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Large trilobites in a stress-free Early Ordovician environment

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Keywords:	Arthropod, Paleozoic, Body-size, Fezouata Shale
Abstract:	<p>Understanding variations in body-size is essential for deciphering the response of an organism to its surrounding environmental conditions and its ecological adaptations. In modern environments, large marine animals are mostly found in cold waters. However, numerous parameters can influence body size variations other than temperatures, such as oxygenation, nutrient availability, predation, or physical disturbances by storms. Here, we investigate trilobite size variations in the Lower Ordovician Fezouata Shale deposited in a cold water environment. Trilobite assemblages dominated by small- to normal-sized specimens that are few cm in length are found in proximal and intermediate settings, while those comprising larger taxa more than 20cm in length are found in the most distal environment of the Fezouata Shale. Drill core material from distal settings shows that sedimentary rocks hosting large trilobites preserved in-situ are extensively bioturbated with a high diversity of trace fossils, indicating that oxygen and nutrients were available in this environment. In intermediate and shallow settings, bioturbation is less extensive and shallower in depth. The rarity of storm events (minimal physical disturbance) and the lack of predators in deep environments in comparison to shallower settings would have also helped trilobites attain larger body sizes. This highly resolved spatial study investigating the effects of numerous biotic and abiotic parameters on body size has wider implications for the understanding of size fluctuations over geological time.</p>

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5 **2 Large trilobites in a stress-free Early Ordovician environment**
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3 **22 Abstract**
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5 23 Understanding variations in body-size is essential for deciphering the response of an organism
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7 24 to its surrounding environmental conditions and its ecological adaptations. In modern
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9 25 environments, large marine animals are mostly found in cold waters. However, numerous
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11 26 parameters can influence body size variations other than temperatures, such as oxygenation,
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13 27 nutrient availability, predation, or physical disturbances by storms. Here, we investigate
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15 28 trilobite size variations in the Lower Ordovician Fezouata Shale deposited in a cold water
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19 30 few cm in length are found in proximal and intermediate settings, while those comprising
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21 31 larger taxa more than 20cm in length are found in the most distal environment of the Fezouata
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25 33 trilobites preserved *in-situ* are extensively bioturbated with a high diversity of trace fossils,
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27 34 indicating that oxygen and nutrients were available in this environment. In intermediate and
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29 35 shallow settings, bioturbation is less extensive and shallower in depth. The rarity of storm
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31 36 events (minimal physical disturbance) and the lack of predators in deep environments in
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33 37 comparison to shallower settings would have also helped trilobites attain larger body sizes.
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43 1. Introduction

44 Considered one of the most important aspects of animal biology (Bonner, 2006), body size
45 results from numerous biotic and abiotic factors (Bell, 2014). Vertebrate size variations over
46 geological time have received considerable attention (Sander & Clauss, 2008; Geiger et al.,
47 2013). Comparatively, marine invertebrates have been less studied (Lamsdell & Braddy,
48 2009; Klug et al., 2015; Sigurdson & Hammer, 2016). For instance, it is well agreed that low
49 temperatures can be responsible of the large sizes of modern marine invertebrates (i.e.
50 Bergmann's rule; Timofeev, 2001; Moran & Woods, 2012). Nevertheless, if this was the sole
51 parameter controlling body size, all taxa at high latitudes should be larger than genera found
52 at lower latitudes. This is rarely the case because size variations occur locally in a specific
53 paleoenvironment, owing to changes in water depth, oxygenation, predation, nutrient
54 availability or even physical disturbances caused by storm events (Saleh et al., 2018).

55 During the Ordovician, Morocco was part of the Gondwana margins, at high latitudes, close
56 to the South Pole. The Fezouata Shale was deposited near the Zagora region in Morocco,
57 under cold waters at the transition between two major evolutionary events: the Cambrian
58 Explosion and the Great Ordovician Biodiversification Event (Martin et al., 2016a). In this
59 formation, two sedimentary intervals have yielded thousands of exceptionally preserved
60 fossils belonging to different groups such as arthropods, echinoderms, mollusks, and sponges
61 (Vinther et al., 2008, 2017; Van Roy et al., 2010, 2015a; Martí Mus, 2016; Lefebvre et al.,
62 2019). A striking feature of this formation is extreme body size fluctuations at both taxon and
63 assemblage scales between localities and even between different levels of the same locality
64 (for further details see Ebbestad, 2016; Lefebvre et al., 2016; Martin, 2016; Saleh et al.,
65 2018). Trilobites occur in all sites from the Fezouata Shale and show a large body-size range
66 in this formation. Abundant and spectacular specimens of very large trilobites were found at
67 Ouled Slimane near the Tanskhit bridge (Rábano, 1990; Fortey, 2009; Lebrun, 2018). In this

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3 68 study, the sedimentological and taphonomic contexts of levels with large trilobites from the
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5 69 Fezouata Shale are elucidated, in order to contribute to the understanding of body-size
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7 70 fluctuations in the geological record (see also Lamsdell & Braddy, 2009; Klug et al., 2015;
8
9 71 Sigurdson & Hammer, 2016).

12
13 72

14 73 **2. Geological and paleoenvironmental context**

17 74 A long term transgression at the beginning of the Ordovician created epicontinental seas on
18 75 the Gondwana margins in the Southern Hemisphere (Torsvik & Cocks, 2011; 2013). The
19 76 Fezouata Shale Formation (Fig. 1a) was deposited in a cold water sea, at high latitudes (over
20 77 60°S) close to the South Pole (Fig. 1b) (Torsvik & Cocks, 2013; Martin et al., 2016b).
21 78 Sedimentary rocks of this formation consist of blue-green to yellow-green siltstones
22 79 (Destombes et al., 1985). The 900 m-thick succession of the Fezouata Shale (Fig. 1a) was
23 80 deposited in a storm/wave dominated environment with a minor influence of tides (Vaucher et
24 81 al., 2016). In this environment, sedimentological structures **indicate** a deepening trend from
25 82 the SE to the NW (Fig. 1c) as shown in Vaucher et al. (2017). Thus, the most proximal
26 83 settings in the Late Tremadocian (*A. murrayi* Zone) occur near Tamegroute (about 20 km
27 84 ESE of Zagora; Fig. 1c) (see, Saleh et al., 2018). In this locality, sedimentary rocks are
28 85 constituted of coarse siltstones to fine grained sandstones showing hummocky cross
29 86 stratifications (HCS) of cm- to dm-scale wavelengths (Vaucher et al., 2016) (Fig. 1d).
30 87 Intermediate settings of the Fezouata Shale occur in Bou Izargane in the Ternata plain about
31 88 20 km N of Zagora (Fig. 1c). In this setting, sedimentary rocks are characterized by finer
32 89 siltstones and more abundant background sediments than in Tamegroute, in addition to the
33 90 presence of storm events with up to cm-scale HCS (Saleh et al., 2019) (Fig. 1d). The average
34 91 sedimentation rate in this area was estimated ~79 m/Ma (Saleh et al., 2019). The progradation
35 92 model proposed by Vaucher et al., (2017) suggests that the Ouled Slimane area is associated

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3 93 with more distal settings (Fig. 1c). A field campaign was organized in 2019 to better constrain
4
5 94 the depositional environment of this locality (see section 3).
6

7
8 95 As for the faunal content of the different sites, all three sites yielded diverse assemblages of
9
10 96 marine invertebrates (Saleh et al., 2018). However, Tamegroute is characterized by sessile
11
12 97 epibenthic taxa (bivalves, brachiopods) that are about half the size of those in Bou Izargane
13
14 98 (Saleh et al., 2018). Size variations in the Fezouata Shale between localities are not limited to
15
16 99 brachiopods and bivalves. Trilobites also show body-size discrepancies between localities.
17
18
19 100 The largest trilobites from the Fezouata Shale are found at Ouled Slimane (Rábano, 1990;
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21 101 Fortey, 2009; Lebrun, 2018).
22

23
24 102 <insert figure 1>
25

26 103 3. Material and methods

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28
29 104 Two successive field campaigns were carried out in the Zagora region in 2018 and 2019 and
30
31 105 two cores were obtained. The first core (~13m) was drilled in the intermediate settings of Bou
32
33 106 Izargane. The second core (~2.5m) was made in Ouled Slimane, crossing the interval in
34
35 107 which large trilobites were discovered. Both cores correspond strictly to the same
36
37 108 stratigraphic interval in the *Araneograptus murrayi* biozone (see Vaucher et al., 2016; Saleh
38
39 109 et al., 2018; and references therein for correlations). Cores were described for their lithology,
40
41 110 grain size, depositional sedimentary structures and bioturbation intensity and size at the
42
43 111 University of Lausanne, Switzerland, and are currently deposited at the University of Brest.
44
45 112 All levels crossed by cores were repeatedly sampled from 2004 to 2017, and yielded a large
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47 113 number of fossils (most of them are deposited in the collections of the Cadi-Ayyad
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49 114 University, Marrakesh). Trilobite taxa and assemblages discovered in these levels are
50
51 115 determined at the specific or at the generic level. Size distribution of trilobites was
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53 116 investigated between localities by measuring the full length of individuals from the anterior
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55 117 margin of the cephalon to the posterior margin of the pygidium. The sizes of representatives
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3 118 of the trilobite genus *Platypeltoides*, which occurs in all localities (Table 1), were measured
4
5 119 based on the sagittal length of the pygidium including articulation half ring.
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8 120 <insert table 1>
9

10 121 The current taxonomy of *Platypeltoides* is uncertain. *Platypeltoides magrebiensis* Rábano,
11
12 122 1990, was the only species of this genus reported from the Fezouata Shale (Rábano, 1990;
13
14 123 Martin et al., 2016a). Recently, Corbacho et al. (2018) described four species of
15
16 124 *Platypeltoides* from Morocco. The differences between these species are based on genal spine
17
18 125 morphologies, the position of the eyes and the presence/absence of an anterior border
19
20 126 (Corbacho et al., 2018). There are several issues with the definition of the new species. First,
21
22 127 the morphology of the genal spine changes remarkably during ontogeny (Chatterton, 1980;
23
24 128 Chatterton & Speyer, 1997; Park & Choi, 2009; Laibl et al., 2015) and differences in the
25
26 129 position of eyes can be an effect of taphonomic compression (see Hughes & Rushton, 1990
27
28 130 for detailed explanation). Second, genal spines in Moroccan trilobites are often artificially
29
30 131 modified by local collectors (Gutiérrez-Marco & García-Bellido, in press). Most importantly,
31
32 132 species other than *P. magrebiensis* are based on the description of a single specimen (*P.*
33
34 133 *hammondi* Corbacho & López-Soriano, 2016; *P. carmenae* Corbacho et al., 2017), or four
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36 134 specimens (*P. cuervoae* Corbacho & López-Soriano, 2012). Consequently, until more
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38 135 material is found and a comprehensive revision of the genus is performed, we consider *P.*
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40 136 *magrebiensis* as the only valid species and refer all our material to it.
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49 138 **4. Results**

50 51 139 **4.a. Trilobite size and preservation**

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53 140 The most diverse trilobite assemblage is found in the intermediate setting locality, Bou
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55 141 Izargane (i.e. 7 taxa; Table 1). Four of these taxa are also found in the more proximal site of
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57 142 Tamegroute. *Platypeltoides magrebiensis* is the only taxon that is found across the proximal-
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3 143 distal axis (Table 1). The mean **total** sagittal length of all trilobite taxa recorded in the distal
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5 144 site of Ouled Slimane is 32.4 cm (median = 31.9; standard deviation sd = 1.41; n = 31), which
6
7 145 is four times larger than the mean **total sagittal length of all trilobites** recorded in Bou
8
9 146 Izargane (mean = 7.37 cm; median = 5.9 ; sd = 1.21; n = 14), and eight times larger than the
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11 147 mean **total sagittal length of all trilobites** recorded in Tamegroute (mean = 3.78 cm; median =
12
13 148 3.7 ; sd = 1.24; n = 15) (Fig. 2a; and Tab. 1 in supplementary material for detailed
14
15 149 measurements). **Total sagittal lengths of trilobite forming the assemblages in Ouled Slimane,**
16
17 150 **Bou Izargane, and Tamegroute are statistically normally distributed** (Shapiro-Wilk test, p -
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19 151 value= 0.97, p -value =0.23, p -value =0.4 respectively). **Trilobite** size variations between two
20
21 152 contiguous localities (i.e. Ouled Slimane and Bou Izargane, Bou Izargane and Tamegroute)
22
23 153 are significantly different (t-test, p -value = $3.85 \cdot 10^{-14}$, p -value = 0.006 respectively; cf. Tab. 4
24
25 154 in supplementary material). The increase in size between proximal and distal sites is not only
26
27 155 evidenced between assemblages but also between different species belonging to the same
28
29 156 group (e.g. *Asaphellus* belonging to asaphids, and both *Platypeltoides* and *Symphysururs*
30
31 157 belonging to nileids; Table 1).
32
33 158 The mean pygidial sagittal length including axial half ring of *Platypeltoides* in Ouled Slimane
34
35 159 is 6.3 cm (median = 6.2; sd = 0.5; n = 9), which is twice longer than the mean pygidial sagittal
36
37 160 length recorded in Bou Izargane (mean = 3.3 cm; median = 3.5 ; sd = 0.84; n = 5), and four
38
39 161 times larger than the mean **mean pygidial sagittal length** recorded in Tamegroute (mean =
40
41 162 1.29 cm; median = 1.32 ; sd = 0.35; n = 5) (Fig. 2b, see supplementary material for detailed
42
43 163 measurements). Pygidial sagittal length measurements for *Platypeltoides* are normally
44
45 164 distributed in Ouled Slimane, Bou Izargane, and Tamegroute (Shapiro-Wilk test, p -value=
46
47 165 0.39, p -value =0.76, p -value =0.19 respectively; cf. Tab. 7 in supplementary material).
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49 166 Pygidial sagittal length variations for *Platypeltoides* between Ouled Slimane and Bou
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3 167 Izargane, in addition to those between Bou Izargane and Tamegroute are statistically
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5 168 significantly different (t-test, p -value = 0.0012, p -value = $3.5 \cdot 10^{-6}$ respectively).
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7
8 169 <insert figure 2>
9

10 170 Trilobites from Ouled Slimane are preserved in silicified, quartz-rich concretions. Some are
11
12 171 disarticulated and other are complete (Fig. 3a–e). Trilobites from the two other localities are
13
14 172 preserved in shales (Fig. 3f–h).
15

16
17 173 <insert figure 3>
18

19 174 **4.b. Sedimentological context**

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21 175 The background sediments of both cores from Bou Izargane and Tamegroute in the Fezouata
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23 176 Shale consist of very fine siltstones to claystones (Fig. 4a–d). In Bou Izargane, coarse
24
25 177 siltstone event deposits are abundant (Fig. 4e). Event deposits have an erosive base and show
26
27 178 occasionally HCS (Fig. 4e). In Ouled Slimane, event deposits are rare and consist of quartz
28
29 179 silts that are finer than in Bou Izargane (generally $< 40 \mu\text{m}$) (Fig. 4a). When they occur, they
30
31 180 do not exceed 1 cm in thickness and lack HCS (Fig. 4a). Bioturbation occurs in all cores but it
32
33 181 shows variations in both depth and intensity. Some intervals are only lightly bioturbated with
34
35 182 a bioturbation depth of around 1 mm, while others are highly bioturbated with a bioturbation
36
37 183 depth of few centimeters (Fig. 4f). Intensity of bioturbation varies from light (less than 10%
38
39 184 of sedimentary rocks showing evidence of biological activity) to moderate (between 10 and
40
41 185 30% of sedimentary rocks showing evidence of biological activity), high (between 30 and
42
43 186 70% of sedimentary rocks affected by biological activity), and extreme (over 70% of
44
45 187 sedimentary rocks reworked by biological activity). **The used scale for the studied cores is**
46
47 188 **simplified after the bioturbation index in Taylor & Goldring, 1993.** However, there is no
48
49 189 direct correlation between bioturbation depth and intensity. Some intervals can be extremely
50
51 190 bioturbated with a bioturbation depth that does not exceed few millimeters (Fig. 4c).
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53 191 Generally, sediments from Ouled Slimane are more extensively bioturbated than in Bou
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3 192 Izargane in terms of both traces intensity and depth (Fig. 4f). In Bou Izargane, bioturbation is
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5 193 generally less than 1 cm in depth (Fig. 4f).
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8 194 <insert figure 4>
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10 195 **5. Interpretation and discussion**

11 12 13 196 **5.a. Depositional environment and preservation**

14
15 197 In marine settings, grain sizes are indicative of the distance from the source traveled by
16
17 198 sediments (Nichols, 2009). In the Fezouata Shale, coarse grains are found towards the south
18
19 199 east, closer to the source, when compared to finer sediments that are mainly deposited in the
20
21 200 basin (Vaucher et al., 2016, 2017). Furthermore, the abundance of storm events is indicative
22
23 201 of the energy of the depositional environment (Nichols, 2009; Perillo et al., 2014). Stacked
24
25 202 storm events designate a shallow unstable environment that is constantly agitated by waves
26
27 203 (Nichols, 2009). In these agitated settings, waves generate orbitals in the water column that
28
29 204 decrease in size with depth leaving oscillation traces such as HCS on the sea floor (Vaucher et
30
31 205 al., 2016, 2017). The deeper the water column is, the smaller these HCS are. Thus, the
32
33 206 presence in the Fezouata Shale of very fine siltstones to claystones with a scarce presence of
34
35 207 storm events and an absence of HCS, all indicate that the sedimentary succession at Ouled
36
37 208 Slimane was deposited relatively far from the source, in a stable environment that was rarely
38
39 209 agitated by storm waves. In the Fezouata Shale, Ouled Slimane is the most distal locality.
40
41 210 Despite being distal in position, an abundant bioturbation (i.e. light, high, and extreme) with
42
43 211 variable depth (from a few millimeters to 4 cm) and a high diversity of trace fossils are
44
45 212 observed in the sedimentary succession in Ouled Slimane. This validates that this
46
47 213 environment was colonized by benthic organisms and shows that little to no chemical stress
48
49 214 (i.e. related to nutrients and oxygen availability) occurred in the bottom of the water column
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51 215 but also, at least, in surface sediments.
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3 216 In the Fezouata Shale, two modes of preservation have been evidenced. The first one,
4
5 217 consisting of the preservation of both mineralized and soft bodied taxa in shales, is well
6
7 218 understood (Martin et al., 2016b; Saleh et al., 2019). Living organisms of the Fezouata Biota
8
9 219 colonized the sea floor and were repeatedly buried *in situ* by event deposits (Vaucher et al.,
10
11 220 2017). The second mode consists of preservation in concretions, and the processes underlying
12
13 221 it are more complex (McCoy et al., 2015a,b). Siliceous concretions similar to the ones
14
15 222 preserving large trilobites at Ouled Slimane have been described from distal settings of the
16
17 223 Fezouata Shale by Vaucher et al. (2017) and Gaines et al., (2012). The original siliceous
18
19 224 material for the formation of these concretions comes from more proximal localities (Vaucher
20
21 225 et al., 2017). However, the growth of these concretions was controlled by the decay rates of
22
23 226 dead animals covered by event deposits (Gaines et al., 2012). When a large carcass is
24
25 227 decaying, permissive anoxic conditions are established leading to mineral overgrowth around
26
27 228 decaying carcasses (Gaines et al., 2012). This model was used to explain the preservation of
28
29 229 giant and complete invertebrates *in situ* in the Fezouata Shale (i.e. radiodonts such as
30
31 230 *Aegirocassis*; Gaines et al., 2012; Van Roy and Briggs, 2011; Van Roy et al., 2015b). The
32
33 231 presence of partially articulated and complete large trilobites in the concretions from Ouled
34
35 232 Slimane argue, in a similar way to *Aegerocassis*, in favor to an autochthonous preservation. If
36
37 233 transport occurred, it was most likely limited and from the same distal setting (i.e. few meters
38
39 234 only).

235 **5.b. Body-size fluctuations**

236 Many trilobite genera included in this study have been also discovered from other high
237 latitude (peri)Gondwanan localities. For instance, the Třenice and Mílina formations (late
238 Tremadocian; Czech Republic) have yielded a large number of trilobites comparable in size to
239 those found in Tamegroute and Bou Izargane (i.e. total sagittal length of *Anacheirurus* ~
240 3.5cm; *Euloma* ~ 2.5cm; *Platypeltoides* ~ 5.5cm; *Geragnostus* ~ 0.6cm; see e.g. Mergl,

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3 241 2006). Other assemblages of similarly sized trilobites are known in the late Tremadocian
4
5 242 Saint-Chinian Formation, France (i.e. total sagittal length of *Euloma* ~ 3.3cm, *Geragnostus* ~
6
7 243 1.1cm ; *Megistaspis* ~ 3.9cm ; *Symphysurus* ~ 3.4cm; Thoral, 1935; Capéra et al., 1975, 1978;
8
9
10 244 Courtessole & Pillet, 1975; Courtessole et al., 1981). *Euloma* was also found in the late
11
12 245 Tremadocian Vogtendorf Formation of Germany with a total sagittal length of size ~ 5.5cm
13
14 246 (Sdzuy et al., 2001).

16
17 247 Although rare in the fossil record, occurrences of large trilobites are not restricted to the lower
18
19 248 part of the Fezouata Shale. Other known occurrences include e.g. the Cambrian Series 2 Emu
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21 249 Bay Shale, Australia (Holmes et al., 2020), the Cambrian Series 2 to Miaolingian Jbel
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23 250 Wawrmast Formation of Morocco (Geyer, 1993), the Early Ordovician ‘Schistes à Gâteaux’
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25 251 Formation, France (Thoral, 1946; Bérard, 1986), the Middle Ordovician Valongo Formation,
26
27 252 Portugal (Rábano, 1990; Gutiérrez-Marco et al., 2009), the Late Ordovician Churchill River
28
29 253 Group, Canada (Rudkin et al., 2003), and the Middle Devonian Onondaga Limestone, NY
30
31 254 USA (Whiteley et al., 2002). In general, the largest trilobites occur in a wide array of
32
33 255 environments. Some of them were reported from low latitude nearly equatorial areas, in
34
35 256 shallow-water carbonates (Whiteley et al., 2002; Rudkin et al., 2003) or deeper, but still
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37 257 nearshore siliciclastic deposits (Paterson et al., 2016). Others come from high latitudes (over
38
39 258 60°S) of the West Gondwana margin, where they are preserved either in distal mudstones
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41 259 (Gutiérrez-Marco et al., 2009), fine grained sandstones and shales (Geyer, 1993), and
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43 260 concretions (Thoral, 1946; Bérard, 1986). The best analog for the Ouled Slimane assemblage
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45 261 is thus probably the Early Ordovician fauna described in the ‘Schistes à Gâteaux’ of the
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47 262 Cabrières area (eastern-most part of the southern Montagne Noire; Berard, 1986). In this
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49 263 region, similarly sized concretions (70 to 100 cm in diameter) formed under comparable
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51 264 depositional settings yielded abundant remains of both disarticulated and fully articulated
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53 265 large trilobites belonging to Asaphidae and Nileidae (Bérard, 1986). During the Early
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3 266 Ordovician, the Montagne Noire area was situated at relatively high latitudes, not far away
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5 267 from the Anti-Atlas area, on the western margin of Gondwana. In general, high latitudes, and
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7 268 consequently low temperatures are often considered as the main explanatory factor for
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9 269 trilobite gigantism (Gutiérrez-Marco et al., 2009; Klug et al., 2015). Given the widespread
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11 270 distribution of large trilobites in various latitudes and facies, it is unlikely that there is only
12
13 271 one single controlling mechanism of trends toward larger sizes. Indeed, the trilobite size
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15 272 fluctuations within the Fezouata Shale in a comparatively restricted area suggest, that despite
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17 273 high latitudes, other factors must be taken into consideration.

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21 274 In the Fezouata Shale, differences in size distribution between localities can be the result of
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23 275 numerous mechanisms and conditions (ontogeny, size sorting due to transport, oxygenation,
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25 276 nutrient availability; Saleh et al., 2018). Transport-induced size sorting is unlikely to explain
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27 277 size discrepancies of trilobites in general and *Platypeltoides* in particular. When current-
28
29 278 related sorting happens in marine environments, small individuals are more easily transported
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31 279 than large ones, and they are consistently displaced towards more distal settings (Johnson,
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33 280 1960; Fagerstrom, 1964). The opposite pattern for trilobites is observed in the Fezouata Shale.
34
35 281 Furthermore, all previous surveys made on brachiopods, bivalves, echinoderms, and trilobites
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37 282 from this part of the Fezouata Shale have concluded that most fossils were preserved *in situ*
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39 283 (with occasional limited transport), because delicate anatomical structures were preserved
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41 284 (Saleh et al., 2018 and references therein). Brachiopods of the Fezouata Shale have frequently
42
43 285 their setae preserved (Saleh et al., 2018) and in many cases, the most fragile skeletal elements
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45 286 of stylophoran echinoderms remained connected to the rest of the body (Martin et al. 2015;
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47 287 Lefebvre et al., 2016, 2019). As trilobites had a chitinous, partially biomineralized
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49 288 exoskeleton (Teigler & Towe, 1975), their remains are frequently preserved in marine
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51 289 Paleozoic deposits (Speyer & Brett, 1986). Given that post-mortem processes are insufficient
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53 290 to explain the size distribution seen in the Fezouata Shale (this study; Saleh et al., 2018), the
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3 291 presence of large trilobites in only the most distal paleoenvironments is taken as representing
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5 292 the original size distribution of organisms. The increase in trilobite size from shallow
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8 293 proximal to deep distal localities in the Fezouata Shale is consistent with observations of
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10 294 crustacean body size fluctuations in modern marine environments, in which large animals are
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12 295 found in deep-water settings (Horikoshi, 1986; Timofeev, 2001).

14 296 The increase in size between proximal and distal localities may be related to ontogeny (e.g.
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16
17 297 Laibl et al., 2014), with younger -and therefore smaller- developmental stages favoring
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19 298 shallower environments, and older and larger ones preferring deeper settings. If this was the
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21 299 case, all taxa should be found in all localities, which is not true for the Fezouata Shale. For
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23 300 instance, Ouled Slimane seems to entirely lack small and medium-sized taxa (e.g. *Bavarilla*,
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25 301 *Anacheirurus*, *Euloma*), with the exception of *Platypeltoides magrebiensis* (Tab. 1).
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27 302 *Dikelokephalina* and *Ogyginus* are present in Ouled Slimane, but are absent in more proximal
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29 303 sites (Tab. 1). Ontogeny alone does not explain size discrepancies observed for *Platypeltoides*
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31 304 *magrebiensis*, because the material measured here consistently excluded juvenile stages
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33 305 (defined by the number of thoracic segments). Even if future work shows a correlation
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35 306 between changes in habitats and developmental stages of some trilobites, this fails to explain
36
37 307 why older and bigger individuals preferred deeper environments. Therefore, there must have
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39 308 been external biotic and abiotic conditions that selected for larger bodies in deeper setting and
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41 309 smaller bodies in more proximal environments.

46 310 Oxygen availability is an abiotic parameter that can influence the body-size distribution of
47
48 311 marine taxa (Zeuthen, 1953). It is suggested that large sizes are dictated by oxygen
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50 312 availability rather than by temperature in modern polar ecosystems (Chapelle & Peck, 1999).
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52 313 Oxygen concentration correlates with the general trend in marine gigantism during the
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54 314 Paleozoic (Vermeij, 2016), and a direct connection (i.e. in magnitude) between Paleozoic
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56 315 gigantism and atmospheric hyperoxia was also established using a mathematical model based
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3 316 on oxygen transport limitation (Payne et al., 2012). In contrast, benthic individuals tend to
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5 317 have smaller sizes in oxygen minima zones (i.e. Lilliput effect; Twitchett, 2007). However,
6
7 318 for instance in Tamegroute, the bottom of the water column was oxic, leading to the
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9 319 development of diverse assemblages on the sea floor (Saleh et al., 2018).
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11 320 Another abiotic factor that can limit size growth is nutrient availability (Booth et al., 2008).
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13 321 Nutrients are generally more abundant in proximal sites near the source (Rowe et al., 1975;
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15 322 Philippart et al., 2000; Wang et al., 2003). The occurrence of a relatively high and diverse
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17 323 bioturbation in Ouled Slimane (Fig. 4a-d) suggests that nutrients were not a limiting
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19 324 parameter. This interpretation is in accordance with the presence of diverse planktonic
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21 325 microorganism assemblages in the deepest settings of the Fezouata Shale (Nowak et al.,
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23 326 2016).
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25 327 Storm turbulences generate another abiotic stress in shallow environments (Barry & Dayton,
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27 328 1991; McAlister & Stancyk, 2005). Storms transport sediments that can cause the suffocation
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29 329 of both sessile and mobile invertebrate taxa in proximal sites (Tabb & Jones, 1962). Storms
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31 330 can also increase the input of fresh water to the sea, with the resulting change in water column
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33 331 salinity causing heavy mortalities (Tabb & Jones, 1962; Barry & Dayton, 1991). Furthermore,
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35 332 although exoskeleton formation in arthropods is mainly constrained by biotic parameters, the
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37 333 major source of calcium used for exoskeleton calcification is exogenous, and comes from
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39 334 from the waters where the organisms live (Luquet, 2012). In seawater, the concentration of
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41 335 calcium is generally very high (Luquet, 2012), but fresh water input during a storm may alter
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43 336 calcium availability for biomineralization in shallow waters, inhibiting marine arthropods
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45 337 from attaining large sizes. However, in the Ordovician, even the shallowest settings from the
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47 338 Fezouata Shale in Morocco were extremely far from the shore (more than 1000 km away;
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49 339 Guiraud et al., 2004). Thus, it is more likely that the impact of storms on living organisms
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51 340 was more related to transport of sediment and obrution events rather than calcium and salinity
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3 341 fluctuations. This sediment-induced stress was evidenced in proximal localities of the
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5 342 Fezouata Shale, regularly killing sessile epibenthic taxa and thus inhibiting them from
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7 343 attaining large sizes (Saleh et al., 2018). This stress decreased from proximal to distal
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9 344 localities, allowing organisms to attain larger sizes in deeper environments (Saleh et al.,
10
11 345 2018). However, mass mortality is not generally the trend for arthropods in storm-dominated
12
13 346 modern shallow marine environments, except in the cases of supercritical events (Conner et
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15 347 al., 1989). In regions that are seasonally affected by storms, arthropods are able to migrate to
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17 348 more stable environments (Conner et al., 1989). Pink shrimp individuals are known to leave
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19 349 shallow waters to deeper environments about 60 miles offshore during a hurricane (Tabb &
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21 350 Jones, 1962), and similar shelter-seeking behavior is observed during the storms season in
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23 351 spiny lobsters (Hunt et al., 1994). It is likely that trilobites, similarly to modern vagile
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25 352 arthropods, were able to adapt against physical instabilities and were little affected by storm
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27 353 turbulences. Some of them even showed collective behavior by migrating during storm
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29 354 seasons, in a similar way to extant spiny lobsters (Vannier et al., 2019).

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31 355 The occurrence of large trilobite individuals in deep waters may also indicate a lack of
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33 356 predators in these settings (Rex, 1976), as heavy predation is known to limit body size
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35 357 (Horikoshi, 1986). Cephalopods, major predators in both Ordovician and modern marine
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37 358 ecosystems (Cherel & Hobson, 2005; Kröger et al., 2009a), are absent in Ouled Slimane,
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39 359 although they are relatively common in more proximal localities of the Fezouata Shale
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41 360 (Kröger & Lefebvre, 2012). Their absence from the distal setting preserved at Ouled Slimane
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43 361 is in good accordance with the observation that their initial Furongian–Early Ordovician
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45 362 diversification was restricted to relatively shallow environments (Kröger et al., 2009b). The
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47 363 lack of predation pressure from cephalopods in distal marine environments in general during
48
49 364 the Cambrian to Early Ordovician period may explain the numerous occurrences of large
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51 365 trilobites in distal settings globally during this time interval (e.g. Fezouata Shale, ‘Schistes à
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3 366 Gâteaux', see also introduction), and the rarity of large trilobites in younger deposits more or
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5 367 less coincides with the paleoecological diversification of cephalopods into deeper settings
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7 368 during the Middle Ordovician (Kröger et al., 2009a). Thus, the environmental conditions of
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9 369 the distal Fezouata Shale setting were characterized by a lack of storms and predators, and an
10
11 370 abundance of oxygen and nutrients, all of which are conducive to the local occurrence of large
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13 371 trilobites.
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18
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645

646 **Figure captions**

647 Figure 1. (Colour online) General geographical context of the Fezouata Shale. (a)
 648 Stratigraphic sequence of the Fezouata Shale with the studied interval. (b) Location of
 649 Morocco in the Early Ordovician near the South Pole (modified from Vaucher *et al.*,
 650 2017). (c) Deepening trend in the Fezouata Shale from the SE to the NW (modified from
 651 Vaucher *et al.*, 2017), with the study localities Ouled Slimane, Bou Izargane, and
 652 Tamegroute indicated. (d) Proximal to distal relative position of the three localities
 653 studied here: Ouled **Slimane**, Bou Izargane, and Tamegroute.

654 Figure 2. (Colour online) Trilobite size fluctuations in the Fezouata Shale. (a) General body
 655 size patterns, all taxa included, in Ouled Slimane, Bou Izargane, and Tamegroute. (b)
 656 Differences in the pygidial sagittal length of *Platypeltoides magrebiensis* between
 657 localities.

658 Figure 3. (Colour online) Trilobites from the Fezouata Shale, Morocco. (a-e) Large trilobites
 659 from Ouled Slimane preserved in concretions. (a) External moulds of trilobites non
 660 picked up by collectors. (b) Thorax and pygidium of *Platypeltoides magrebiensis*. (c)
 661 Incomplete cranidium of *Platypeltoides* sp. (d) Part of the thorax and pygidium of
 662 *Dikelokephalina brenchleyi* (e) Pygidium of *Asaphellus stubbsi*. (f) Normal-sized
 663 *Symphysurus* sp. from Bou Izargane. (g-h) Normal sized *Platypeltoides magrebiensis*
 664 from Bou Izargane (g) and Tamegroute (h) preserved in shales.

665 Figure 4. (Colour online) Drilled sedimentary rocks from Ouled Slimane and Bou Izargane.

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3 666 (a) Core sediments from Ouled Slimane showing the dominance of background clayey to
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5 667 silty sediments with rare, coarser grain event deposits. Bioturbation intensity variations
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7 668 between intervals at Ouled Slimane from light (a) to high (b) and extreme (c). (d)
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10 669 Bioturbation depth of few centimeters in Ouled Slimane. (e) Core sediments from Bou
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12 670 Izargane are less bioturbated and more affected by storm deposits. (f) Bioturbation
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14 671 intensity and depth along the core in Ouled Slimane and Bou Izargane. All scale bars are
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17 672 1cm in length.

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For Peer Review

673 Table 1. Trilobite diversity, abundances and sizes in the studied localities from the Lower
 674 Ordovician of the Fezouata Shale.

Locality	Trilobite	N	Size range (cm)
Tamegroute	<i>Anacheirurus adserai</i> (Vela, & Corbacho, 2007)	2	4-4.8
	<i>Asaphellus</i> sp. aff. <i>jujuanus</i> Harrington, 1937	2	3.7-4.1
	<i>Bavarilla</i> sp.	4	2.2-2.8
	<i>Euloma</i> sp.	2	3.1
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	5	3.3-6.2
Bou Izargane	<i>Asaphellus</i> sp. aff. <i>jujuanus</i> Harrington, 1937	2	3.9-6.2
	<i>Bavarilla</i> sp.	2	3.7-4.1
	<i>Euloma</i> sp.	1	3.8
	<i>Geragnostus</i> sp.	1	0.9
	<i>Megistaspis</i> sp.	1	5.6
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	5	8.5-16.1
Ouled Slimane	<i>Symphysurus</i> sp.	2	3.9-4.2
	<i>Asaphellus stubbsi</i> Fortey, 2009	7	24.1-38
	<i>Dikelokephalina brenchley</i> Fortey, 2010	13	24.2-33.7
	<i>Ogyginus</i> sp.	7	39.2-49.1
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	4	18-23

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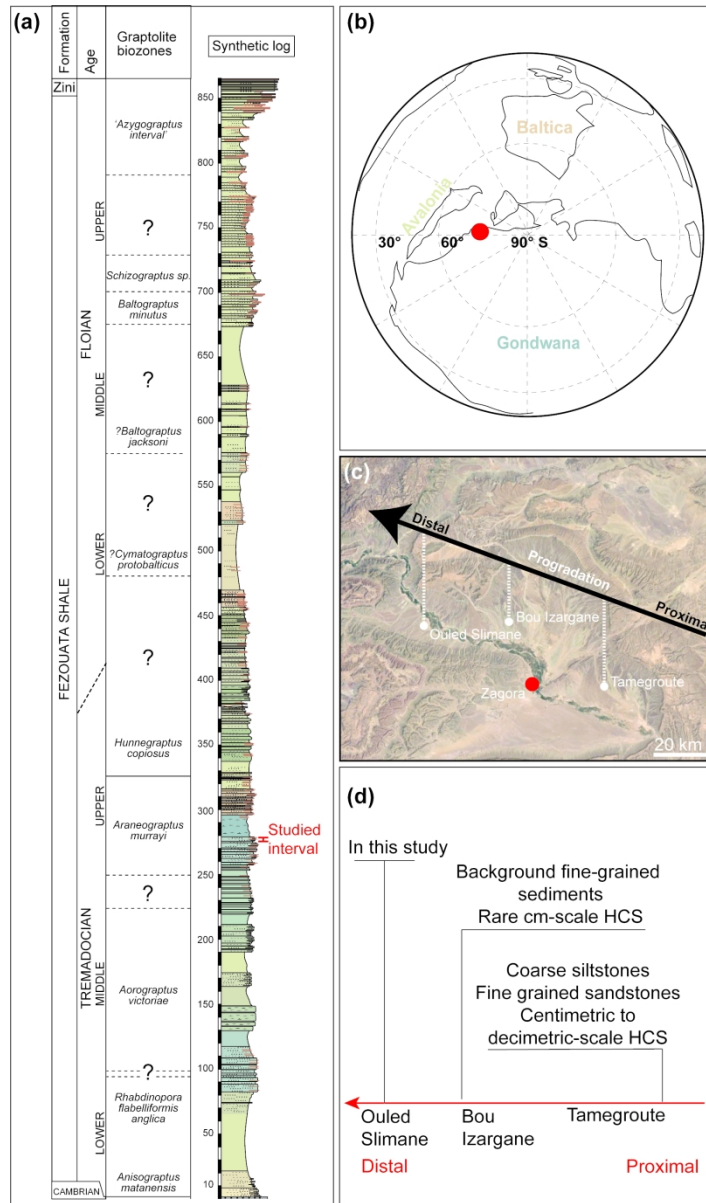


Figure 1. (Colour online) General geographical context of the Fezouata Shale. (a) Stratigraphic sequence of the Fezouata Shale with the studied interval. (b) Location of Morocco in the Early Ordovician near the South Pole (modified from Vaucher et al., 2017). (c) Deepening trend in the Fezouata Shale from the SE to the NW (modified from Vaucher et al., 2017), with the study localities Ouled Slimane, Bou Izargane, and Tamegroute indicated. (d) Proximal to distal relative position of the three localities studied here: Ouled Slimane, Bou Izargane, and Tamegroute.

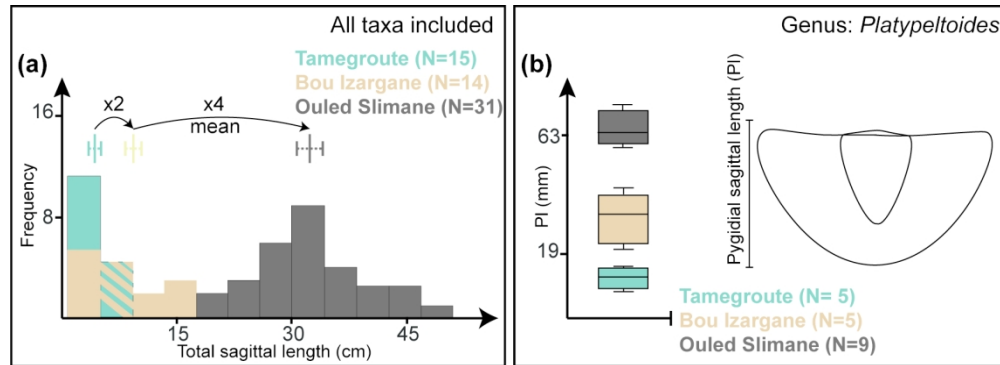


Figure 2. (Colour online) Trilobite size fluctuations in the Fezouata Shale. (a) General body size patterns, all taxa included, in Ouled Slimane, Bou Izargane, and Tamegroute. (b) Differences in the pygidial sagittal length of *Platypeltoides magrebiensis* between localities.

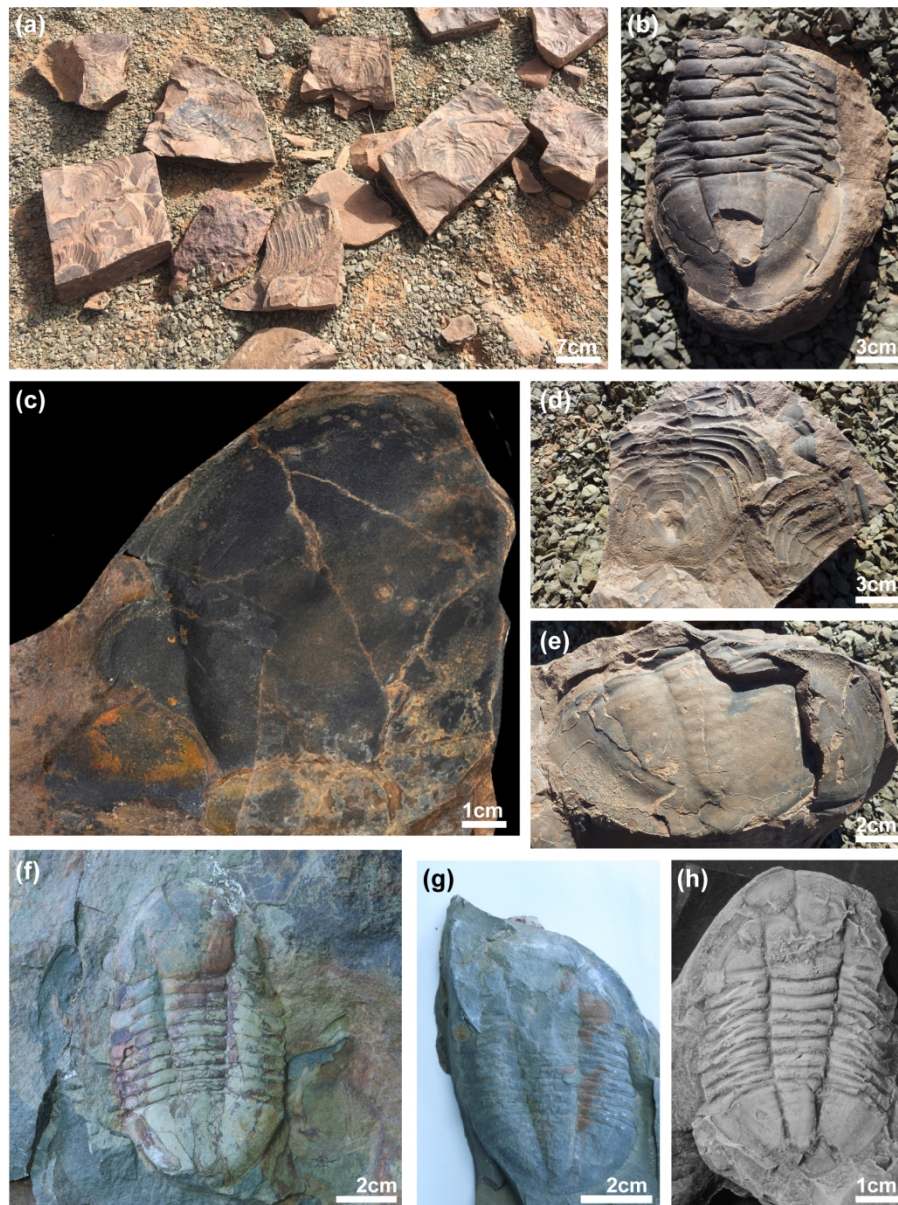


Figure 3. (Colour online) Trilobites from the Fezouata Shale, Morocco. (a-e) Large trilobites from Ouled Slimane preserved in concretions. (a) External moulds of trilobites non picked up by collectors. (b) Thorax and pygidium of *Platypeltoides magrebiensis*. (c) Incomplete cranium of *Platypeltoides* sp. (d) Part of the thorax and pygidium of *Dikelocephalina brenchleyi* (e) Pygidium of *Asaphellus stubbsi*. (f) Normal-sized *Symphysurus* sp. from Bou Izargane. (g-h) Normal sized *Platypeltoides magrebiensis* from Bou Izargane (g) and Tamegroute (h) preserved in shales.

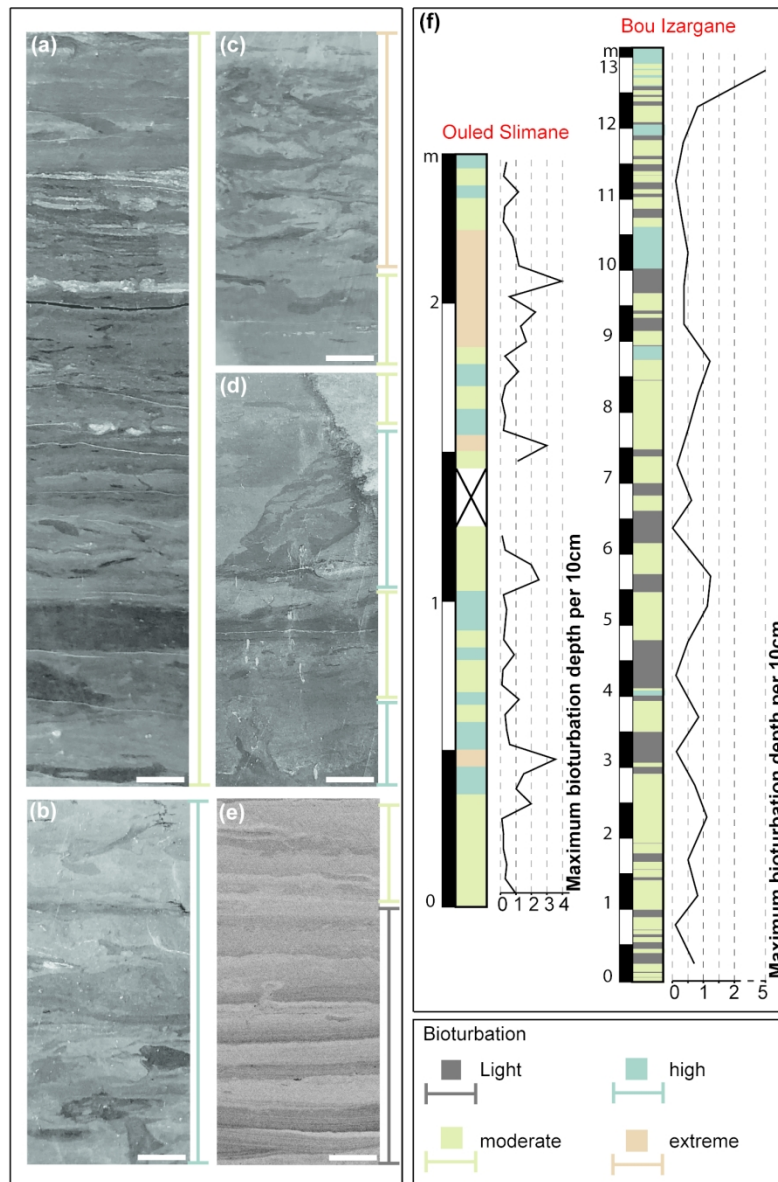


Figure 4. (Colour online) Drilled sedimentary rocks from Ouled Slimane and Bou Izargane. (a) Core sediments from Ouled Slimane showing the dominance of background clayey to silty sediments with rare, coarser grain event deposits. Bioturbation intensity variations between intervals at Ouled Slimane from light (a) to high (b) and extreme (c). (d) Bioturbation depth of few centimeters in Ouled Slimane. (e) Core sediments from Bou Izargane are less bioturbated and more affected by storm deposits. (f) Bioturbation intensity and depth along the core in Ouled Slimane and Bou Izargane. All scale bars are 1cm in length.

Supplementary Material

Large trilobites in a stress-free Early Ordovician environment

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Short running title: Large Ordovician trilobites

Complete trilobites sizes (cm)		
Tamegroute	Bou Izargane	Ouled Slimane
4.9	9.8	18
3.3	13	19.1
6	14.2	21.5
6.2	16.1	23
3.7	8.5	24.2
2.2	3.7	26
2	4.1	26.7
2.8	3.8	27.2
2.9	6.2	28.4
4	3.9	28.5
4.8	0.9	29.7
3.1	5.6	30.1
3.1	9.3	31.3
3.7	4.2	31.6
4.1		31.9
		33.4
		33.7
		34.2
		24.1
		33.5
		35.2
		36.4
		37.3
		38
		39.2
		39.6
		41.7
		42.9
		43.2
		47
		49.1

	<i>Platypeltoides magrebiensis</i> (Rábano, 1990)
	<i>Bavarilla</i> sp.
	<i>Anacheirurus adserai</i> (Vela, J.A. & Corbacho, 2007)
	<i>Euloma</i> sp.
	<i>Asaphellus</i> sp. aff. <i>jujanus</i> (Harrington, 1937)
	<i>Geragnostus</i> sp.
	<i>Megistaspis</i> sp.
	<i>Symphysurus</i> sp.
	<i>Dikelokephalina brenchley</i> (Fortey, 2010)
	<i>Asaphellus stubbsi</i> (Fortey, 2009)
	<i>Ogyginus</i> sp.

Table 1. Raw trilobites measurements in the studied localities.

Summary statistics					
Tamegroute		Bou Izargane		Ouled Slimane	
N	15	N	14	N	31
Min	2	Min	0,9	Min	18
Max	6,2	Max	16,1	Max	49,1
Sum	56,8	Sum	103,3	Sum	1005,7
Mean	3,786667	Mean	7,378571	Mean	32,44194
Std. error	0,3221751	Std. error	1,219853	Std. error	1,415633
Variance	1,556952	Variance	20,83258	Variance	62,12452
Stand. dev	1,247779	Stand. dev	4,564272	Stand. dev	7,881911
Median	3,7	Median	5,9	Median	31,9
25 prcntil	2,9	25 prcntil	3,875	25 prcntil	26,7
75 prcntil	4,8	75 prcntil	10,6	75 prcntil	38
Skewness	0,6465317	Skewness	0,6577487	Skewness	0,1820401
Kurtosis	-0,1826851	Kurtosis	-0,6027403	Kurtosis	-0,4525136
Geom. mean	3,601623	Geom. mean	5,939102	Geom. mean	31,48845
Coeff. var	32,95191	Coeff. var	61,85848	Coeff. var	24,29544

Table 2. Summary statistics on trilobite sizes from the Tamgroute, Bou Izargane and Ouled Slimane.

Normality test					
Tamegroute		Bou Izargane		Ouled Slimane	
N	15	N	14	N	31
Shapiro-Wilk W	0,9424	Shapiro-Wilk W	0,9175	Shapiro-Wilk W	0,9879
p(normal)	0,4138	p(normal)	0,2021	p(normal)	0,9732
Anderson-Darling	0,3422	Anderson-Darling	0,5364	Anderson-Darling	0,09692
A		A		A	
p(normal)	0,4423	p(normal)	0,1385	p(normal)	0,9963
p(Monte Carlo)	0,4561	p(Monte Carlo)	0,1391	p(Monte Carlo)	0,9997
Jarque-Bera JB	0,9986	Jarque-Bera JB	1,18	Jarque-Bera JB	0,5749
p(normal)	0,6069	p(normal)	0,5545	p(normal)	0,7502
p(Monte Carlo)	0,361	p(Monte Carlo)	0,2449	p(Monte Carlo)	0,6932

Table 3. Normality tests for the studied sites showing that size distributions are normal.

Significant differences					
Tamegroute vs Bou Izargane			Bou Izargane vs Ouled slimane		
t :	2,9361	p (same mean): 0,006 7168	t :	-11,047	p (same mean): 3,86 E-14
Uneq. var. t :	2,8469	p (same mean): 0,012 365	Uneq. var. t :	-13,412	p (same mean): 2,09 E-16
Monte Carlo permutation:	p (same mean): 0,005		Monte Carlo permutation:	p (same mean): 0,0001	

Table 4. t-test showing that size differences between sites are significant.

Pygidial sagittal length for <i>Platypeltoides</i> (cm)		
Tamegroute	Bou Izargane	Ouled Slimane
1.3	2.6	5,7
0.8	3.5	7,1
1.6	3.8	6,5
1.6	4.3	6
1	2.2	6,2
		7
		5,9
		6,9
		5,7

Table 5. Raw pygidial sagittal length in the studied localities.

Summary statistics					
Tamegroute		Bou Izargane		Ouled Slimane	
N	5	N	5	N	9
Min	0,8855	Min	2,2638	Min	5,7
Max	1,6709	Max	4,3428	Max	7,1
Sum	6,49056	Sum	16,5935	Sum	57
Mean	1,298112	Mean	3,3187	Mean	6,333333
Std. error	0,158821	Std. error	0,3823575	Std. error	0,186339
Variance	0,1261206	Variance	0,7309864	Variance	0,3125
Stand. dev	0,3551346	Stand. dev	0,8549774	Stand. dev	0,559017
Median	1,32386	Median	3,5112	Median	6,2
25 prcntil	0,9394	25 prcntil	2,45245	25 prcntil	5,8
75 prcntil	1,64395	75 prcntil	4,0887	75 prcntil	6,95
Skewness	-0,133172	Skewness	-0,1776892	Skewness	0,2802879
Kurtosis	-2,713525	Kurtosis	-1,867874	Kurtosis	-1,78304
Geom. mean	1,257634	Geom. mean	3,226366	Geom. mean	6,311613
Coeff. var	27,35778	Coeff. var	25,76242	Coeff. var	8,826584

Table 6. Summary statistics on pygidial length in Tamegroute, Bou Izargane, and Ouled Slimane.

Normality test					
Tamegroute		Bou Izargane		Ouled Slimane	
N	5	N	5	N	9
	0,896		0,953		0,889
Shapiro-Wilk W	6	Shapiro-Wilk W	6	Shapiro-Wilk W	7
	0,391		0,763		0,198
p(normal)	3	p(normal)	2	p(normal)	2
Anderson-Darling A	9	Anderson-Darling A	6	Anderson-Darling A	6
	0,297		0,209		0,400
	0,426		0,711		0,283
p(normal)	8	p(normal)	9	p(normal)	6
	0,490		0,807		0,301
p(Monte Carlo)	1	p(Monte Carlo)	5	p(Monte Carlo)	2
	0,593		0,460		
Jarque-Bera JB	5	Jarque-Bera JB	2	Jarque-Bera JB	0,965
	0,743		0,794		0,617
p(normal)	2	p(normal)	5	p(normal)	2
	0,394		0,602		0,244
p(Monte Carlo)	7	p(Monte Carlo)	3	p(Monte Carlo)	4

Table 7. Normality test on pygidial lengths showing normal distributions.

Significant differences					
Tamegroute vs Bou Izargane			Bou Izargane vs Ouled slimane		
t :	-4,8803	p (same mean): 0,001 2239	t :	-8,0391	p (same mean): 3,58E -06
Uneq. var. t :	-4,8803	p (same mean): 0,003 8096	Uneq. var. t :	-7,0875	p (same mean): 0,000 4085
Monte Carlo permutation:	p (same mean):	0,0076	Monte Carlo permutation:	p (same mean):	0,0005
Exact permutation:	p (same mean):	0,00396 83	Exact permutation:	p (same mean):	0,00049 95

Table 8. t-test showing significant differences in pygidial lengths between sites.