1 **The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: age,**
2 **environment and evolutionary perspectives**

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29 **ABSTRACT**

30 The Lower Ordovician Fezouata Konservat-Lagerstätte from southern Morocco has been one
31 of the major palaeontological discoveries of the last decade. It provides a unique insight into
32 one of the most critical periods in the evolution of marine life: the Cambrian-Ordovician
33 transition. However, its potential for deciphering key trends in animal diversification was
34 hitherto largely limited by major uncertainties concerning its stratigraphic position, age and
35 environmental setting. Based on extensive fieldwork, fossil evidence, and facies recognition,
36 our study provides clarification on these three crucial issues. Exceptional preservation is
37 limited to two intervals within the Fezouata Shale. Graptolites indicate a late Tremadocian
38 age for the Fezouata Konservat-Lagerstätte as a whole, which is supported by
39 biostratigraphical evidence provided by acritarchs. Sedimentological features and
40 reconstructed patterns of relative sea-level changes indicate relatively shallow-water
41 environmental conditions, under distal storm influence, in an offshore to lower shoreface
42 siliciclastic ramp setting. The Fezouata Biota represents a unique and exceptional window
43 into the palaeobiodiversity in open-marine conditions, thus contrasting with the other
44 Ordovician Konservat-Lagerstätten presently known. In our analyses of this new set of data,
45 we pave the way for accurate temporal, faunal and environmental comparisons with other
46 Lower Palaeozoic Konservat-Lagerstätten, and unlock the full potential of the Fezouata Biota
47 to better understand the processes and scenarios of early animal radiations.

48

49 *Keywords:* Konservat-Lagerstätten, sedimentology, Ordovician, Gondwana, Morocco,
50 Fezouata.

52 1. Introduction

53 The Cambrian-Ordovician time interval (*c.* 541-443 Ma) is characterised by the evolution and
54 radiation of animals that led to irreversible changes in marine ecosystems (Bambach et al.,
55 2007; Vannier et al., 2007; Butterfield, 2011; Erwin and Valentine, 2013). Triggered by
56 complex interacting factors (Smith and Harper, 2013; Maruyama et al., 2014; Santosh et al.,
57 2014; Zhang et al., 2014), the Cambrian Explosion is the initial visible phase of animal
58 diversification and is defined by the appearance in the fossil record of a wide spectrum of new
59 anatomies and functionalities, and by complex ecological systems that have no counterparts in
60 the Precambrian (Erwin et al., 2011; Shu et al., 2014). This evolutionary and ecological
61 revolution is evidenced by several early to middle Cambrian Konservat-Lagerstätten (*sensu*
62 Seilacher, 1970; termed “Lagerstätten” below; Fig. 1), which have yielded abundant and
63 diverse remains of both shelly and non-biomineralised organisms such as those of Chengjiang
64 (Hou et al. 2004; Zhao et al., 2009), Sirius Passet (Peel and Ineson, 2011), Emu Bay (Paterson
65 et al., *in press*), or the Burgess Shale (Caron and Jackson, 2008) [Figure 1 nearby]. They
66 provide detailed information on the anatomy, lifestyles, and behaviours of early animals and
67 also on their interactions within the evolving trophic web (Dunne et al., 2008; Vannier, 2011).
68 Postdating the Cambrian Explosion, the Great Ordovician Biodiversification Event (GOBE)
69 represents the second major burst in marine biodiversity. During most of the Ordovician
70 Period, a sustained exponential diversification took place within almost all animal phyla
71 (Harper, 2006; Servais et al., 2008, 2010). Unlike the Cambrian Explosion, the GOBE is
72 primarily recognised from diversity analyses based on the fossil record of shelly faunas and
73 microfossils. Indeed, Ordovician Lagerstätten are rare and most of them occur in the Upper
74 Ordovician, long after the initial stages of the GOBE (Fig. 1). Moreover, they typically
75 contain low diversity faunas that lived in restricted marine environments (e.g. Beecher’s

76 Trilobite Bed from the Lorraine Group, Farrell et al., 2013; Soom Shale, Gabbott, 1998;
77 William Lake Biota of Manitoba, Young et al., 2007).

78 The recent discovery of a Burgess Shale-type Lagerstätte in the Lower Ordovician of
79 Morocco (Zagora area, Central Anti-Atlas, Fig. 2A; Van Roy et al., 2010) provided
80 unexpected and unprecedented possibilities to obtain high-resolution information on both the
81 aftermath of the Cambrian Explosion and the very beginning of the Ordovician radiation
82 event [Figure 2 nearby]. Although still largely undescribed, the diverse fossil assemblages of
83 the Fezouata Biota (Fig. 3) are characterised by the co-occurrence of organisms typical of
84 Cambrian Burgess Shale-type biotas (Van Roy et al., 2010), such as anomalocaridids (Van
85 Roy and Briggs, 2011; Gaines et al., 2012a) and some demosponges (Botting, 2007) with
86 classical Ordovician faunal elements. The biomineralised component of the Fezouata Biota is
87 dominated by trilobites (e.g. Destombes, 1972; Rábano, 1990; Henry et al., 1992; Vidal,
88 1998a, 1998b; Chatterton and Fortey, 2008; Fortey, 2009, 2011a, 2011b) and echinoderms
89 (Ubaghs, 1963; Chauvel, 1966, 1969, 1971a, 1971b, 1978; Donovan and Savill 1988; Chauvel
90 and Régnault, 1986; Lefebvre and Botting, 2007; Noailles et al., 2010; Sumrall and Zamora,
91 2011). The fauna also contains a great abundance of xiphosurid arthropods (Van Roy et al.,
92 2010), palaeoscolecidan worms, annelids (machaeridians, Vinther et al., 2008), molluscs
93 (Babin and Destombes, 1990; Horný, 1997; Kröger and Lefebvre, 2012), hyolithids (Marek,
94 1983; Valent et al., 2013), brachiopods (Havlíček, 1971; Mergl, 1981, 1988), and conularids
95 (Destombes et al., 1985) [Figure 3 nearby]. Graptolites are also abundant but have not been
96 studied in detail so far (Destombes and Willefert, 1959; Willefert in Destombes et al., 1985;
97 Aceñolaza et al., 1996). Despite this remarkable diversity, two main obstacles have so far
98 limited the impact of the Fezouata Lagerstätte. First, most fossils were collected from isolated
99 excavations lacking an accurate positioning within the lithological succession. This led Van
100 Roy et al. (2010) to hypothesise that the Fezouata Lagerstätte could span a time period of

almost 10 Myr (late Tremadocian to late Floian). Second, major uncertainties remained concerning the environmental setting of the Fezouata Biota, especially in terms of bathymetry, energy and oxygenation. The Lower Ordovician succession in the Zagora area has remained virtually unstudied since the pioneering work of Destombes et al. (1985). Based on extensive fieldwork in the Zagora area, new fossil studies, and facies recognition, we here provide clarification on these two crucial chronological and environmental issues, making it possible for the first time 1) to establish precise comparisons with other Lower Palaeozoic Lagerstätten and 2) to test the potential of the Fezouata Lagerstätte in resolving the pace and amplitude of the animal diversification in the Early Palaeozoic.

110

111 **2. Geological setting**

In the Anti-Atlas of south-eastern Morocco, the Cambrian-Ordovician transition is exposed in the Ternata plain, 30 km north of Zagora. The Guzhangian (Cambrian series 3) sandstones of the Tabanite Group are unconformably overlain by the Tremadocian to Floian (Lower Ordovician) deposits of the Lower Fezouata, the Upper Fezouata, and the Zini formations, which, together with the Tachilla Formation (Middle Ordovician), form the Outer Feijas Group (Destombes et al., 1985; Geyer and Landing, 2006). The Lower and Upper Fezouata formations constitute a thick (up to 1200 m) and rather monotonous sequence dominated by silty and micaceous argillites. A glauconitic and ferruginous horizon has often been used as a possible lithological marker for the boundary between the two formations, which have been regarded as Tremadocian and Floian in age respectively (Destombes et al., 1985). However, this horizon is missing in the Zagora area, where the Fezouata Lagerstätte is located. Consequently, the Lower and Upper Fezouata formations are here considered together as a single lithological unit: the Fezouata Shale, which is topped by the sandstone-dominated Zini Formation (Destombes, 1962; Destombes et al., 1985).

126 During the Early Ordovician, the Anti-Atlas was located on the southern margin of Gondwana
127 and situated in the southern hemisphere at high latitudes (*c.* 65°S), relatively close to the
128 South Pole (Fig. 2B, Cocks and Torsvik, 2004; Torsvik and Cocks, 2011, 2013). The Lower
129 Ordovician sediments were deposited in a rifting context associated with the northward drift
130 of Avalonia away from the Gondwanan palaeocontinent (Cocks and Torsvik, 2004).

131 **3. Material and methods**

132 **Exceptional preservation**– The Fezouata Lagerstätte is a Konservat-Lagerstätte that is by
133 definition characterised by the occurrence of exceptionally well-preserved fossils (EPF). In
134 the Fezouata Lagerstätte, EPF were soft-bodied and lightly sclerotised organisms (e.g. worms,
135 sponges, arthropods) that are usually preserved via pyritisation and subsequent weathering to
136 iron oxides, giving the fossils a reddish colour. EPF typically display more or less complete
137 anatomical (e.g. digestive features) and exoskeletal features (e.g. arthropod appendages).

138 **Fieldwork**–The whole Lower Ordovician succession exposed in the Zagora area (Central
139 Anti-Atlas, Morocco; Fig 2C) was logged at a decimetre scale from fourteen different sections
140 (black and red crosses on Fig. 2C). Data were compiled in a single, synthetic *c.* one thousand-
141 metre-thick stratigraphic column. All localities yielding EPF mentioned in the original
142 contribution of Van Roy et al. (2010) were included in this study, except one located *c.* 15 km
143 west of the main outcrop area (blue asterisk on Fig. 2C). EPF localities were carefully located
144 and positioned along the stratigraphic column based on their lithological characteristics
145 (colour, composition, marker beds) and faunal elements (mostly graptolites, trilobites, and to
146 a lesser extent echinoderms). Graptolites were collected throughout the succession, but
147 particular attention was paid to horizons yielding EPF. Changes in lithology and sedimentary
148 structures were observed throughout the succession and were used to reconstruct short-term
149 and long-term relative sea-level changes. EPF and graptolites were photographed with a
150 Nikon D3X camera (with a Micro-Nikkor AF 60mm f/2.8D macrolens) and with a Leica

151 MZ75 binocular microscope. When necessary, fossils were immersed under dilute ethanol in
152 order to enhance contrast and avoid reflective spots. All fossil specimens are deposited in the
153 collections of the Cadi Ayyad University, Marrakech (Faculté des Sciences et Techniques,
154 Guéliz; sample number prefix AA), except for one, which is deposited in the palaeontological
155 collections of Lyon 1 University, Villeurbanne (sample number prefix FSL).

156 **4. Results and Interpretations**

157 ***4.1. Stratigraphic distribution and age of the Fezouata Biota***

158 The lithology of the Fezouata Shale Formation is fairly homogeneous and largely dominated
159 by fine-grained siliciclastic deposits, except in its lowermost and uppermost parts. The lower
160 part of the Fezouata Shale is characterised by a transgression from a foreshore environment,
161 whereas its upper part records a regressive trend. The distribution of EPF throughout the
162 thousand-metre-thick Fezouata Shale shows that exceptional preservation occurs within a
163 restricted interval in the lower part of the succession [Figure 4 nearby]. Figure 4 summarises
164 the stratigraphic distribution of graptolites across this interval and its facial characteristics
165 (colour, lithology, sedimentary structures). About three hundred well-preserved graptolite
166 specimens were collected, identified, and used for dating the lower part of the Fezouata Shale.
167 Graptolites also occur locally as monospecific mass-occurrences of *Araneograptus murrayi*
168 (Hall) and “*Tetragraptus*” *bulmani* Thomas. The facies evolution within the entire succession
169 and the structural context of the Lower Ordovician in the area of Zagora are beyond the scope
170 of this contribution and will be the subjects of a separate study.

171

172 The studied succession is rather homogeneous, being composed of mainly thinly-bedded
173 argillites with frequent intercalations of silts and millimetre- to centimetre-thick silty to sandy
174 beds. Facies variations consist of slight differences in argillite composition (e.g. presence of
175 silts or micas), or in diagenesis (e.g. induration, bedding). EPF are restricted to a 70-metre-

176 thick interval developed between 260 and 330 metres above the basal contact with the
177 Guzhangian Tabanite Group and are usually found in relatively fine facies, the beds overlying
178 them being coarser. They occur within two distinct intervals of *c.* 25 (interval 1) and 15
179 (interval 2) metres in thickness respectively, separated by a *c.* 30-metre-thick interval where
180 only biomineralised remains are found (e.g. brachiopods, echinoderm exoskeletons, trilobite
181 carapaces).

182 Eleven graptolite species have been recognised through the studied succession (Fig. 5) [Figure
183 5 nearby]. These include the index species of the *Araneograptus murrayi* and *Hunnegraptus*
184 *copiosus* graptolite biozones, which are the uppermost graptolite zones of the Tremadocian
185 (Loydell, 2012). *A. murrayi* occurs in great abundance from 240 to 295 metres above the base
186 of the Fezouata Shale. EPF-bearing Interval 1 falls within the *Araneograptus murrayi*
187 Biozone. EPF-bearing Interval 2 mainly belongs to the upper part of the *A. murrayi* Biozone.
188 Only the uppermost part of this interval corresponds to the following *Hunnegraptus copiosus*
189 Biozone, as indicated by the first occurrence of *H. copiosus*. EPF-bearing interval 1 and 2 are
190 thus both of late Tremadocian age and correlate with the Tr3 substage of Bergström et al.
191 (2009).

192

193 **4.2. Environmental setting of the Fezouata Biota**

194 Ripple marks, hummocky cross-stratification (HCS), and normally-graded tempestites are
195 repeatedly found throughout the section, including in the two intervals with EPF (Fig. 6A-D)
196 [Figure 6 nearby]. These sedimentary structures are interpreted as being induced by storm
197 wave action on the sea floor (Harms et al., 1975; Duke, 1985; Duke et al., 1991; Gupta, 1998)
198 and suggest a depositional environment at or above storm wave-base. However, HCS
199 observed in the studied succession are only at a millimetre- to centimetre-scale, whereas they
200 can reach several decimetres elsewhere in the succession (e.g., near the contact with the Zini

201 Formation). These small-scale HCS suggest a relatively shallow depositional environment,
202 most probably located within the offshore to lower shoreface (as defined by McLane, 1995;
203 Fig. 6E).

204 Three long-term cycles of relative sea-level fluctuations are recognised in the entire Fezouata
205 Shale, but only the first and the second of them are documented in the studied section (Fig. 4).
206 All are composed of a transgressive phase marked by an evolution from silt-dominated to
207 clay-dominated intervals and a regressive phase marked by the opposite trend. Exceptional
208 preservation occurs at the end of the regressive phase of the first cycle and at the beginning of
209 the transgressive phase of the second cycle (Fig. 4). Additionally, facies changes towards
210 more argillaceous sedimentary deposits and fewer silty tempestites, or towards more silty
211 argillites interrupted by more frequent silty or fine-sandy tempestites are interpreted as
212 transgressive and regressive phases of short-term cycles respectively. Two of them are
213 associated with the preservation of EPF.

214

215 **5. Discussion**

216 ***5.1. Exceptional preservation: stratigraphic distribution and environmental factors***

217 The distribution of EPF within the Fezouata Shale is restricted to two narrow stratigraphic
218 intervals, which contradicts earlier assessments (Van Roy et al., 2010) that exceptional
219 preservation occurs throughout the Fezouata Shale. This is a common point shared with most
220 major Cambrian and Ordovician Lagerstätten in which exceptional preservation is limited to a
221 relatively narrow stratigraphic interval, ranging from a few metres - e.g. Sinsk (Russia;
222 Ivantsov et al., 2005), Emu Bay (Australia; Gehling et al., 2011), the Spence Shale (USA;
223 Liddell et al., 1997), the Burgess Shale (Canada; Collom et al., 2009), or the Llanfawr
224 Mudstones (UK; Botting et al., 2011) - to a few tens of metres, as in Chengjiang (China;

225 Babcock and Zhang, 2001), the Pioche Shale (USA; Moore and Lieberman, 2009), Wheeler
226 Formation (USA; Brett et al., 2009), or the Soom Shale (South Africa; Aldridge et al., 1994).
227 An exception is the Guanshan Biota (China; Hu et al., 2010), which seems to occur
228 throughout the entire Wulongqing Formation, and can reach up to 60 metres in thickness.
229 Environmental conditions maintained over a relatively short timespan may account for the
230 preservation of EPF within a narrow stratigraphic interval (Hagadorn, 2002). Exceptional
231 preservation is often associated with the rapid burial of organisms, which is supposed to
232 promote oxygen restriction and to favour the preservation of soft tissues and lightly
233 sclerotised features (Gaines et al., 2012b). Different mechanisms of entombment have been
234 proposed. For example, a mostly turbiditic origin is often suggested for the mudrock-
235 siltstones of the Burgess Shale (Gabbott et al., 2008), with probably a rhythmic deposition
236 from waxing and waning density currents (Gabbott and Zalasiewicz (2009). Recent studies of
237 the Burgess Shale communities (Caron and Jackson, 2008; Caron, 2009) show that the fauna
238 was mostly preserved *in situ* and only moderately disturbed by the event of burial. Most
239 organisms were buried *in situ* by distal mudflow events. In Chengjiang, a typical sedimentary
240 succession is recognised (Hu, 2005). It consists of background layers dominated by
241 hemipelagic mud, which are interrupted by event layers that contain soft-bodied fossils. These
242 event layers are generated by bottom-flowing density currents, which are responsible for the
243 burial of the fauna.

244 Although storms played an important role in the overall depositional mode of the Fezouata
245 Shale (as indicated by the presence of numerous HCS and tempestites), the storm waves seem
246 to have had a limited influence on the relatively distal deposits that contain EPF. Indeed,
247 storm currents were weak in this area, as attested by the relatively small scale of the HCS
248 found, resulting from a mainly oscillatory movement at the seafloor. The animal communities
249 of the Fezouata Shale were probably buried *in situ* during storm events, which mobilised

250 more proximally a large amount of coarser sediments. Between two storm events, the
251 background sedimentation resulted from the decantation of mud suspended by wave action. It
252 is not associated with any sedimentological structures, such as HCS and tempestites. This
253 depositional scenario would be comparable to the one invoked for the Chengjiang and other
254 Burgess Shale-type Lagerstätten (Gaines et al., 2012b).

255 The geochemical context of the Fezouata Shale has not yet been explored and will be
256 investigated on fresh rocks obtained from drilled cores (in-progress). No detailed information
257 is available on the redox conditions that prevailed at the water-sediment interface and within
258 the sediment. However, the presence of iron oxides in the majority of the weathered EPF
259 suggests that an early mineralisation of pyrite took place on both soft and sclerotised tissues
260 and was induced by microbial activity under anaerobic conditions (Gabbott et al., 2004;
261 Vinther et al., 2008; Van Roy et al., 2010). This taphonomic pathway, rather unusual among
262 Burgess Shale-type Lagerstätten, led to the exceptional preservation of giant anomalocaridids
263 in silica-chlorite concretions and possibly involved the dissolution of volcanic ashes in the
264 sediment (Gaines et al., 2012a). Field observations indicate that bioturbation associated with
265 EPF-bearing intervals was limited to mostly narrow horizontal burrows, very close to the
266 water-sediment interface. This supports a low infaunal activity, possibly related to
267 dysoxic/anoxic conditions within the sediment.

268

269 **5.2. Dating the Fezouata Lagerstätte**

270 Graptolites (*Araneograptus murrayi* and *Hunnegraptus copiosus* biozones) indicate a late
271 Tremadocian age for the EPF-bearing intervals of the Fezouata Shale. Therefore, the Fezouata
272 Lagerstätte does not extend to the Floian as suggested previously (Van Roy et al., 2010). It
273 cannot be entirely ruled out that *H. copiosus* occurs lower in the stratigraphy. As the base of
274 the *H. copiosus* Biozone is defined by the First Appearance Datum of this biozonal marker

275 graptolite (Egenhoff et al., 2004), a larger portion of the interval 2 may belong to the
276 *Hunnegraptus copiosus* Biozone. However, the resulting changes would be of little
277 significance regarding the age of the Fezouata Biota, which would remain late Tremadocian
278 (Tr3 of Bergström et al., 2009).

279 The only excavation that was not re-studied in detail (blue asterisk in Fig. 2C) yielded the
280 graptolite *Clonograptus*, associated with the trilobite *Dikelocephalina brenchleyi*. Both would
281 suggest a late Tremadocian age (Fortey, 2009, 2011b).

282 Graptolites are both abundant and well preserved throughout the Fezouata Shale (Fig. 5).
283 They are reliable markers for dating and correlations, especially in the Ordovician (Webby et
284 al., 2004; Sadler et al., 2009). The graptolite assemblages of the Fezouata Shale are dominated
285 by planktonic forms that are assumed to have lived in epipelagic niches (Cooper et al., 1991,
286 2012a), with a small percentage of rooted benthic dendroids (Fig. 5C and J). The planktonic
287 ones have a cosmopolitan distribution and have been widely used for global correlations.
288 They occur in Scandinavia (Lindholm, 1991), North America (Williams and Stevens, 1991;
289 Maletz, 1997; Jackson and Lenz, 2003), South America (Maletz and Egenhoff, 2001; Ortega
290 and Albanesi, 2005), China (Feng et al., 2009) and southwestern Europe (Aceñolaza et al.,
291 1996; Pillola et al., 2008).

292 Microfossils, such as acritarchs, chitinozoans, and conodonts, are also accurate
293 biostratigraphic markers, but their study requires fresh material (e.g. from well drillings or
294 boreholes; Elaouad-Debbaj, 1988) for high-resolution dating. Acritarchs typical of the late
295 Tremadocian to lower Floian *messaoudensis-trifidum* assemblage occur in the lower part of
296 the Fezouata Shale below and within EPF-bearing interval 1. This particular acritarch
297 assemblage indicates a late Tremadocian age, correlating to the top of the *A. murrayi* and the
298 base *H. copiosus* graptolite biozones (Molyneux et al., 2007). A drill core, which presumably

299 crosses the Fezouata Shale, about 300 km southwest of Zagora, yielded comparable acritarch
300 assemblages equally pointing to a late Tremadocian age (Nowak et al. *in press*).

301

302 **5.3. Environmental setting: implications**

303 Sedimentological features indicate that the Fezouata Shale was deposited above storm wave-
304 base, in a relatively shallow, open-marine environment (offshore to lower shoreface, Fig 6e).

305 Based on comparisons with the depth of storm influence in modern oceans (Immenhauser,
306 2009), a palaeodepth ranging from 50 to 150 m is proposed for the depositional area of the
307 Fezouata Shale. The Fezouata Biota also delivers interesting indications of water depths.

308 Based on the characteristics of the mitrate (Echinodermata, Stylophora) *Peltocystis cornuta*
309 from the Fezouata Formation, Lefebvre and Botting (2007) conclude that the environment
310 was shallow and of moderately high energy. In addition, non-calcareous algae are present in
311 the fauna (Van Roy et al., 2010), but they might also have been transported in from shallower
312 waters. Thus, their presence should be considered with caution and is not a reliable depth
313 indicator. In this respect, the visual systems of the articulated benthic trilobites are probably
314 more useful. All trilobites of this stratigraphic interval seem to have eyes (except *Ampyx* cf.
315 *priscus*; Vidal, 1998a, 1998b). This would suggest that there must have been at least some
316 visible light, but not necessarily enough for photosynthesis. As a consequence, a maximum
317 depth of 150 metres might be overestimated, given the low insolation received in high
318 latitudes (Kirk, 2011). The weak contrasts in lithology and facies throughout the cycles of
319 short- and long-term sea-level changes indicates relatively low-amplitude sea-level
320 fluctuations and thus, a relatively stable sea level close to storm wave-base over a relatively
321 long time span (at least from the *A. murrayi* to the *H. copiosus* biochrons that represent a
322 duration of about 2 Myr; Cooper et al., 2012b).

323 The palaeoenvironmental setting (open shelf close to the limit between the lower shoreface
324 and the offshore) of the Fezouata Biota differs markedly from that of all Ordovician
325 Lagerstätten presently known (Fig. 1), which are associated with particular marine
326 environments. Indeed, the Winneshiek Biota (USA) lived in a possible estuarine embayment
327 (Liu et al., 2006), the Beecher's Trilobite Bed (USA) was deposited under dysoxic conditions
328 in an environment of deposition of distal turbidites (Farrell et al., 2013), the Llanfawr
329 mudstones (UK) represented deep-water or abyssal environments (Botting et al., 2011), the
330 Letná Formation (Czech Republic; Fatka et al., 2013), the Airport Cove and William Lake
331 (Canada; Young et al., 2007) were located in shallow peritidal settings and the Soom Shale
332 (South Africa) was close to a retreating ice front (Aldridge et al., 2001).

333 Therefore, the Fezouata Lagerstätte opens a unique and exceptional window into the marine
334 biodiversity within open-marine environments during the Early Ordovician and makes it
335 possible for the first time to establish accurate comparisons with the older well-documented
336 open-marine exceptional biotas from the Cambrian. Among them, the Burgess Shale (Canada;
337 Collom et al. 2009), Kaili (China; Zhao et al., 2005), Sinsk (Russia; Ivantsov et al., 2005), and
338 Sirius Passet (Greenland; Ineson et al., 2011) Lagerstätten are associated with distal offshore
339 environments, whereas the Emu Bay Shale Lagerstätte (Australia; Gehling et al., 2011) is
340 characterised by a relative nearshore setting affected by the tectonics of an active margin. In
341 terms of environmental setting, the Fezouata Lagerstätte may best compare with the Guanshan
342 and Chengjiang Lagerstätten (Hu, 2005; Hu et al., 2010; MacKenzie et al., 2015), although
343 the environmental conditions that prevailed at Chengjiang are still debated (see Zhao et al.,
344 2012). A lower shoreface/offshore depositional environment has been inferred for these three
345 localities, in which early diagenetic pyritization represents the dominant mode of soft-tissue
346 preservation (Gabbott et al., 2004; Van Roy et al., 2010; Vinther et al., 2008).

347 Another important characteristic of the Fezouata Lagerstätte is its high latitudinal position (c.
348 65°S) compared with that of other Ordovician and Cambrian Lagerstätten (Fig. 2B, Cocks and
349 Torsvik, 2004; Torsvik and Cocks, 2011). The Hirnantian Soom Shale Lagerstätte (South
350 Africa) was previously thought to be located at 60°S, but more recent palaeogeographic
351 reconstructions suggest a much lower latitude (i.e. 35°S; Whittle et al, 2007; Torsvik and
352 Cocks, 2013). Unlike the Soom Shale (Gabbott, 1998), no glaciogenic sediments are
353 associated with the Fezouata Biota. This raises the important question of the climatic
354 conditions and seawater temperature that prevailed and may have influenced the diversity and
355 composition of the Fezouata Biota. Nevertheless, the very nature of the global climate state
356 during the Early and Middle Ordovician is under discussion (Trotter et al., 2008;
357 Vandenbroucke et al., 2009; Nardin et al., 2011; Turner et al., 2011).

358

359 *5.4. A Late Tremadocian Lagerstätte : evolutionary perspectives*

360 The Fezouata Biota is a key source of information for understanding the biotic turnover that
361 took place during the Cambrian-Ordovician transition, i.e. after the Cambrian Explosion and
362 before the GOBE. The co-existence of Burgess Shale-type faunal elements (such as
363 marrellomorphs and anomalocaridids) with remarkably derived, typical post-Cambrian
364 organisms (such as crinoids, ostracods and xiphosurids) indicates that the transition between
365 the Cambrian and Palaeozoic Evolutionary Faunas (Sepkoski, 1979) was more complex and
366 extended than hitherto realised. Moreover, the presence of several surprisingly advanced
367 forms in the biota, such as xiphosurid arthropods, machaeridians, or cheloniellids (Van Roy et
368 al., 2010), suggests that at least in some non-biomineralised groups, the GOBE started earlier
369 than previously thought. This supports the idea that, rather than being two distinct events, the
370 Cambrian Explosion and the GOBE might in fact represent different phases of the same
371 dynamic of diversification (Droser and Finnegan, 2003; Van Roy et al., 2010).

372

373 6. Conclusions

374 Exceptional preservation in the Fezouata Shale is restricted to two relatively narrow intervals
375 that belong to the upper Tremadocian (*A. murrayi* to basal-most *H. copiosus* graptolite
376 biozones). The animal communities of the Fezouata biota lived in an open-marine
377 environment, in a relatively shallow setting (offshore to lower shoreface transition) close to
378 the storm wave-base. Organisms were very likely buried *in situ* during storm events, with a
379 background sedimentation resulting from the decantation of mud suspended by wave action.
380 By offering better chronological and environmental constraints, our results reveal the
381 potential of the Fezouata Biota for understanding the early steps of animal life. Future
382 investigations will concentrate on the identification of the taphonomic and/or abiotic factors
383 controlling the restricted stratigraphic distribution of EPF within the thousand-metre-thick
384 Fezouata Shale.

385

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 733

733 **Figure Captions**

734

735 **Figure 1.** Stratigraphic distribution of the main diverse exceptionally preserved faunas from
736 the Cambrian and the Ordovician.

737

738 **Figure 2.** A, Lower Ordovician outcrops of northern Morocco and location of Zagora; B,
739 Palaeogeography of Africa (blue star represents Zagora) in the Early Ordovician (modified
740 from Cocks and Torsvik, 2004; Torsvik and Cocks, 2011); C, Lower Ordovician outcrops in
741 the Zagora area. Small black crosses indicate logged sections and red crosses the three key
742 sections used to build the composite stratigraphic column (Figure 4). Small grey crosses and
743 blue asterisk indicate the inspected and non-inspected localities that yielded EPF respectively
744 (Van Roy et al., 2010; modified).

745

746 **Figure 3.** Examples of exceptionally preserved fossils from the Fezouata Biota (latest
747 Tremadocian; Zagora area, Morocco). A, unidentified palaeoscolecid worm, AA-BGF2-OI-1;
748 B, *Pirania auraeum* Botting, 2007, demosponge, AA-JBZ-OI-115; C–E, arthropods with
749 preserved appendages (arrows); C, *Furca* sp. (Marrellomorpha), AA-BIZ31-OI-39; D,
750 Xiphosuran (Chelicerata) with fully segmented opisthosoma, FSL 712 411; *Bavarilla* sp.
751 (Trilobita), AA-BIZ15-OI-16. All specimens were photographed under alcohol. Scale bars:
752 A–C, 5 mm; D–E, 2 mm.

753

754 **Figure 4.** Partial composite section of the Fezouata Shale (Lower Ordovician, Zagora area)
755 showing the distribution of the main levels (except one, see discussion 4.1) yielding
756 Exceptionally Preserved Fossils (EPF; red stars) and the vertical range of diagnostic

757 graptolites. Right columns modified from (1) Loydell (2012) and (2) Bergström et al. (2009).

758 The colours in the logged section roughly correspond to the colours of outcropping rocks.

759

760 **Figure 5.** Graptolites of the Fezouata Biota (late Tremadocian; Zagora area, Morocco). A,

761 *Araneograptus murrayi* (Hall, 1865), AA-BIZ3-OI-35 showing nematularium (upper left) and

762 distal end on another young colony (center-right); B, *Paradelograptus tenuis* Lindholm, 1991,

763 AA-OFTa-OI-23; C, *Koremagraptus* sp., AA-FETi-OI-1; D, *Clonograptus rigidus* (Hall,

764 1858), AA-JTZb-OI-19; E, *Paradelograptus norvegicus* (Monsen, 1937), AA-JTZ-OI-10; F,

765 “*Tetragraptus*” *bulmani* Thomas, 1973, AA-BIZ13-OI-9; G, “*Didymograptus* sp. 1” (cf.

766 Lindholm, 1991), AA-BIZ31-OI-40; H–I, *Paratemnograptus magnificus* (Pritchard, 1892),

767 fragment of a large rhabdosome (F, AA-BZG-OI-13) and detail of a stipe showing plaited

768 thecal structure (triad budding without bithecae), AA-BIZ13-OI-10; J, *Dictyonema?* sp., AA-

769 BZG-OI-14; K–M, “*Kiaerograptus*” *supremus* Lindholm, 1991, K= AA-BGF2-OI-7; L= AA-

770 BGF2-OI-6, with detail of the proximal end (M) showing sicular bitheca (arrow); N–O,

771 *Hunnegraptus copiosus* Lindholm, 1991, N= AA-JBZ-OI-117; O= AA-JBZ-OI-116; P,

772 *Paradelograptus* sp., AA-JTZ-OI-9. All specimens, excepting A, H, I and M, were

773 photographed under alcohol. Scale bars: A, D, and H, 20 mm; E, 10 mm; C, F, K, L, and J, 5

774 mm; B, G, N, and O, 3 mm; I, and P, 2 mm; M, 0.5 mm.

775

776 **Figure 6.** Typical sedimentary structures used to characterise the palaeoenvironment of the

777 Fezouata Shale. A–B, 2D-wave ripples in a distal tempestite, in section and slab surface,

778 respectively. C, small, centimetre-scale hummocky cross stratifications (HCS) from the top of

779 the section. D, thin, possibly wave-induced cross-laminated structures in a distal silty

780 tempestite. E, general palaeoenvironmental reconstruction for the Fezouata Shale deposition.

781 Terminology of depth zones follows the definition of McLane (1995). Scale bars: A–B, 1 cm;

782 C–D, 3 cm.

783

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6