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- 1 Taphonomic bias in exceptionally preserved biotas
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15 ABSTRACT

16 Exceptionally preserved fossil biotas provide crucial data on early animal evolution. 17 Fossil anatomy allows for reconstruction of the animal stem lineages, informing the stepwise 18 process of crown group character acquisition. However, a confounding factor to these 19 evolutionary analyses is information loss during fossil formation. Here we identify a clear 20 taphonomic differentiation between the Cambrian Burgess Shale and Chengjiang Biota, and 21 Ordovician Fezouata Shale. In the Fezouata Shale, soft cellular structures are most commonly 22 associated with partially mineralized and sclerotized tissues, which may be protecting the soft 23 tissue. Also, entirely soft non-cuticularized organisms are absent from the Fezouata Shale. 24 Conversely, the Cambrian sites commonly preserve entirely soft cellular bodies and a higher 25 diversity of tissue types per genus. The Burgess and Chengjiang biotas are remarkably 26 similar, preserving near identical proportions of average tissue types per genus. However, the 27 Burgess shale has almost double the proportion of genera that are entirely soft as compared to 28 the Chengjiang Biota, indicating that the classic Burgess Shale was the acme for soft tissue 29 preservation. Constraining these biases aids the differentiation of evolutionary and 30 taphonomic absences, which is vital to incorporating anatomical data into a coherent 31 framework of character acquisition during the earliest evolution of animals.

32

33 INTRODUCTION

34 Exceptionally preserved biotas have revolutionized our understanding of animal 35 origins and evolution owing to the preservation in these deposits of soft-bodied and lightly 36 sclerotized organisms, which under normal circumstances have little to no fossilization 37 potential (Butterfield, 1995). Burgess Shale-type (BST) preservation deposits including the 38 Burgess Shale (Wuliuan, Miaolingian; ~505 Ma, Canada) and the Chengjiang Biota (Stage 3, 39 Cambrian Series 2; ~530 Ma, China) are particularly famous Lagerstätten, yielding hundreds 40 of exceptionally preserved Cambrian taxa (Fig. 1a-c) critical to our understanding of the 41 earliest metazoan-dominated communities and evolutionary events such as the Cambrian 42 Explosion (Daley et al., 2018). The youngest of these deposits, the Fezouata Shale, is the only Ordovician (Tremadocian; ~479-478 Ma, Morocco) Lagerstätte to yield a diverse 43

44 exceptionally preserved fauna (Fig. 1d-f). With over 185 taxa of marine invertebrates (Van 45 Roy et al., 2015a) recovered from specific intervals in the Zagora area (Lefebvre et al., 2018; 46 Saleh et al., 2018, 2019), this formation offers new insights into the diversification of 47 metazoans, at a key interval between the Cambrian Explosion and the Ordovician Radiation 48 (Van Roy et al., 2010, 2015b; Lefebvre et al., 2019). Despite being anatomically and 49 biologically informative, even these spectacular fossil localities inevitably have taphonomic 50 biases, because no fossil site can ever be a perfect replication of all the anatomical and 51 ecological information of a living community (Butterfield, 2003; Brasier et al., 2010; Landing 52 et al., 2018). Gathering "complete" data is impossible even in studies on modern living 53 communities. It is therefore essential to understand what factors may be affecting the fossil 54 preservation at a community level in order to properly reconstruct ancient ecosystems and 55 biodiversity fluctuations over geological time.

56 The aim of this study is to examine the taphonomic signal of these deposits, allowing a solid 57 understanding of the preservation bias at play in each locality. For this reason, a taphonomic 58 classification of all eumetazoan genera from the Fezouata Shale (N=178) was established, 59 and compared with the preservation of genera from the Burgess Shale (N=103) and the 60 Chengjiang Biota (N=133) based on the presence / absence of different types of anatomical 61 structures: (A) biomineralized skeletons, (B) sclerotized parts (i.e. possessing an organically 62 strengthened part or organ) (C) soft with an unsclerotized cuticle (i.e. a non-cellular outer body surface that is either collagenous or formed by polymerized polysaccharides), (D) soft 63 64 cellular outer layer defining at least a part of the body (e.g. tentacles of hyoliths), and (E) soft 65 internal cellular organ/tissue (e.g. digestive or nervous systems) (Fig.1).

66

67 MATERIAL AND METHODS

In order to define the preservation pattern in all three exceptionally preserved biotas, the various possible co-occurrences of characters A (biomineralized), B (sclerotized), C (unsclerotized, cuticularized), D (cellular body walls), and E (internal tissues) were tallied (e.g. AB, AC, CDE, and ABCDE) (Tab. 1). To avoid any overlap between categories, the data were analyzed on a five-fold Venn diagram per site. In order to see if there is any difference

73 between sites, the total number of genera having just one character regardless of its nature 74 (e.g. A, or B, or C, or D, or E) was plotted against the number of genera that have pairs (e.g. 75 AB), threes (e.g. ABC) or fours (e.g. ABCD) for all exceptionally preserved biotas (Fig. 2). 76 Afterward, the average number of tissue types per genus, as derived from the dataset, was 77 calculated by adding the probability of the occurrence of all classes of structures A, B, C, D, 78 and E (Tab. 2). In order to constrain the categories causing the biggest variations in 79 preservation between sites, plots were made to show the proportion of paired and triple 80 categories in localities (Fig. 3).

81 The association of soft internal organs (E) with other structures, in all three localities 82 was also investigated. For this, the probabilities of discovering two classes of structures 83 together having already found one of them were calculated (Tab. 3). For example, p(E|A) is 84 the probability of E occurring if A has occurred. The reverse conditional approach was also 85 made and the probability of finding A given that E has been found p(AlE) was also calculated 86 (Tab. 3). Then, the likelihood of producing the distribution of combinations of structures 87 found in the Burgess Shale and the Chengjiang Biota assuming that the Fezouata Shale has 88 the "true" preservation regime was investigated using the following parametrized binomial 89 $P(x \ge n) | Bi(n, p):$

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

90 In this equation, p = p(E|A) for the Fezouata Shale, q = 1-p, n is the number of genera 91 preserving an A in the Burgess Shale or the Chengjinag Biota, and x is the number of desired 92 success which is, in this case, at least the actual number n of genera preserving both A and E 93 in the Burgess Shale/Chengjiang Biota. All calculated probabilities are added up and the 94 probability $P(x \ge n) \mid Bi(n, p)$, of producing the actual Burgess Shale/Chengjinag Biota AE 95 category, considering that the Fezouata Shale regime is "true", is then obtained (Tab. 4). This 96 was then performed for other tissues combinations (i.e. BE, CE, and DE) (Tab. 4). This 97 approach was then extended to the assumption that the Burgess Shale preservation 98 distribution is "true" and finally assuming that the Chengjiang Biota preservation distribution 99 is the "true" preservation model (Tab. 5).

Finally, the probability of finding organisms with only soft cellular tissues (both internal and external to the exclusion of everything else with A' for instance indicating the set that is defined as not containing and members of A) $p(A' \cap B' \cap C' \cap D \cap E|E)$ for all three *Lagerstätten* was calculated.

104

105 **RESULTS**

106 All three Lagerstätten preserve numerous biomineralized skeletons (A), sclerotized 107 parts (B), unsclerotized, soft cuticular parts (C), and internal soft parts (E) (Tab. 1). However, 108 genera having cellular body walls defining the entire body (i.e. D, DE), with or without 109 internal organs (E) are absent in the Fezouata Shale. In comparison the Chengjiang Biota (9 110 genera) and the Burgess Shale (13 genera) have a considerable number of entirely soft 111 organisms preserved (Tab. 1). Further, numerous biomineralized and sclerotized genera in the 112 Burgess Shale and the Chengjiang Biota preserve external soft tissues defining a part of the 113 body (i.e. AD, BD, BDE, ACDE) (Tab. 1). These genera are absent from the Fezouata Shale, 114 with the exception of two specimens of aculiferan molluscs (both, however, densely covered 115 by sclerites). The Burgess Shale and the Chengjiang Biota preserve almost twice as many 116 tissues per genus as the Fezouata Shale (Fig. 2), with the mean number of tissue types per 117 genus in the Cambrian sites being 2.2 (Burgess = 2.206; Chengjiang = 2.185) whilst it is 118 1.316 for the Fezouata Shale (Tab. 2). The overall distribution of tissue frequency by genus 119 are similar for the Burgess Shale and the Chengjiang Biota, with mean and variance 120 suggesting they are drawn from comparable if not identical populations (variance Burgess 121 Shale = 0.026; Chengjiang Biota = 0.030; t = -0.45, p(same mean) = 0.6532; F = 1.154, 122 p(same variance) = 0.454). However, the distribution for the Fezouata Shale is very different 123 (variance = 0.08034), with both t and F-tests reporting significance for the mean and variance 124 respectively when compared to Burgess Shale (t = 29.53, p(same mean) = 1.035×10^{37} ; F = 125 3.0685, p(same variance) = $3.195 \times 10^{\circ}$) and the Chengjiang Biota (t = 32.34, p(same mean) = 126 3.414×10^{101} ; F = 2.5591, p(same variance) = 1.718×10^{8}).

127 The three studied localities show a dominance of both BCE and ACE categories (Fig.128 3). This is at least partly linked to the high number of arthropods found at all localities, with

129 their external anatomy often consisting of ventral unsclerotized cuticle (C) and a reinforced 130 dorsal area consisting of a biomineralized exoskeleton (A) or scleritized cuticle (B), found in 131 conjunction with internal soft parts (E). However, when the preservation of two tissue types 132 occurs in the Fezouata Shale, it consists mostly of the association of biomineralized skeletons 133 and internal soft tissues (AE is 9 of the 21 pairs that consist of the possible sets AB, AC, AD, 134 AE, BC, BD, BE, CD, CE, DE), sclerotized tissue and internal soft tissue (7 of the 21 pairs), 135 and biominerals and sclerotized tissue (3 of 21 pairs). All other tissue associations are rare or 136 absent. In the Burgess Shale, the dominant association is between cellular soft bodied tissues 137 and internal organs (13 of 36 pairs), with sclerotized and cuticularized tissues also commonly 138 associated (7 of 36 pairs). In the Chengjiang Biota, the dominant association is between 139 sclerotized and cuticularized tissues (16 of 57 pairs), with additional common associations 140 between cuticularized tissues and internal organs (12 of 57 pairs), cellular soft bodied tissues 141 and internal organs (9 of 57 pairs), and biominerals and sclerotized tissues (8 of 57 pairs) 142 (Fig. 3). The probabilities of finding internal soft tissues in a given fossil genus, in co-143 occurrence with any of the other types of structures, show that the distribution of tissues in the 144 Burgess Shale and the Chengjiang Biota are much more similar to each other (Tab. 3) and are 145 significantly different from the Fezouata Shale (Tab. 4). In the Fezouata Shale, only a small 146 proportion of all biomineralized genera also preserve internal organs (p(E|A) = 0.162) (Tab. 147 3), but of the genera that do have internal organs the majority are associated with biominerals 148 ((A|E) = 0.667) (Tab. 3). This means that although a biomineral does not guarantee the 149 preservation of internal anatomies, it could still be seen as a very helpful pre-requisite in the 150 Fezouata Shale. Conversely, biominerals in paleoenvironments such as the Burgess Shale and 151 the Chengjiang Biota do not seem to have any role in soft tissue preservation (p(A|E) = 0.183)152 and p(A|E) = 0.273 for the Burgess Shale and the Chengjiang Biota respectively, which are 153 not significantly different to chance association (Tab. 3). The result of probabilistic modelling 154 (Tab. 4) shows that the distributions of tissue associations found at the Fezouata Shale cannot 155 be generated by randomly sampling a biota with a similar composition to that of either the 156 Chengjiang Biota or the Burgess Shale, and in all possible soft tissue combinations the 157 Fezouata Shale is statistically significantly different to both of the Cambrian biotas studied 158 (Tab. 4). Finally, it is worth noting that the absence of entirely soft bodied organisms at the 159 Fezouata Shale is not just a striking observation, but it is also statistically significant from the 160 proportions found at the Cambrian sites. The absence of entirely soft bodied organisms at the 161 Fezouata Shale cannot be generated by randomly sampling a population like that found in the 162 Cambrian sites with any confidence (with p-values of 0.00137 and 0.03819 for Burgess Shale 163 and Chengjiang Biota models respectively). Therefore, the Burgess Shale $(p(D \cap E|E) =$ 164 0.2167) and the Chengjiang Biota ($p(D \cap E|E) = 0.113$) both show significantly higher 165 probabilities of recovering entirely soft bodied genera. The preservation of entirely soft 166 bodied genera is also different between the Chengjiang Biota and the Burgess Shale (Tab. 3), 167 with the higher incidence being found in the Burgess Shale. This difference is significant and 168 could not be generated by chance or subsampling (Tab. 5).

169

170 **DISCUSSION**

171 Soft part preservation in the Fezouata Shale is strikingly different from the 172 preservation in the Chengjiang Biota and the Burgess Shale. This difference in the occurrences of soft tissues cannot result from a collection bias, because all three localities 173 174 were subjected to collecting efforts that actively focused on finding and sampling fossils with 175 labile soft part in various depositional settings and stratigraphic levels. Instead, the observed 176 pattern of preservation suggests that the presence of non-cellular layers covering internal 177 anatomies in the Fezouata Shale was essential for exceptional preservation, unlike at the 178 Burgess Shale and Chengjiang Biota. The near complete absence of preserved external soft 179 tissues is possibly related to them being less decay-resistant than mineralized, sclerotized or 180 even cuticularized structures. Under most circumstances, even unsclerotized soft cuticle is 181 more decay resistant than cellular tissue, because cuticular structures are not subject to 182 autolysis, and the composition of complex polymerized polysaccharides means cuticle is more 183 difficult to break down than cellular tissues (Briggs and Kear, 1993). The decay-resistance of 184 complex biopolymers found in the cuticle was also recently invoked to explain the rare but 185 selective preservation of cuticularized organisms in coarse clastic sediments (MacGabhann et 186 al., 2019).

7

187 In the Fezouata Shale, there was a pathway of preservation in place that systematically 188 failed to preserve (i) almost all soft-bodied organisms lacking a cuticular cover in particular, 189 and (ii) external soft cellular tissues in general. In this deposit, dead individuals experienced 190 harsh decay prior to their preservation owing to a relative burial tardiness in comparison with 191 the Burgess Shale and the Chengjiang Biota in which fossils were killed and preserved 192 directly during an obrution event (Saleh et al., 2018). This decay may also have been retarded 193 by berthierine, a mineral that can slow down microbial activity through the oxidative damage 194 of bacterial cells (McMahon et al., 2016; Anderson et al., 2018; Saleh et al., 2019). Therefore, 195 in contrast to the Burgess Shale and the Chengjiang Biota, the external conditions at the 196 Fezouata Shale were generally less permissive for the preservation of external soft tissues. 197 However, resistant skeletal parts and cuticular external surfaces created isolated environments 198 within the carcasses that maintained a chemical equilibrium conducive to the preservation of 199 internal organs.

200 The systematic taphonomic bias described here for the Fezouata Shale has 201 implications for understanding the original faunal community assemblage, specifically in 202 regard to the proportions of genera preserved in the fossil record. The systematic removal of 203 all soft-bodied organisms, lacking a non-cellular external envelope (cuticle), and external 204 cellular soft tissues leads to an underestimation of the original diversity at the Cambro-205 Ordovician transition and distorts faunal composition to a greater extent than in the Burgess 206 Shale or the Chengjiang Biota. Many animal groups could have lived in the Fezouata Shale 207 environment but left little to no trace behind, such as chordates (e.g. Pikaia, Metaspriggina). 208 A corollary of this finding is that it is now possible to differentiate between ecological and 209 taphonomic absences of numerous genera. For example, the absence of priapulids such as 210 Ottoia in the Fezouata Shale (Van Roy et al., 2015a) is likely a real aspect of the fauna, since 211 these cuticle-bearing soft-bodied animals would not have been affected by the same 212 taphonomic bias responsible for the removal of the majority of soft-bodied genera lacking a cuticle. 213

Now that a source of systematic taphonomic bias operating in the Fezouata Shale has been identified (Fig. 4), and most importantly, compared to the biases in play in the Burgess Shale and the Chengjiang Biota (Fig. 4), it can be accounted for in future paleoecological and evolutionary analyses. This will facilitate more accurate comparisons of faunal community compositions between these biotas in particular, and when comparing exceptionally preserved faunas in general, as similar restrictive mechanisms are likely active to a varying extent at other localities.

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284

285 TABLES AND FIGURES

Table 1. Number of genera in different categories in all exceptionally preserved biotas.

Table 2. Proportion of each type of tissue in all categories combined in the Fezouata Shale, the Burgess Shale and the Chengjiang Biota. The probability of preserving cuticularized and cellular tissues, in addition to the number of tissue per genus in the Fezouata Shale are lower than in the Chengjiang Biota and the Burgess Shale.

Table 3. Probabilities of finding internal soft tissues in a fossil given that another tissue was found and vice versa. The obtained numbers for the Burgess Shale and the Chengjiang Biota are more similar to each other than to the Fezouata Shale.

Table 4. Probabilities of reproducing patterns of preservation of the Burgess Shale and the Chengjiang Biota assuming that the Fezouata Shale preservation regime is true. All probabilities are smaller than 0.05 showing that the preservation regime in the Fezouata Shale is different from both the Chengjiang Biota and the Burgess Shale.

Table 5. A: Probabilities of reproducing patterns of preservation of the Burgess Shale assuming that the Chengjiang biota preservation regime is true. B: Probabilities of reproducing patterns of preservation of the Chengjiang Biota assuming that the Burgess Shale preservation regime is true. Some tissue associations are not reproducible in both models (i.e. marked as "No" in the "Pass" column), showing that the pattern of preservation between theBurgess Shale and the Chengjiang Biota is not exactly the same.

304 Figure 1. Fossils from the three studied exceptionally preserved biotas showing examples of 305 tissue associations. (a) Burgess Shale Eldonia USNM57540b preserving soft cellular body 306 walls and internal organs (i.e. DE). (b) Branchiocaris pretiosa from the Burgess Shale 307 USNM189028nc showing the association of sclerotized and cuticularized parts in addition to 308 internal organs (BCE). (c) Anomalocaris saron ELRC20001a from the Chengjiang Biota 309 belonging as well to the BCE category. (d) Marrellid arthropod from the Fezouata Shale AA-310 BIZ31-OI-39 preserving both sclerotized and cuticularized structures (BC). (e) Fezouata Shale stylophoran AA.BIZ.15.OI.259 showing the association of biominerals and internal 311 312 organs (AE). (f) Solutan from the Fezouata shale belonging also to the AE category.

Figure 2. Differences in proportions of genera (Y axis) between single, paired, triple and quadruple character categories (marked as 1, 2, 3, and 4 on the X axis) between the Fezouata Shale, the Burgess Shale and the Chengjiang Biota. The Fezouata Shale shows a dominance of genera preserving only one tissue when compared to the Burgess Shale and Chengjiang Biota.

Figure 3. Pie charts showing the differences in paired and triple character categories betweenthe Fezouata Shale, the Burgess Shale, and the Chengjiang Biota.

Figure 4. Preservation differences between exceptionally preserved biotas and one non-*Lagerstätte* (i.e. preservation of only mineralized genera). The Chengjiang biota and the Burgess Shale preserve more tissue-types than the Fezouata Shale in which soft tissues in direct contact with sea water are not preserved.









Burgess Shale & Chengjiang biota

	Fezouata Shale	Burgess Shale	Chengjiang Biota
А	90	15	4
В	41	7	9
С	3	0	6
D	0	1	4
E	1	0	0
AB	3	5	8
AC	0	2	2
AD	1	1	0
AE	9	1	0
BC	7	7	16
BD	0	1	4
BE	1	2	6
CD	0	0	0
CE	0	4	12
DE	0	13	9
ABC	0	2	0
ABD	0	0	0
ABE	5	0	2
ACD	0	0	0
ACE	1	8	19
ADE	0	0	0
BCD	0	0	0
BCE	7	28	28
BDE	0	2	1
CDE	0	0	0
ABCD	0	0	0
ABCE	3	1	1
ACDE	0	1	0
ACDE	0	0	0
BCDE	0	0	0
ABCDE	0	0	0

	Fezouata Shale	Burgess Shale	Chengjiang Biota
	N(total)=173	N(total)=101	N(total)=133
А	N(A)=112	N(A)= 36	N(A) = 36
	p(A)=0.647	p(A)=0.356	p(A) = 0.270
В	N(B)=67	N(B)=55	N(B)=75
	p(B) = 0.387	p(B)=0.544	p(B)=0.563
С	N(C)=21	N(C)=53	N(C)=84
	p(C) = 0.121	p(C)=0.524	p(C)=0.631
D	N(D)=1	N(D)=19	N(D)=18
	p(D)=0.005	p(D)=0.188	p(D)=0.135
E	N(E)=27	N(E)=60	N(E)=78
	p(E)=0.156	p(E)=0.594	p(E)=0.586
Total = tissue/genus	1.316	2.206	2.185

	Fezouata Shale	Burgess Shale	Chengjiang Biota
p(ElA)	0.162	0.306	0.611
p(ElB)	0.239	0.607	0.507
p(ElC)	0.524	0.789	0.714
p(ElD)	0	0.842	0.556
p(AlE)	0.667	0.183	0.278
p(BIE)	0.593	0.567	0.481
p(ClE)	0.407	0.683	0.759
p(DIE)	0	0.267	0.127

	Burgess Shale	Chengjiang Biota
p(E A)	P(X≥11) Bi(36, 0.162)	P(X≥22) Bi(36, 0.162)
	= 0.0235	< 0.000001
p(E B)	P(X≥34) Bi(56, 0.239)	P(X≥38) Bi(75, 0.239)
	< 0.000001	< 0.000001
p(E C)	P(X≥41) Bi(52, 0.524)	P(X≥60) Bi(84, 0.524)
	= 0.0000738	= 0.000291
p(E D)	0	0