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1 **Taphonomic bias in exceptionally preserved biotas**

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14 **Keywords:** Exceptional preservation, taphonomy, Cambrian, Ordovician

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
43 Ordovician (Tremadocian; ~479-478 Ma, Morocco) *Lagerstätte* to yield a diverse

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
63 body surface that is either collagenous or formed by polymerized polysaccharides), (D) soft
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**

68 In order to define the preservation pattern in all three exceptionally preserved biotas,
69 the various possible co-occurrences of characters A (biomineralized), B (sclerotized), C
70 (unsclerotized, cuticularized), D (cellular body walls), and E (internal tissues) were tallied
71 (e.g. AB, AC, CDE, and ABCDE) (Tab. 1). To avoid any overlap between categories, the data
72 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(A|E) 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 $P(x \geq n) | \text{Bi}(n, p)$:

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

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 $P(x \geq n) | \text{Bi}(n, p)$, 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).

100 Finally, the probability of finding organisms with only soft cellular tissues (both
101 internal and external to the exclusion of everything else with A' for instance indicating the set
102 that is defined as not containing and members of A) $p(A' \cap B' \cap C' \cap D \cap E | E)$ for all three
103 *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; $t = -0.45$, $p(\text{same mean}) = 0.6532$; $F = 1.154$,
122 $p(\text{same variance}) = 0.454$). 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 ($t = 29.53$, $p(\text{same mean}) = 1.035 \times 10^{-57}$; $F =$
125 3.0685 , $p(\text{same variance}) = 3.195 \times 10^{-9}$) and the Chengjiang Biota ($t = 32.34$, $p(\text{same mean}) =$
126 3.414×10^{-101} ; $F = 2.5591$, $p(\text{same variance}) = 1.718 \times 10^{-8}$).

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 sclerotized 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
173 occurrences of soft tissues cannot result from a collection bias, because all three localities
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).

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
213 cuticle.

214 Now that a source of systematic taphonomic bias operating in the Fezouata Shale has
215 been identified (Fig. 4), and most importantly, compared to the biases in play in the Burgess

216 Shale and the Chengjiang Biota (Fig. 4), it can be accounted for in future paleoecological and
217 evolutionary analyses. This will facilitate more accurate comparisons of faunal community
218 compositions between these biotas in particular, and when comparing exceptionally preserved
219 faunas in general, as similar restrictive mechanisms are likely active to a varying extent at
220 other localities.

221

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272

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284

285 **TABLES AND FIGURES**

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

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

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

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

298 Table 5. A: Probabilities of reproducing patterns of preservation of the Burgess Shale
299 assuming that the Chengjiang biota preservation regime is true. B: Probabilities of
300 reproducing patterns of preservation of the Chengjiang Biota assuming that the Burgess Shale
301 preservation regime is true. Some tissue associations are not reproducible in both models (i.e.

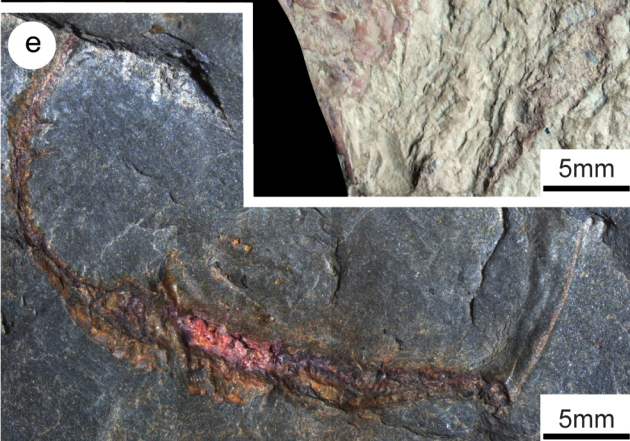
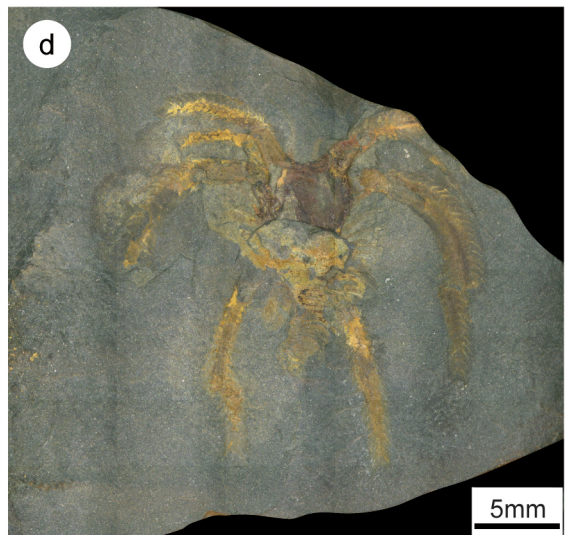
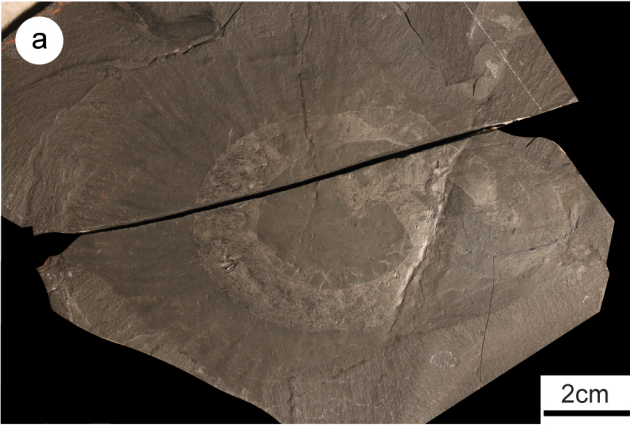
302 marked as “No” in the “Pass” column), showing that the pattern of preservation between the
303 Burgess Shale and the Chengjiang Biota is not exactly the same.

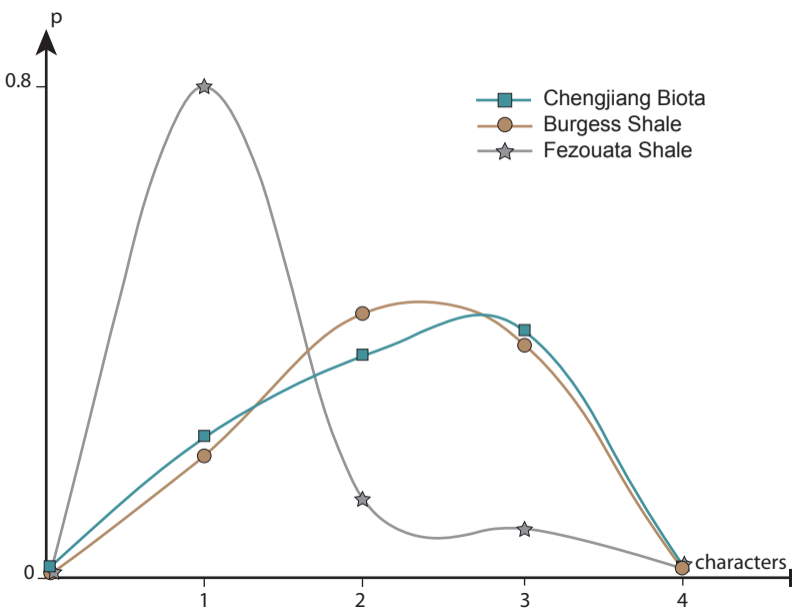
304 Figure 1. Fossils from the three studied exceptionally preserved biotas showing examples of
305 tissue associations. (a) Burgess Shale *Eldonia* USNM57540b preserving soft cellular body
306 walls and internal organs (i.e. DE). (b) *Branchiocaris pretiosa* from the Burgess Shale
307 USNM189028nc showing 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
311 Shale stylophoran AA.BIZ.15.OI.259 showing the association of biominerals and internal
312 organs (AE). (f) Solutan from the Fezouata shale belonging also to the AE category.

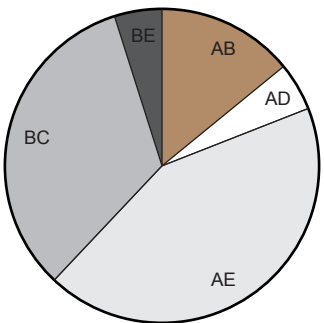
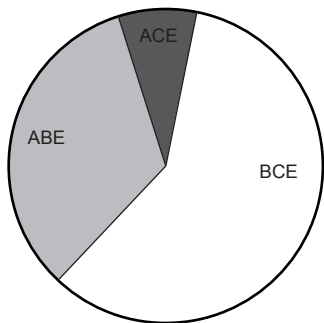
313 Figure 2. Differences in proportions of genera (Y axis) between single, paired, triple and
314 quadruple character categories (marked as 1, 2, 3, and 4 on the X axis) between the Fezouata
315 Shale, the Burgess Shale and the Chengjiang Biota. The Fezouata Shale shows a dominance
316 of genera preserving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

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

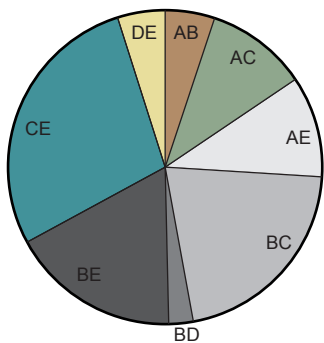
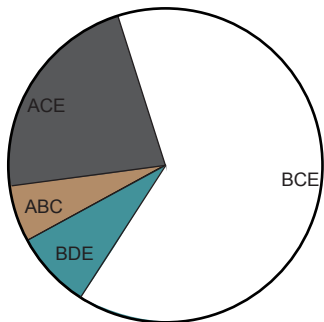
320 Figure 4. Preservation differences between exceptionally preserved biotas and one non-
321 *Lagerstätte* (i.e. preservation of only mineralized genera). The Chengjiang biota and the
322 Burgess Shale preserve more tissue-types than the Fezouata Shale in which soft tissues in
323 direct contact with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



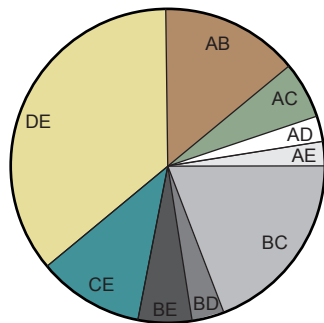
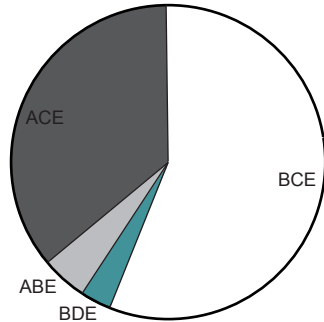




Fezouata Shale

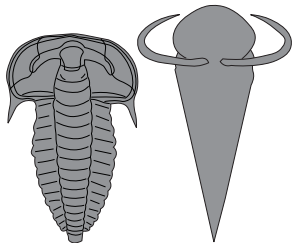


Chengjiang Biota

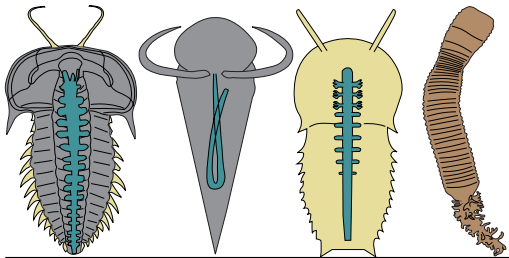


Burgess Shale

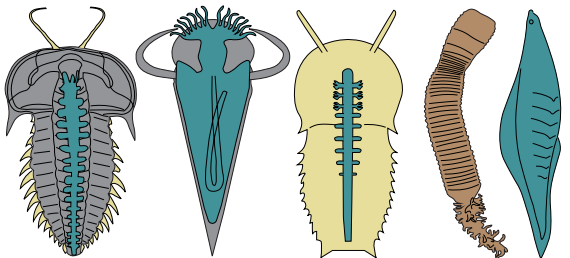
A: Biomineralized B: Sclerotized C: Cuticularized D: Outer cellular tissues E: Internal cellular tissues



Non-Lagerstätte



Fezouata Shale



Burgess Shale & Chengjiang biota

- Cellular tissues
- Cuticularized
- Sclerotized
- Biomineralized

	Fezouata Shale	Burgess Shale	Chengjiang Biota
A	90	15	4
B	41	7	9
C	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

Table 1

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

Table 2

	Fezouata Shale	Burgess Shale	Chengjiang Biota
p(E A)	0.162	0.306	0.611
p(E B)	0.239	0.607	0.507
p(E C)	0.524	0.789	0.714
p(E D)	0	0.842	0.556
p(A E)	0.667	0.183	0.278
p(B E)	0.593	0.567	0.481
p(C E)	0.407	0.683	0.759
p(D E)	0	0.267	0.127

Table 3

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

Table 4