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1 **New fossil assemblages from the Early Ordovician Fezouata Biota**

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33 **ABSTRACT**


34 The Fezouata Biota (Morocco) is a unique Early Ordovician fossil assemblage. The discovery of  
35 this biota revolutionized our understanding of Earth's early animal diversifications – the Cambrian  
36 Explosion and the Ordovician Radiation – by suggesting an evolutionary continuum between both  
37 events. Herein, we describe Taichoute, a new fossil locality from the Fezouata Shale. This locality  
38 extends the temporal distribution of fossil preservation from this formation into the upper Floian,  
39 while also expanding the range of depositional environments to more distal parts of the shelf. In  
40 Taichoute, most animals were transported by density flows, unlike the *in-situ* preservation of  
41 animals recovered in previously investigated Fezouata sites. Taichoute is dominated by three-  
42 dimensionally preserved, and heavily sclerotized fragments of large euarthropods – possibly  
43 representing nektobenthic/nektic bivalved taxa and/or radiodonts. Resolving whether this  
44 dominance reflects a legitimate aspect of the original ecosystem or a preservational bias requires  
45 an in-depth assessment of the environmental conditions at this site. Nevertheless, Taichoute  
46 provides novel preservational and palaeontological insights during a key evolutionary transition in  
47 the history of life on Earth.

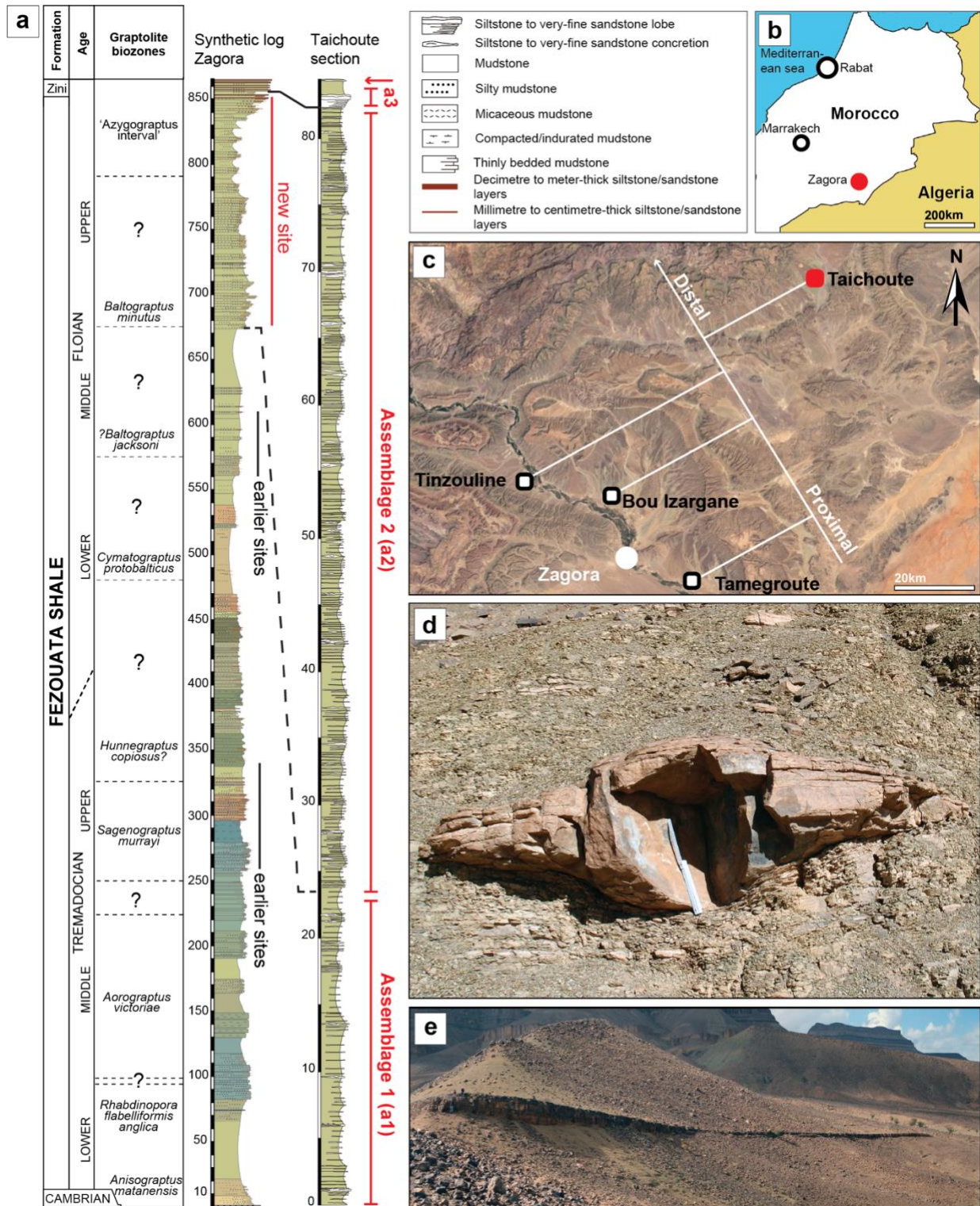
48

49 **KEYWORDS:** Palaeozoic, Morocco, exceptional preservation, taphonomy, arthropods

50

51 **INTRODUCTION**

52 The Early Ordovician Fezouata Biota of Morocco is an exceptionally-preserved fossil assemblage  
53 that contains a combination of non-mineralized extinct organisms that have become synonymous  
54 with the Cambrian Explosion, such as radiodonts, halkieriids, lobopodians, nektaspidids, and  
55 marrellomorphs, alongside more derived forms that are representative of typical Palaeozoic faunas,  
56 such as xiphosurans, cheloniellids, and machaeridians<sup>1,2</sup>. To date, most palaeobiological research<sup>1-  
57 25</sup> has focused on Fezouata fossils that occur in either upper Tremadocian or middle Floian deposits  
58 in the Zagora region (Fig. 1a, b)<sup>26</sup>, covering to some extent, the proximal-distal axis of an ancient  
59 marine environment (Fig. 1c)<sup>27, 28</sup>. This environment was dominated by wave/storm processes<sup>29,  
60 30</sup>. The exceptionally well-preserved fossils in these deposits were buried *in situ* by storm-induced  
61 deposits close to the storm wave base (SWB)<sup>29-31</sup>. Lightly biomineralized or sclerotized animals  
62 in the Fezouata Biota are most commonly preserved in shales as weathered carbonaceous material  
63 (compressed to different degrees) and authigenic minerals<sup>32, 33</sup>. Preservation within concretions  
64 has also been reported from this formation (Fig. 1d), but this mode of fossilization is more  
65 restricted compared to shale-hosted macrofossils<sup>34</sup>. Most Fezouata Shale fossil collections are  
66 based on discoveries around the Zagora region in Morocco (e.g., Tamegroute, Bou Izargane, and  
67 Tinzouline) (Fig. 1b)<sup>32</sup>; with little effort spent prospecting fossiliferous localities outside this area.  
68 Here, we report a new and continuous fossiliferous section from the Fezouata Shale discovered in  
69 Taichoute, 80km away from previously investigated localities (Fig. 1a, c). We discuss the  
70 palaeontology, sedimentology, and possible preservational biases operational at this site.  
71 Taichoute expands the range of depositional environments yielding non-biomineralized fossils,  
72 reveals new modes of preservation from the Fezouata Shale, and expands the occurrence of fossil-  
73 bearing strata within this formation 

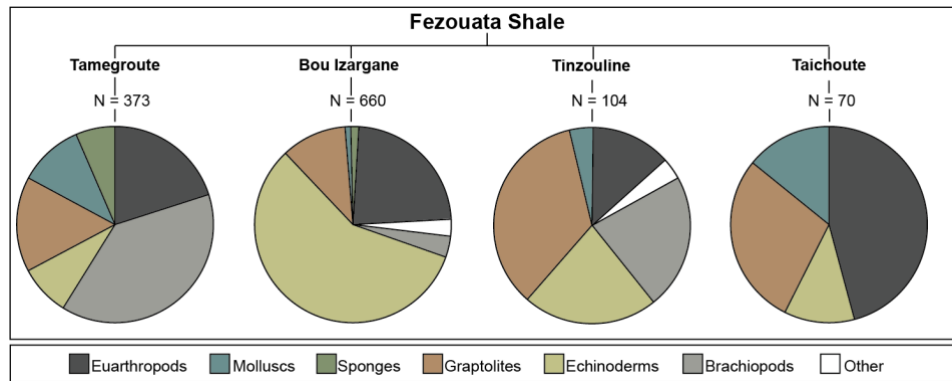


74  
 75 **Figure 1.** (a) Stratigraphic column for the Lower Ordovician Fezouata Shale and Zini Formation including the  
 76 Taichoute locality divided into three fossil assemblages. The red arrow in (a) indicates an accumulation level of  
 77 brachiopods and bryozoans at the top of the Taichoute section. (b) Zoom on the Zagora Region where the Fezouata  
 78 Shale is discovered. (c) Taichoute is the most distal site in the depositional environment of the Fezouata  
 79 Shale. (d) Concretion from the Zagora region. (e) A large lobe from the Fezouata Shale at the upper part of the succession (a3)  
 80 and interpreted as a density-flow deposit.

## 81 RESULTS AND DISCUSSION

### 82 Faunal content

83 Euarthropods, brachiopods, echinoderms, and graptolites constitute together most of the preserved  
84 biodiversity in the Fezouata Biota<sup>32</sup>, and this pattern is replicated in the newly described Taichoute  
85 locality (Fig. 2). Some animal groups such as sponges, found in some other localities (e.g.,  
86 Tamegroute and Bou Izargane), remain, so far, absent from Taichoute (Fig. 2).

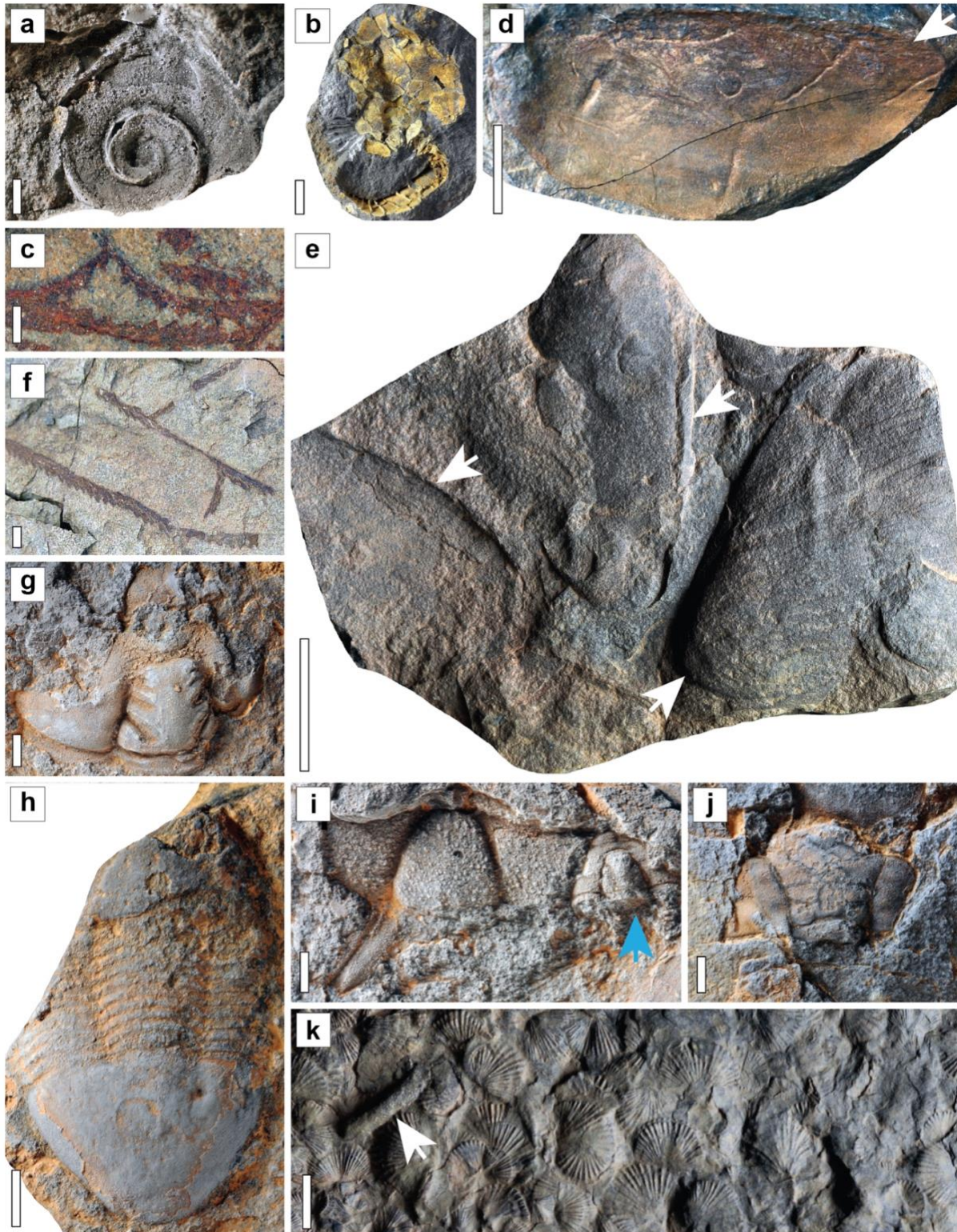


87  
88 **Figure 2.** Faunal composition and specimen abundances for each animal group at different Fezouata Shale localities  
89 based on the Marrakech Collections of the Cadi Ayyad University (Morocco). Note that the pie chart for Taichoute  
90 excludes the accumulation level of brachiopods and bryozoans (above a3, at the top of the succession), as it is  
91 impossible to count fossil specimens on this bed. This figure does not account for all specimens recovered/observed  
92 at outcrops. For information on how this data was collected and plotted, kindly refer to the Material and Methods  
93 section.




94  
95 Taichoute can be categorized by three distinct assemblages based on their diversity and  
96 preservation (a1, a2, and a3; Fig. 1a). The lowermost assemblage (a1) consists of brachiopods,  
97 molluscs (Fig. 3a), echinoderms (Fig. 3b), and graptolites (Fig. 3c). A middle Floian age for  
98 assemblage a1 can be inferred by the occurrence of *Baltograptus* gr. *deflexus*<sup>8</sup> (Fig. 3c). Fossils  
99 from this interval are mainly found in concretions that typically contain a single specimen (e.g.,  
100 Fig. 3b). The preservation of minute details, showing various stages of disarticulation and the *in-*  
101 *situ* collapse of echinoderms, with no evidence of abrasion (Fig. 3b), indicate that these animals  
102 were not transported, and concretions formed while organisms were decaying on the seafloor  
103 below the SWB in a similar way to some previously described concretion-based preservation from  
104 the Zagora region<sup>2</sup>. Another type of concretion, preserving unrecognizable bioclasts transported  
105 by storm events and formed above the SWB, has also been previously described from the Zagora  
106 region<sup>29</sup>, but has not been found at Taichoute.

107 The intermediate interval a2 (Fig. 1a) yields concretions with low taxonomic diversity consisting  
108 mainly of nautiloid cephalopods, euarthropod fragments (Fig. 3d, e; 4), and graptolites (Fig. 3f),  
109 Although there is some variability in their morphology and appearance, the euarthropod carapaces  
110 are typically oval-shaped to elongate, and they are preserved with substantial convexity and/or  
111 artefacts of previous relief that suggests a heavily sclerotized original constitution (Fig. 3d, e; 4).  
112 Coupled with their large size, ranging from ca. 5 to 15cm in length (Fig. 3d, e, 4), and the presence  
113 of thickened marginal rims, we tentatively interpret them as corresponding to bivalved  
114 euarthropods and possibly elements of radiodonts (Fig. 3d, e, 4). Whilst preliminary, we argue that  
115 these affinities are the most plausible for the fragments considering the known diversity of  
116 euarthropods during the Early Ordovician, and the fact that giant radiodonts are well known from  
117 the Fezouata Shale<sup>5, 6</sup>. The observed euarthropod carapaces (Fig. 3d, e; 4) from Taichoute are

118 considerably larger than those described from early- and mid-Cambrian sites [e.g., *Balhuticaris*<sup>35</sup>;  
119 *Isoxys*<sup>36, 37</sup>; *Tuzoia*<sup>37, 38</sup>; *Branchiocaris*<sup>39,40</sup>, and *Tokummia*<sup>41</sup>], and are more comparable in size to  
120 stratigraphically younger euarthropods (e.g., phyllocarids) discovered in Silurian and Devonian  
121 taxa<sup>42, 43</sup>.

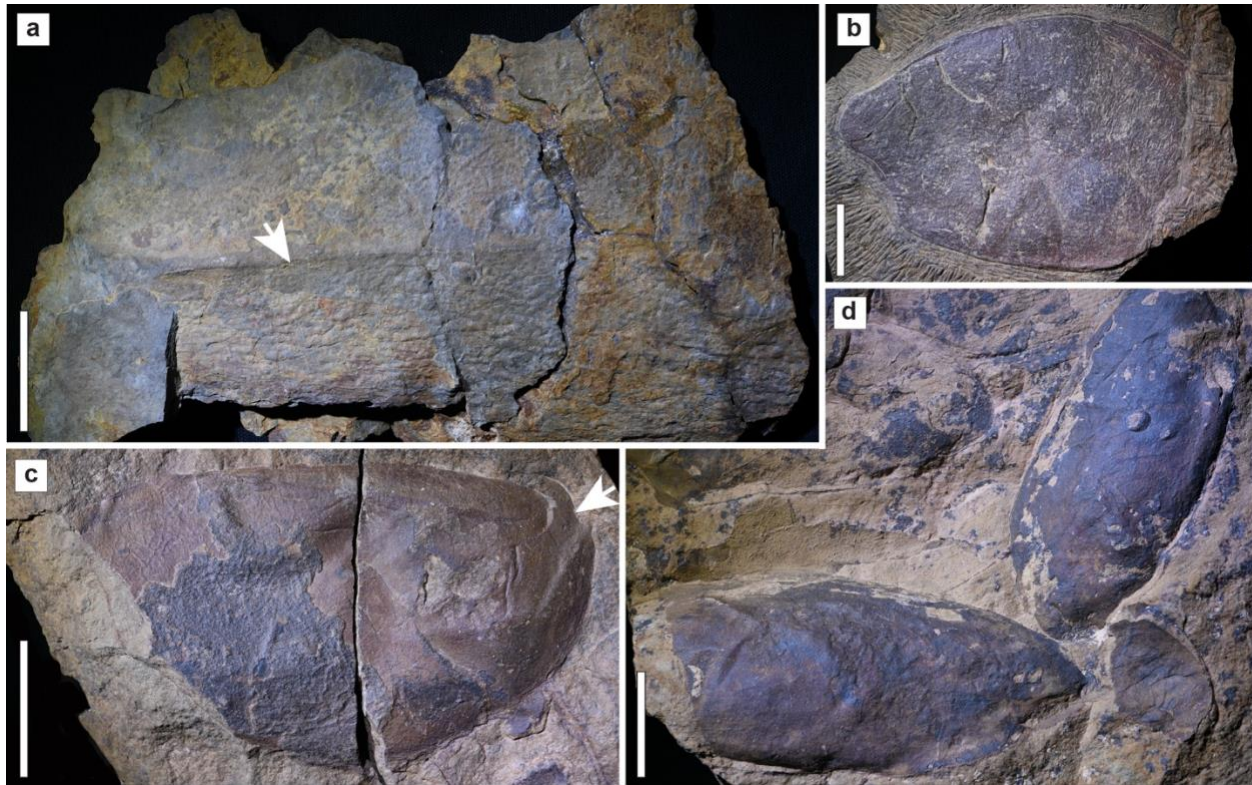


122

123 **Figure 3.** Fossils from the Taichoute locality (a1: A-C, a2: D-F, a3: G-J). (a) The gastropod *Lesueurilla prima*. (b)  
124 The solutan echinoderm *Plasiacystis mobilis*. (c) The graptolite *Baltograptus* gr. *deflexus*. (d-e) Giant euarthropod  
125 carapaces indicated with white arrows. (d) Carapace likely belonging to previously documented to bivalved arthropods  
126 from the Fezouata Biota<sup>59</sup>. (e) Two incomplete but tapering carapaces (left and center) adjacent to a structure that  
127 bears possible resemblance to a block of radiodont setal blades (right), consisting of a series of parallel elongated  
128 blades a few millimetres wide separated by slight changes in sediment level and/or by intervening sediment, with an  
129 overall tapering outline, similar to the setal blade blocks of hurdiids such as *Hurdia* from the Burgess Shale<sup>60</sup>. (f) The  
130 multiramous graptolite *Holograptus* sp. (g) The calymenid trilobite *Colpocoryphe* cf. *thorali*. (h) The illaenid trilobite  
131 *Ectillaenus?* sp. (i) The calymenid trilobite *Neseuretus* cf. *attenuatus* (blue arrow) and Lichidae gen. indet. (to the left  
132 of the blue arrow). (j) The dalmanitid trilobite, subfamily Zeliszskellinae. (k) Accumulations of specimens of a new  
133 genus of orthidine brachiopod and bryozoans (white arrow) on top of a3. Scale bars = 5mm in a, f, g, h, i, j; 10 mm in  
134 b, c and k; 25 mm in d; 50mm in e. By order from a to j: AA.TAI2.OI.9; ML20-259357; AA.TAI3.OI.2;   
135 AA.TAI6.OI.  AA.TAI6.OI.6; AA.TAI13.OI.1; AA.TAI13.OI.2; AA.TAI13.OI.3; AA.TAI13.OI.4;  
136 AA.TAI14.OI.  All specimens are housed at the Marrakech Collections of the Cadi Ayyad University.

137  
138 Bivalved euarthropods and radiodonts are generally interpreted as primarily nektic or nektobenthic  
139 components of Palaeozoic ecosystems. The dominance of nektic/nektobenthic euarthropod taxa,  
140 nautiloids, and planktonic graptolites in a2 suggests that the seafloor, above which they lived, was  
141 not suitable to sustain a diverse and abundant benthic community. However, this environment does  
142 not necessarily correspond to Taichoute, mainly because a2 concretions differ from those found in  
143 a1 in terms of their quality of fossil preservation. Specimens in a2 are fragmented (Fig. 3d, e, 4).  
144 The disarticulated nature of specimens could result from prolonged decay, which may have started  
145 in the water column during the bloating and floating stage of initial decomposition, concurrent  
146 with processes such as carcass scavenging. Disarticulation may have also resulted from fossil  
147 transport, especially that, unlike a1, a2 concretions are generally not formed of a single specimen,  
148 and numerous fragments were often trapped within sediments, that were later consolidated in  
149 concretions (e.g., Fig. 3e). Some of these carapaces are covered by meandering traces of varying  
150 sizes across their surface, and rare brachiopod epibionts are found on some carapaces (Fig. 3d)  
151 indicating that they could have acted as nutrient sources for the community and/or as a stable  
152 substrate for brachiopods to attach to, following their transport to Taichoute, and prior to their  
153 consolidation in concretions in a2<sup>44</sup>.

154 The upper interval a3 (Fig. 1a) consists of a large sedimentary lobe yielding fragmented bryozoans  
155 and trilobites (Fig. 3g-j). These large sedimentary bodies in the Fezouata Shale (Fig. 1e) are  
156 considered as the stratigraphically distal equivalent to the overlying proximal Zini Formation (Fig.  
157 1a). Due to the degree of fossil disarticulation and fragmentation within this lobe, it is certain that  
158 carcasses were transported prior to their preservation. The uppermost interval, above this lobe  
159 shows an accumulation level preserving rhynchonelliform brachiopods and bryozoans in minute  
160 detail (on planar bedding surfaces, and not within concretions) with very little evidence of physical  
161 abrasion (Fig. 3k).



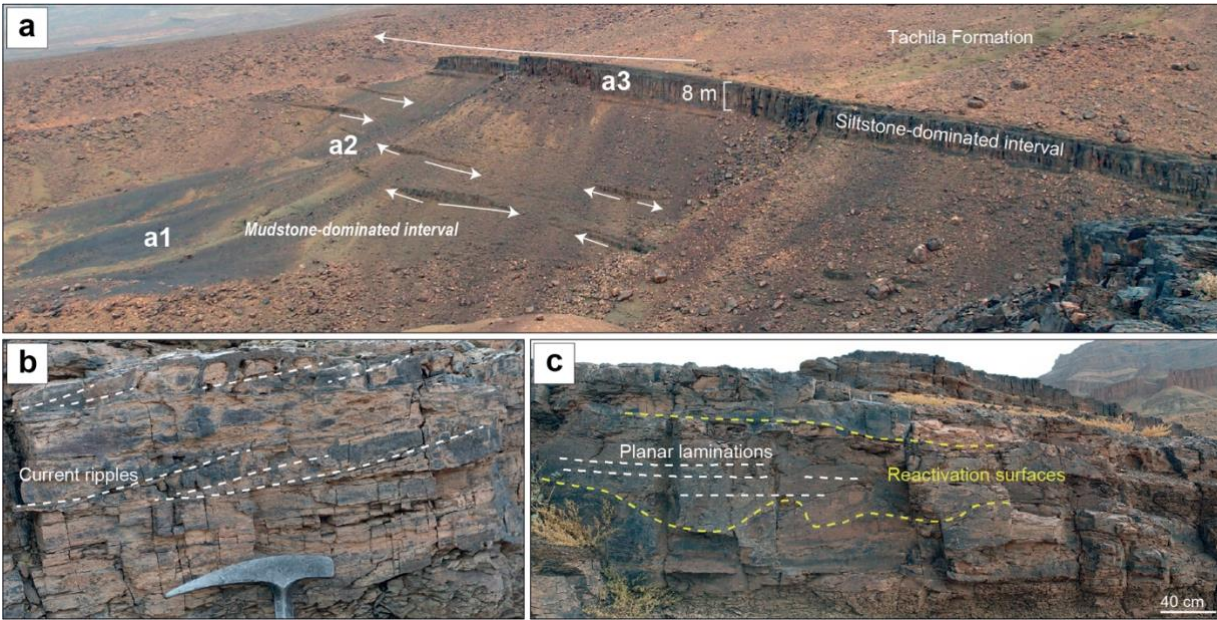
162  
 163 **Figure 4.** Euarthropod fossils from Taichoute interval a2. (a) Large carapace with central carina (white arrow), similar  
 164 to that seen in *Aegirocassis* carapace elements<sup>6</sup>. (b) Carapace with an asymmetrically rounded outline with an anterior  
 165 protrusion similar to that seen in the P-elements of *Hurdia* and other hurdiids<sup>60</sup>. (c) Carapace with an asymmetrically  
 166 rounded outline with one side bearing a structure similar to the upturned projection (white arrow) described for  
 167 *Aegirocassis* lateral carapace elements<sup>6</sup>. (d) Assemblage with at least three carapaces together, some of which are  
 168 elongated and tapering at one end, with a partial outline possibly resembling that of carapace elements of  
 169 *Aegirocassis*<sup>6</sup>. Scale bars are 4cm in a, and 3cm in b, c, d. By order from a to d: MCZ.TAI001, MCZ.TAI002,  
 170 MCZ.TAI003, and MCZ.TAI004. All four specimens are housed at the University of Harvard.

171  
 172 **Sedimentary environment**

173 The Fezouata Shale sequence shallows upwards, but this is mainly evident in the Zagora area,  
 174 where it ends with the deposition of the Zini Formation (Fig 1a), interpreted as nearshore  
 175 sandstones<sup>30, 45</sup>. However, the entire environment represents a proximal-to-distal gradient from the  
 176 southeast (in Algeria) to the northwest<sup>30, 46</sup>. Thus, the shallowing-upwards sequence is not  
 177 expressed in terms of facies everywhere in the Fezouata Shale. In this formation, the emplacement  
 178 of large siltstone lobes, similar to the one deposited in a3, reflects an increase in the sediment  
 179 supply into the basin linked to a lowering of the base level and an increase of erosion in the  
 180 shallower-water southeastern area. These large hectometric lobes that are siltstone-dominated (Fig.  
 181 5a) with minor very fine sandstone components, and displaying dominantly planar lamination,  
 182 asymmetrical cross-laminations, and reactivation surfaces (Fig. 5b, c), have been described as  
 183 storm-induced, density-flow deposits in the most distal setting of the Fezouata Shale<sup>30</sup>. The  
 184 interpretation of Taichoute as the most distal section is in accordance with its position in the basin  
 185 and the previously defined proximal-distal axis<sup>30</sup> (Fig. 1c). This study is the first to document fossil  
 186 preservation in association with such settings in the Fezouata Shale, regardless of the fidelity or  
 187 quality of this preservation. Considering the deposition continuity between a1, a2, and a3 (Fig.  
 188 5a), it is likely that all three intervals represent lateral variations of deposition, from normal



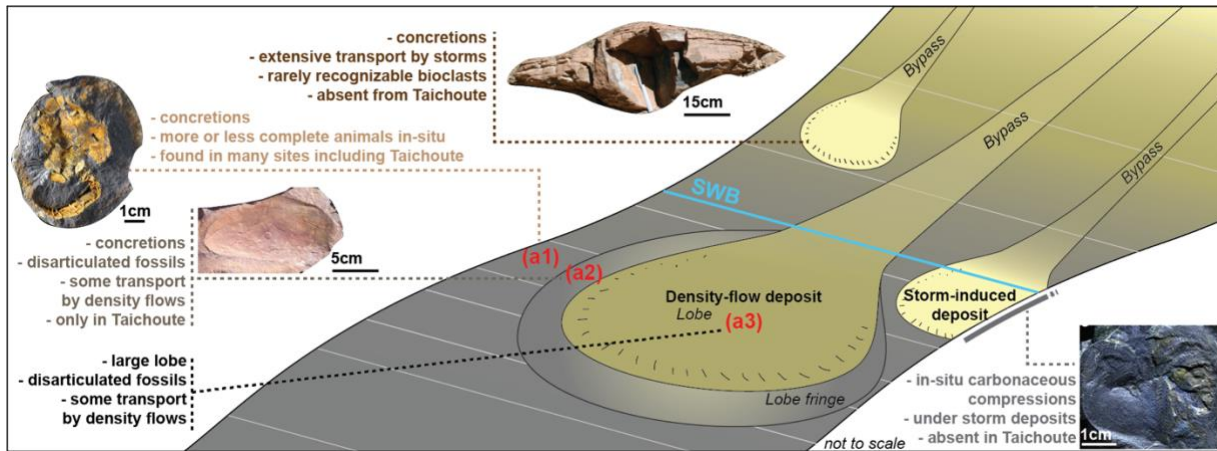
189 sedimentation on the seafloor (a1), passing through lobe fringe (a2) to lobe centre (a3) within the  
 190 same shelf setting (Fig. 6).



191  
 192 **Figure 5.** Sedimentary context of Taichoute. (a) Overview of the upper part of the Fezouata Shale displaying a  
 193 transition between a1, a2, and a3. The large siltstone-lobes of a3 transition upward into the overlying Middle  
 194 Ordovician Tachilla Formation. The white arrows show the lateral discontinuity, characteristic of the siltstone lobes.  
 195 (b) The asymmetrical cross-laminations form current ripples displayed in the siltstone lobes. (c) Reactivation surfaces  
 196 occur frequently in the siltstone lobes, attesting to the turbulence of repeated density flows. These deposits also display  
 197 planar laminations.

198  
 199 These sedimentological interpretations complement previous studies made on the Fezouata Shale  
 200 that highlighted a difference in the mechanism of fossil preservation between this Ordovician site  
 201 and other Cambrian deposits preserving labile anatomies such as the Chengjiang Biota (China)  
 202 and the Walcott Quarry from the Burgess Shale (Canada). It was suggested that most animals  
 203 preserved near the Zagora region were preserved *in-situ*<sup>13, 29, 31</sup> with little to no evidence of  
 204 transport following death, unlike the aforementioned Cambrian sites where sedimentary flows,  
 205 particularly turbidity currents, were operational, transporting animals from their living  
 206 environment to facies favourable for their preservation<sup>47-50</sup>. The discovery of Taichoute increases  
 207 the similarity between the Fezouata Shale and some Cambrian sites by showing that carcasses  
 208 could be transported within the general context of this formation. However, the Fezouata Shale  
 209 remains a unique formation with various modes of fossilisation including animal preservation (i)  
 210 in accumulation levels (above a3 in Taichoute) (Fig. 1a) (ii) as bioclasts in concretions deposited  
 211 above the SWB (present near Zagora); (iii) in shales around the SWB (dominant near Zagora), and  
 212 (iv) under the SWB: (a) *in-situ*, in concretions of different sizes (similar to a1 in Taichoute and  
 213 some sites near Zagora), (b) transported, in concretions (similar to a2 in Taichoute), and (c)  
 214 transported, in large hectometric lobes (similar to a3 in Taichoute) (Fig. 6). This taphonomic  
 215 variability is likely driven by the wide spatial and temporal distribution of the Fezouata Shale,  
 216 around 850m of sediments (Fig. 1a) over 900km<sup>2</sup> in the Draa Valley, spanning ~11 myr. This  
 217 suggests that the Fezouata Shale is an ideal candidate to further investigate a possible continuum  
 218 between shale and concretion preservation, and untangle the possible environmental conditions

219 responsible for the transition between these two modes which preserve most of exceptionally  
 220 preserved fossils during the Early Palaeozoic.



221  
 222 **Figure 6.** The different modes of preservation within the Fezouata Shale, their distribution, in addition to the  
 223 sedimentary processes at play for their formation. SWB: Storm Wave Base.

224  
 225 **Possible taphonomic biases**

226 Non-biomineralized fossils in Taichoute are restricted to large euarthropod carcasses, consisting  
 227 of heavily sclerotized material, preserved in substantial three-dimensional relief, to the exclusion  
 228 of more delicate structures such as body cuticles, cellular sheets in contact with the water column,  
 229 and internal organs (Fig. 3). As such, it is not possible to exclude a taphonomic filter<sup>51-54</sup> at play  
 230 in Taichoute. This filter could result from a prolonged exposure to decay and both biomineralized  
 231 and heavily sclerotized structures are more resistant to degradation than other tissue-types<sup>51</sup>.  
 232 Furthermore, it was previously shown that big carcasses provide large quantities of decaying  
 233 organic material favouring concretion growth<sup>28, 34</sup>. This resulted in the *in situ* preferential  
 234 preservation of large-bodied remains in concretions in some sites near Zagora<sup>28, 34</sup>. In Taichoute,  
 235 large animals were transported and trapped within sediments, that were later consolidated in a2. It  
 236 is possible, that the organic material generated from these carcasses following their transport,  
 237 facilitated siltstone (i.e., interpreted as lobe-fringe deposits; Fig. 6) consolidation around large  
 238 carcasses. The mineralogy of the surrounding matrix might have also played a role controlling  
 239 what got preserved in Taichoute. Particular mineralogical phases are associated with horizons with  
 240 soft-tissue preservation in the Fezouata Shale<sup>55, 56</sup> and in other deposits bearing exceptional  
 241 preservation around the world<sup>57, 58</sup>. These minerals replicate soft tissues, provide resistance to  
 242 decay, and induce damage to bacterial membranes, facilitating the preservation of labile structures  
 243 in the fossil record. In this sense, the absence of labile tissues and dominance of heavily sclerotized  
 244 structures could also point to a lack of these favourable mineralogical phases in Taichoute  
 245 sediments.

246  
 247 **CONCLUSION AND PERSPECTIVES**

248 Taichoute is a newly described late Floian fossil site in the Fezouata Shale. This discovery  
 249 contributes to our understanding of animal preservation in this unique Lower Ordovician formation  
 250 by showing that some organisms are transported by density flows. Three types of concretion  
 251 preservation exist in Taichoute, expanding the fossilization modes observed within the Fezouata  
 252 Shale. The dominant concretion type preserves large euarthropod carcasses, which, based on their  
 253 morphology and size, might correspond to either bivalved forms and/or possibly radiodonts. Future

254 mineralogical and geochemical investigations on Taichoute have the potential to produce valuable  
 255 preservational insights allowing us to resolve whether the aforementioned ecological observations  
 256 represent legitimate aspects of original ecosystems, or are biased by taphonomic filters.  
 257 Nevertheless, at this stage, and prior to yielding further investigations on Taichoute, this site  
 258 remains a significant fossil locality providing novel sedimentary, taphonomic, and paleontological  
 259 information (Tab. 1) at a key interval in the history of life on Earth – at the transition between the  
 260 Cambrian Explosion and the Ordovician Radiation.

	Traditional Fezouata Shale sites	This study (Taichoute)
<b>Location</b>	Zagora Region, Morocco	Taichoute, 80km NNE of Zagora, Morocco
<b>Age</b>	late Tremadocian to middle Floian	middle to late Floian
<b>Environment</b>	Dominated by tempestites	Dominated by storm-induced density flows
<b>Transport</b>	Limited, mainly <i>in situ</i>	Pronounced in most of the section
<b>Fossil matrix</b>	Shales (relatively rare concretions)	Concretions of different types and sizes
<b>Preservation fidelity</b>	Biom mineralized, sclerotized, and cuticularized structures, and internal organs	Biom mineralized structures, and heavily sclerotized large euarthropod fragments (new taxa)

261 **Table 1.** Comparison between the newly discovered Fezouata Shale locality (Taichoute) and conventional sites.  
 262

## 263 MATERIAL AND METHODS

264 In 2017, a field excavation took place in Taichoute (Lower Ordovician, Morocco), 80km away  
 265 from more traditional Fezouata localities (Fig. 1c). The 85 m-thick sedimentary succession at  
 266 Taichoute was logged at a dm-scale, taking into account, sedimentary structures, grain size, and  
 267 bed geometries. Over 300 fossil samples were observed locally, but only 70 samples were  
 268 transported to the Marrakech Collections of the Cadi Ayyad University in Morocco owing to the  
 269 heavy weight of the concretions and are accounted for in figure 2. Kindly note that more than  
 270 12,000 specimens were transported from Bou Izargane to the Marrakech Collections, but only 660  
 271 specimens were identified and inventoried so far, and are as such considered in figure 2. We  
 272 acknowledge that taxonomic abundances are likely to change following the complete curation of  
 273 specimens from Bou Izargane and new fossil discoveries at Tamegroute, Tinzouline, and  
 274 Taichoute, and these abundances are also likely to fluctuate between fossil collections of different  
 275 institutions (e.g., Cadi Ayyad University, Yale Peabody Museum, University of Lausanne, and  
 276 Harvard University). For these reasons, abundances are not made central to this manuscript.  
 277 However, it is important to emphasize that abundance discrepancies between collections and  
 278 fossiliferous localities do not influence the Taichoute conclusions made within this paper (i.e.,  
 279 location, age, environment, preservation).  
 280

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