

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

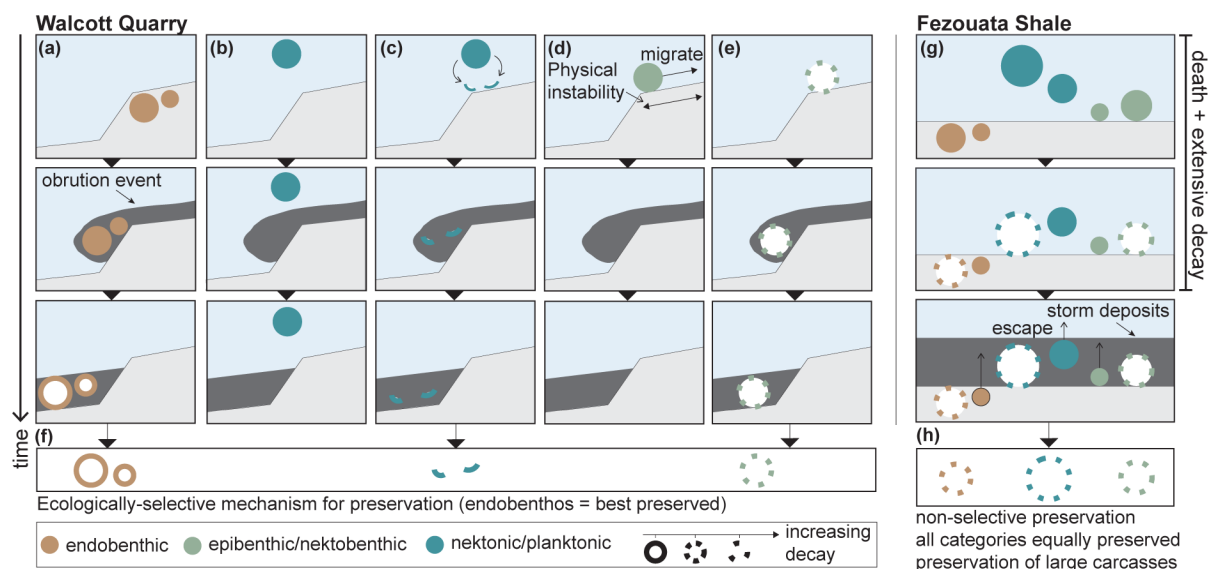


Figure 2. Taphonomic scenarios in the Walcott Quarry and the Fezouata Shale. Walcott Quarry: endobenthic taxa are entrained alive and cannot escape the produced mud-rich deposit and are freshly preserved (a). Nektonic/planktonic taxa living high in the water column can avoid transported sediments (b).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

4.2. Implications in understanding Cambrian ecosystems

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

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

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

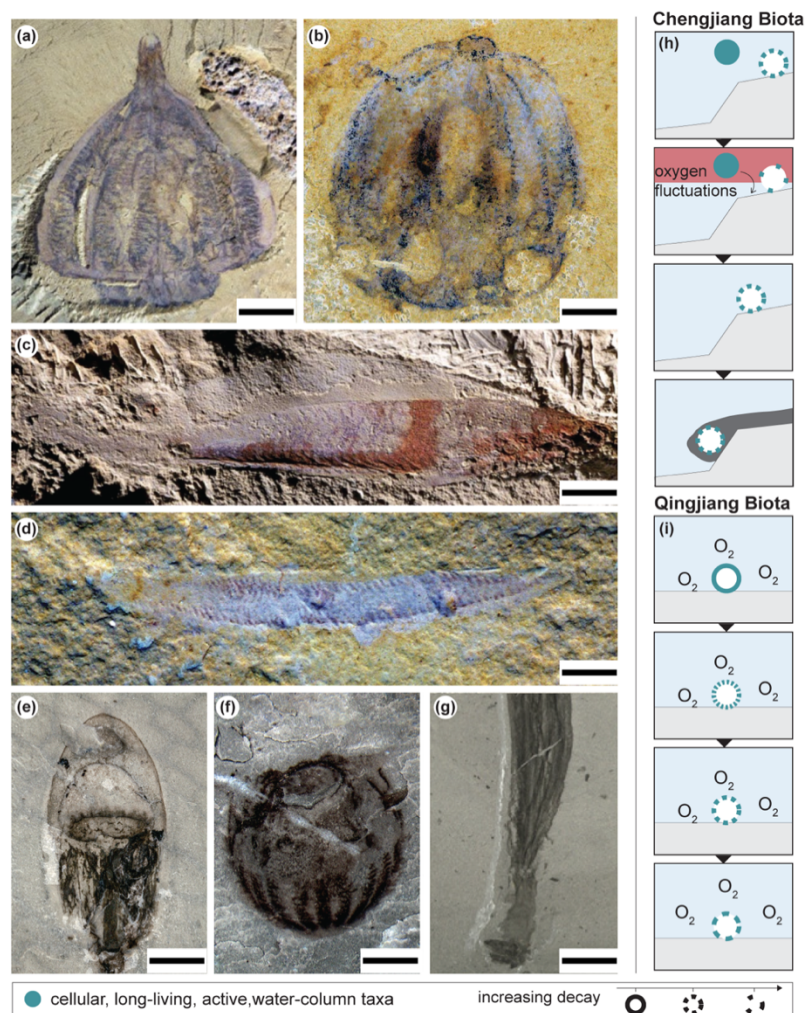


Figure 3. Ecological and preservational discrepancies between Cambrian Burgess Shale-type deposits. Ctenophores from the Chengjiang Biota: (a) *Galeactena hemispherica* (YKLP13810, 5mm scale-bar) (Ou et al., 2015), and (b) *Maotianoascus octonarius* (RCCBYU10217; 1.5mm scale-bar) (Ou et al., 2015). Chordates from the Chengjiang Biota: (c) *Mylokunmingia fengjiao* (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

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

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

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