

1           **STORM-INDUCED COMMUNITY DYNAMICS IN THE FEZOUATA BIOTA**

2   **(LOWER ORDOVICIAN, MOROCCO)**

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12   *RHH: COMMUNITY DYNAMICS IN THE FEZOUATA SHALE*

13   *LRH: F. SALEH ET AL.*

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16   **ABSTRACT**

17   **In the Central Anti-Atlas (Morocco), the lower part of the Fezouata Shale has yielded**  
18   **locally abundant remains of soft-bodied to lightly-sclerotized taxa, occurring in low**  
19   **diversity assemblages characterized by strong spatial and taxonomic heterogeneities, and**  
20   **frequently, by the occurrence of small-sized individuals. Size frequency analyses of**  
21   ***Celdobolus* sp., *Wosekella* sp. (both linguliformean brachiopods) and *Babinka prima***  
22   **(babinkid bivalve) collected in deposits of the Fezouata Shale and associated with distinct**  
23   **paleoenvironmental conditions show that short-lived communities of epifaunal and**  
24   **shallow infaunal taxa were regularly smothered and killed by distal storm deposits. Small-**  
25   **sized individuals more likely represent juveniles, rather than 'dwarfed' adults (Lilliput**

26 **Effect). Consequently, unstable environmental conditions (regular storms, and possibly**  
27 **low oxygenation of the water column) probably explain the unusual community dynamics**  
28 **of late Tremadocian assemblages of the Fezouata Biota (high density of individuals, low**  
29  **$\alpha$ -diversity, and high  $\gamma$ -diversity), interpreted as short-lived, opportunistic populations.**  
30 **This process has wider implications for the understanding of occurrences of small**  
31 **individuals elsewhere in the fossil record.**

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## INTRODUCTION

34 Discovered in the early 2000s in the Central Anti-Atlas of Morocco, the Early Ordovician  
35 Fezouata *Lagerstätte* has dramatically altered evolutionary scenarios on the initial  
36 diversification of metazoans during the Early Paleozoic (Van Roy et al. 2010, 2015a; Lefebvre  
37 et al. 2016a; Martin et al. 2016a). In the Zagora area, the ~900 meter thick siltstones of the  
38 Fezouata Shale (Fig. 1A) have yielded over 200 taxa of marine invertebrates, the majority of  
39 which are shelly organisms typical of the Great Ordovician Biodiversification Event including  
40 asterozoans, bivalves, rhynchonelliformean brachiopods, cephalopods, crinoids, gastropods,  
41 graptolites, ostracods, trilobites (Havlíček 1971; Destombes et al. 1985; Ebbestad 2016;  
42 Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016b; Martin et al. 2016b; Polechová 2016).  
43 The Fezouata Biota also comprises a high number of soft-bodied to lightly sclerotized taxa,  
44 generally preserved as colorful iron oxides, resulting from the weathering of pyrite (Van Roy  
45 2006; Van Roy et al. 2010, 2015a; Lefebvre et al. 2016a; Martin et al. 2016a). Some of these  
46 exceptionally preserved organisms (e.g., cirripede crustaceans, eurypterid and xiphosuran  
47 chelicerates) represent the oldest occurrences of particular marine invertebrates, previously  
48 recorded from younger Paleozoic *Lagerstätten* (Van Roy et al. 2010, 2015a). However, the  
49 Fezouata Biota also includes numerous representatives of soft-bodied to lightly sclerotized  
50 groups typical of early–middle Cambrian, Burgess Shale-type *Lagerstätten* (e.g.,

51 anomalocaridids, protomonaxonids, armoured lobopodians, marrellomorphs, naraoids;  
52 Botting 2007, 2016; Van Roy et al. 2010, 2015b; Van Roy and Briggs 2011; Legg 2016).

53 During the Early Ordovician, the Central Anti-Atlas was located at high latitudes close to  
54 the paleo-South pole (Fig. 1D; see Torsvik and Cocks 2011, 2013). In the Zagora area, the  
55 Fezouata Shale was interpreted to have been deposited in a storm-wave dominated, cold-water,  
56 shallow environment, indirectly influenced by tides (Martin et al. 2016a; Vaucher et al. 2016,  
57 2017). The corresponding paleoenvironment ranges from the shoreface (*sensu* Reading 1996)  
58 to the upper offshore, i.e. close below the storm wave base (Vaucher et al. 2017). In the  
59 Fezouata Shale, the distribution of exceptionally preserved fossils (EPF) is not random, but  
60 associated with a narrow window of favourable environmental conditions, around the storm-  
61 wave base (Martin et al. 2016a; Vaucher et al. 2016, 2017). EPF-bearing levels typically occur  
62 as lenses, located immediately below thin (mm to cm) levels of coarser siltstones to sandstones  
63 (Martin et al. 2015; Vaucher et al. 2016). The Fezouata Biota was thus interpreted as *in situ*  
64 assemblages, smothered by distal storm deposits (Lefebvre et al. 2016a; Martin et al. 2016a;  
65 Vaucher et al. 2016, 2017).

66 In the Lower Ordovician succession of the Zagora area, favourable environmental conditions  
67 for exceptional preservation are located at two distinct stratigraphic intervals (Fig. 1A; Lefebvre  
68 et al. 2016a, 2018; Martin et al. 2016a). Based on acritarchs, conodonts, and graptolites  
69 (Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016a, 2018; Lehnert et al. 2016; Martin et  
70 al. 2016a; Nowak et al. 2016) a late Tremadocian age (Tr3) was proposed for the lower, about  
71 70 m thick interval. The upper EPF-bearing interval is narrower (~50 m thick), and it occurs  
72 about 240 m higher in the succession (Lefebvre et al. 2016a, 2018). Graptolites suggest a mid  
73 Floian age (Fl2) for this upper interval (Gutiérrez-Marco and Martin 2016; Lefebvre et al.  
74 2016a, 2018).

75 Community structures are markedly different in the two EPF-bearing intervals (Lefebvre et  
76 al. 2018). In the Zagora area, all fossiliferous horizons sampled in the upper interval have  
77 yielded comparable, particularly abundant and diverse fossil assemblages (~50 taxa),  
78 dominated by bivalves, rhynchonelliformean brachiopods, cephalopods, gastropods, and  
79 trilobites (Destombes et al. 1985; Vidal 1998; Kröger and Lefebvre 2012; Ebbestad 2016;  
80 Polechová 2016). Exceptionally preserved taxa are rare and constitute a minor component of  
81 the fauna (Van Roy 2006; Van Roy and Tetlie 2006; Botting 2016; Lefebvre et al. 2016a, 2018;  
82 Ortega-Hernández et al. 2016). In contrast, EPF are particularly abundant and diverse in the  
83 lower interval. Both EPF and shelly fossils occur massively in thin, discontinuous levels,  
84 yielding low diversity assemblages generally dominated by one or two taxa, e.g.,  
85 anomalocaridids, linguliformean brachiopods, conulariids, cornute stylophorans, eocrinoids,  
86 graptolites, hyolithids, marrellomorphs, sponges, trilobites, and/or xyphosurans (Botting 2007,  
87 2016; Van Roy et al. 2010, 2015a, 2015b; Van Roy and Briggs 2011; Martin et al. 2015;  
88 Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016b; Van Iten et al. 2016; Allaire et al.  
89 2017). In this interval, each individual horizon has yielded a unique assemblage, in terms of  
90 faunal content and/or relative proportions of occurring taxa. One of the most striking features  
91 of fossil assemblages recovered from the lower EPF-bearing interval is thus their extreme  
92 taxonomic and spatial heterogeneity (Van Roy et al. 2015a; Botting 2016; Lefebvre et al.  
93 2016b). The high cumulative diversity ( $\gamma$ -diversity) recorded in this interval (~150 taxa)  
94 suggests that the low diversity observed for each individual assemblage ( $\alpha$ -diversity) could  
95 represent a kind of random sampling of a larger pool of taxa.

96 Another intriguing feature reported from several upper Tremadocian horizons yielding EPF  
97 in the Zagora area is the repeated occurrence of taxa represented exclusively by small-sized  
98 individuals: this phenomenon has been described in eocrinoid and stylophoran echinoderms  
99 (Lefebvre and Botting 2007; Lefebvre et al. 2016b), gastropods (Ebbestad 2016), and trilobites

100 (Martin 2016). In both echinoderms and gastropods, it is difficult to identify, whether such  
101 assemblages of small-sized individuals are comprised of only juveniles, or if they correspond  
102 to populations of 'dwarfed' adults (Lefebvre and Botting 2007; Ebbestad 2016; Lefebvre et al.  
103 2016b). On the other hand, the assemblage of small-sized trilobites (*Anacheirurus adserai* and  
104 *Bavarilla zemmourensis*) reported by Martin (2016) is apparently composed of meraspid (adult)  
105 individuals, about half their 'standard' size documented in other levels and/or geographic areas.

106 The study of body size is important to understand the biological and ecological adaptations  
107 of an individual to its environment (Jablonski 1996; Vermeij 2016). Previous studies have  
108 explained spatial differences in body sizes in marine settings, either by post-mortem processes  
109 (e.g., fossil sorting and preservation; Brenchley and Harper 1998) or by the pre-mortem  
110 chemical conditions of the water column and sediments. These conditions reflect mainly  
111 oxygen fluctuations (Savrda and Bottjer 1986; Payne and Clapham 2012; He et al. 2017) and  
112 nutrient availability (Twitchett 2007; He et al. 2010). Consequently, the aim of this paper is to  
113 identify the physical mechanisms (e.g., storm influence) possibly involved in body-size changes  
114 in late Tremadocian fossil assemblages of the Fezouata Shale. This study is focused on  
115 brachiopods and bivalves, which constitute a key element of benthic communities in the  
116 Fezouata Biota (Havlíček 1971; Mergl 1981; Babin and Destombes 1990; Destombes et al.  
117 1985; Van Roy et al. 2010, 2015a; Polechová 2016), and the diversification of which was a  
118 major component of the Great Ordovician Biodiversification Event (Harper 2006; Servais and  
119 Harper 2018). The size distribution of three benthic taxa (the bivalve *Babinka* and the two  
120 brachiopods *Celdobolus* and *Wosekella*) is analysed, because they are relatively abundant, well  
121 preserved, easily identifiable and all occur at various horizons spanning a wide range of  
122 environmental conditions in the late Tremadocian EPF-bearing interval of the Zagora area.

123

124

## MATERIAL AND METHODS

125 Over 300 specimens of bivalves and brachiopods were collected from seven different  
126 localities in the lower interval yielding EPF (*Araneograptus murrayi* graptolite Zone, late  
127 Tremadocian) in the Fezouata Shale. The position of these localities along a proximal-distal  
128 axis and in the Zagora area is shown in Fig. 1B and Fig. 1C respectively. For this study, only  
129 specimens belonging to the three genera *Celdobolus*, *Wosekella* and *Babinka* were included  
130 (Fig. 2), because these three taxa are suitably abundant at all sites. This choice was further  
131 motivated by the putative modes of life of these three taxa. *Celdobolus* has been interpreted as  
132 a typical epifaunal genus, possibly epizoic on sponges (Mergl 2002). Cambrian species of  
133 *Wosekella* have been interpreted in some occurrences as semi-infaunal low suspension feeders  
134 (Mergl and Kordule 2008) or epifaunal (attached with the pedicle to the substrate; see  
135 Pettersson Stolk et al. 2010). However, Ordovician *Wosekella* is generally interpreted as  
136 endobenthic (Mergl 2002). *Babinka*, a primitive bivalve, is regarded as a shallow-water infaunal  
137 taxon (Guild G5 suspensivorous – free endofaunal of Sánchez 2008; see also McAlester 1965;  
138 Polechová 2016), based on the subcircular outline and globose profile of the shell. For  
139 measurements and analyses, only complete shells were retained. The width W, the length L,  
140 and the height H of different shells were measured using a Zeiss SteREO Discovery.V8  
141 stereomicroscope linked to a Zeiss AxioCam MRc5 digital camera with a precision of 0.01 mm.  
142 The body size  $G=(L+W)/2$  (Fig. 3) was calculated for brachiopods according to Jablonski  
143 (1996), and for bivalves:  $G=(H+L)/2$  (Fig. 3) according to Carter et al. (2012). Afterward, the  
144 mean size for each genus was determined. Data were plotted as size-frequency histograms in  
145 PAST. Then Shapiro-Wilk test for normality was made. For normal distributions, a Student t-  
146 test was applied to check if there is a significant difference in size between sites (Hammer et  
147 al. 2001).

148 All studied material is registered in the collections of the Cadi Ayyad University, Marrakesh  
149 (Morocco). Precise GPS coordinates of the studied localities are reported on specimen labels,  
150 and are available upon request.

## 151 RESULTS

152 The studied specimens consist of disarticulated valves that do not show any preferential  
153 orientation (simply disarticulated by wave orbitals, with no or limited transport before burial;  
154 Vaucher et al., 2016, 2017). The majority of sampled valves were complete, without any  
155 evidence of damage or abrasion. They were preserved at the base of storm events (covered by  
156 fine sandstones or coarse siltstones showing normal grading or oscillatory structures; Vaucher  
157 et al. 2016, 2017).

158 Both *Celdobolus* and *Babinka* show normal distributions at all sites (Fig. 3A, B) with  
159 an increase in size from proximal to distal localities (Fig. 3A). The difference in body size  
160 between sites is significant (Fig. 3C). *Wosekella* has a normal distribution at all localities (Fig.  
161 3A, B). However, no trend can be observed from shallow to deeper environments (Fig. 3A). In  
162 addition to that, the size differences between sites is not significant (Fig. 3C).

## 163 DISCUSSION

164 The mean size values observed for *Wosekella* at all sites are comparable to those reported  
165 for this genus in Lower Ordovician deposits from other regions (e.g., Bohemia; Mergl 2002).  
166 Similarly, the mean size values obtained for both *Babinka* and *Celdobolus* in the distal-most  
167 site are similar to those described for this genus in other areas (e.g.; Bohemia; McAlester 1965;  
168 Mergl 2002; Polechová 2013). In marked contrast, specimens of both *Babinka* and *Celdobolus*  
169 from Z-F50 are about half the size of those occurring in both Z-F4 and other Early Ordovician  
170 assemblages (McAlester 1965; Mergl 2002; Polechová 2013). This significant difference in the  
171 mean size of *Babinka* and *Celdobolus* from the Fezouata Shale can be explained either by post-  
172 mortem or pre-mortem processes.

173 Post-mortem taphonomic processes include fossil sorting and preservation (Kidwell 1991;  
174 Brenchley and Harper 1998). At all sites, brachiopods and bivalves are apparently preserved *in*  
175 *situ* with little to no evidence of significant lateral transport (disarticulated but complete valves  
176 with no preferential orientation) (Vaucher et al. 2016, 2017), and even minute details of the  
177 shells, such as setae in siphonotretoid brachiopods, are often perfectly preserved. The  
178 preservation of such extremely delicate and brittle structures rather suggests the *in situ* burial  
179 of autochthonous benthic populations by distal storm deposits. Thus, the abundance of small-  
180 sized assemblages of bivalves and *Celdobolus* in proximal sites cannot simply be interpreted as  
181 resulting from sorting and preservation.

182 During pre-mortem processes, chemical parameters (e.g., low oxygen concentrations,  
183 oligotrophic waters) have been frequently invoked to explain severe reductions in the mean size  
184 of adults in populations of marine invertebrates (Tasch 1953; Urlichs 2012; Botting et al. 2013).  
185 This phenomenon ('Lilliput Effect') has been advocated for marine faunas, particularly those  
186 associated with the survival and recovery phases following extinction events (e.g., Huang et al.  
187 2010; Twitchett 2007). The Lilliput Effect generally affects most elements of the biota, across  
188 a wide range of taxonomic levels. In the Fezouata Shale, the possible occurrence of a Lilliput  
189 Effect was questioned for several low-diversity assemblages from the lower EPF-bearing  
190 interval, yielding small-sized trilobites (Martin 2016), echinoderms (Lefebvre et al. 2016b), and  
191 gastropods (Ebbestad 2016). At proximal sites, however, there is no evidence supporting the  
192 existence of a putative Lilliput Effect: with the exception of *Babinka*, *Celdobolus* and possibly  
193 some other co-occurring epibenthic brachiopod genera (*Elliptoglossa*, *Monobolina*, and  
194 *Orbithele*), all other components of the associated benthic fauna (including trilobites and some  
195 brachiopods, such as *Wosekella*; Fig. 2A) do not show any reduction in size. Unfavorable  
196 chemical conditions should have affected the whole benthos. In these sites, small-sized  
197 specimens of *Babinka* thus more likely correspond to juveniles, rather than to 'dwarfed' adults.



198 Physical parameters of the water column (e.g., storm intensity, currents) are other pre-  
199 mortem processes possibly involved in the observed pattern of size distribution. When  
200 entombed by sediment, deep infaunal organisms have a greater chance of physically being able  
201 to react than epifaunal or shallow infaunal ones (Freeman et al. 2013). Taxa like *Wosekella* with  
202 a reduced dorsal pseudointerarea and smooth, elongate suboval valves (Emig 1997; Bassett et  
203 al. 1999) have the capability to re-orient upward and the possibility of burrowing upwards.  
204 Hammond (1983) described that in experimental conditions, 100% of *Lingula anatina* buried  
205 in 5 to 10 cm of sediment survived, and 70% of *L. anatina* with pedicles emerged from 20 cm  
206 of sediment. Moreover, Thayer and Steele-Petrovic (1975) demonstrated that, using modern  
207 genus *Glottidia*, after entombment, reorientation and re-burrowing were successful, even in the  
208 case of animals losing their pedicles. On the other hand, Hutchinson et al. (2016) showed a high  
209 mortality of sessile epibenthic bivalves after their burial by sediment. As it is the case during  
210 storms, even shallow infaunal taxa are subjected to the power of the wave orbitals, which  
211 snatches the animals from their life position in the burrow. The result is that the organisms may  
212 become disoriented and lie in a position that is far from their normal life position.

213 In the Fezouata Shale, the storm record varies between localities and between different levels  
214 at the same locality (Vaucher et al. 2017). During storm events, wave orbitals generated in the  
215 water column, in addition to the quantity of burial material, if any, clearly had an impact on  
216 benthic communities. Proximal, shallow-water settings were more affected by storms and wave  
217 orbitals, and larger amounts of sediment were deposited than in more distal, deeper-water  
218 environments (Vaucher et al. 2016, 2017). In this context, the demographics observed for  
219 *Babinka*, *Celdobolus* and *Wosekella* in the Fezouata Shale can be simply explained by both  
220 their presumed mode of life and physical ability to re-burrow and reorient to their normal life  
221 orientation, and external physical parameters (e.g., storm intensity) depending on their position  
222 along a proximal-distal gradient. In proximal settings (e.g., Z-F50), shallow infaunal taxa (e.g.,

223 *Babinka*) are exclusively represented by small-sized, probably juvenile individuals, whereas  
224 deeper infaunal genera that actively respond to physical stress exhibit a much wider range of  
225 sizes, including putative adult individuals. This suggests that, in shallow-water settings,  
226 populations of *Babinka* were regularly smothered and killed by thin, distal storm deposits, thus  
227 preventing the development of stable communities on the sea floor. In contrast, individuals of  
228 *Wosekella* were less affected and could reach larger sizes. In more distal environments (e.g., Z-  
229 F4), both epibenthic/shallow infaunal (e.g. *Babinka*, *Celdobolus*) and deep infaunal (e.g.  
230 *Wosekella*) communities were little affected by storms, so that individuals could reach larger  
231 sizes and form stable, ageing populations (Fig. 4). Consequently, in the lower EPF-bearing  
232 interval of the Fezouata Shale, reaching large sizes in an environment constantly affected by  
233 storms seems to be related to a better luck when colonizing the sea floor, due to larval transport  
234 by fair weather currents. These currents allowed randomly the (re)colonization of either a high  
235 or a low-energy setting, thus permitting or preventing the growth of *Babinka*, *Celdobolus* and  
236 possibly other epibenthic or shallow infaunal taxa into full-sized adults.

237 In the late Tremadocian of the Zagora area, the persistence of unstable environmental  
238 conditions in shallow settings prevented the colonisation of the sea bottom by stable, long-  
239 ranging communities of sessile or slow-moving epibenthic/shallow infaunal taxa. These  
240 stressful environmental conditions probably explain the high spatial and taxonomic  
241 heterogeneity observed in this interval of the Fezouata Shale, and support the interpretation of  
242 the low-diversity assemblages occurring in these levels as opportunistic populations buried *in*  
243 *situ* by distal storm deposits. This interpretation is in good agreement with previous reports of  
244 similar, low diversity, Early–Mid Ordovician benthic assemblages dominated by primitive  
245 bivalves (Cope 1999; Sánchez and Benedetto 2007) and/or by linguliformean brachiopods  
246 (Popov et al. 2013).

247

248

## CONCLUSIONS

249 The low-diversity, dense assemblages occurring in most fossiliferous horizons of the late  
250 Tremadocian EPF-bearing interval of the Fezouata Shale are not generated by currents, but they  
251 correspond to autochthonous communities smothered by distal storm deposits (Martin et al.  
252 2015, 2016a; Vaucher et al. 2016, 2017). Both the spatial heterogeneity and unusual  
253 demographics displayed by these assemblages can be explained by relatively unstable  
254 environmental conditions, both in terms of oxygenation (dysoxic to anoxic settings; see Botting  
255 2016; Martin et al. 2016b) and storm activity (Vaucher et al. 2016). It is thus very likely that  
256 the particularly dense and patchy, low diversity assemblages observed in this interval  
257 correspond to successive colonizations of the sea floor by opportunistic taxa (Botting 2016;  
258 Lefebvre et al. 2016b). At several horizons, the small size of most individuals suggests that  
259 these epibenthic or shallow infaunal populations were short-lived and repeatedly buried by  
260 distal storm deposits.

261 This study also constitutes the first step to elaborate a proxy, at generic level, relating shell  
262 sizes to bathymetry, in a storm-wave dominated environment. Additionally, it shows that a new  
263 mechanism, related to physical processes, can explain size differences independently from the  
264 chemical conditions of the water column and their related dwarfism. Finally, this study  
265 highlights the utility of understanding life habit and more broadly paleoecology for fully  
266 understanding fossil assemblages.

267

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#### FIGURE CAPTIONS

478 FIG. 1.—Geologic context of the studied material. **A)** Synthetic stratigraphic column of the  
479 Lower Ordovician succession in the Zagora area, Morocco showing the position of the two  
480 intervals yielding exceptionally-preserved faunas (KsL); modified from Gutiérrez-Marco and  
481 Martin (2016) and Lefebvre et al. (2018). Colors on the log correspond to those of the rocks  
482 exposed. **B)** The position of studied levels along a proximal-distal axis. **C)** The position of  
483 studied localities in the Zagora region. **D)** The Early Ordovician and current position of the  
484 Zagora area.

485

486 FIG. 2.—Late Tremadocian babinkid bivalves and linguliformean brachiopods from the  
487 Fezouata Shale, hill east of Tamegroute, Zagora area, Central Anti-Atlas (Morocco). **A–B)**  
488 *Babinka prima* Barrande, 1881; scale bars: 2 mm. **A)** AA-TGR1c-OI-178. **B)** AA-TGR1c-OI-  
489 14. **C–D)** *Wosekella* sp.; scale bars: 2 mm. **C)** AA-TGR1c-OI-102. **D)** AATGR1c-OI-155. **E–**  
490 **F)** *Celdobolus* sp.; scale bars: 2 mm. **E)** AA-TGR1c-OI-78. **F)** AA-TGR1c-OI-62.

491

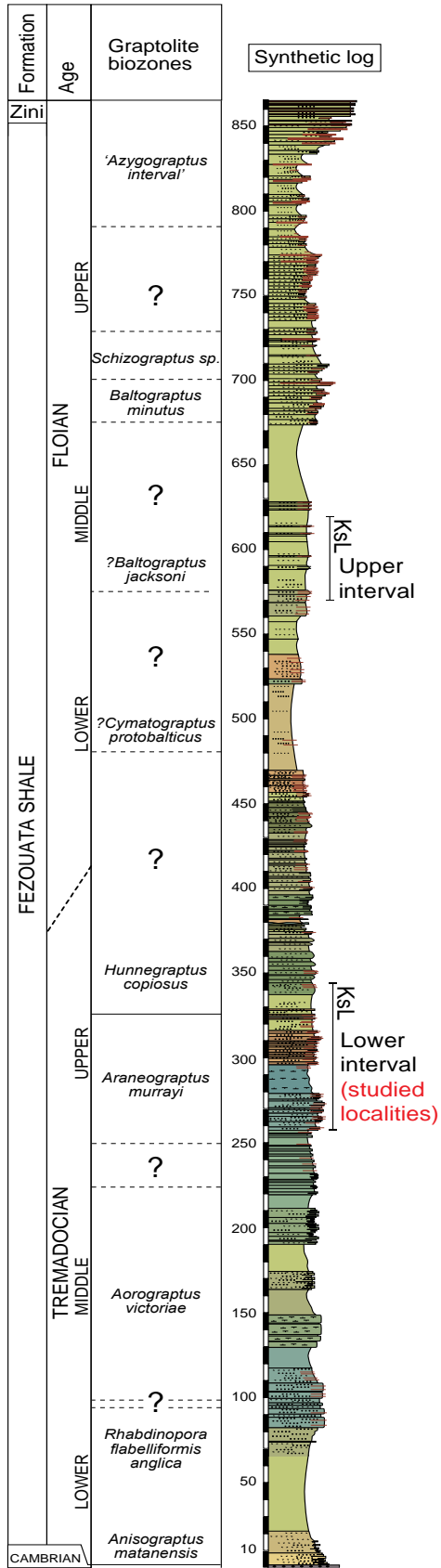
492 FIG. 3.— Statistical analysis on brachiopods and bivalves in the Fezouata Shale, Zagora area  
493 (Morocco). **A)** Size distribution for *Celdobolus* sp., *Babinka prima* Barrande, 1881 and  
494 *Wosekella* sp. at all sites. **B)** Shapiro-Wilk p-values for normality. **C)** t-test p-values for  
495 significant differences in size between sites.

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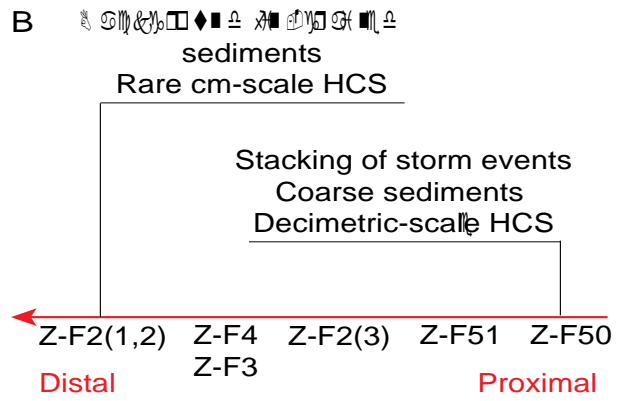
497 FIG. 4.—Model explaining the influence of storms on brachiopod and bivalve communities in  
498 the lower part of the Fezouata Shale (upper Tremadocian), Zagora area (Morocco).

499

A



B

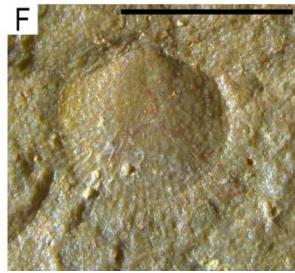
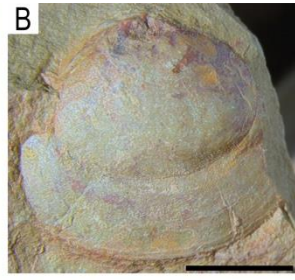
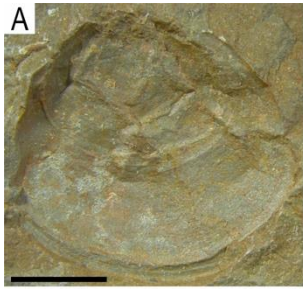


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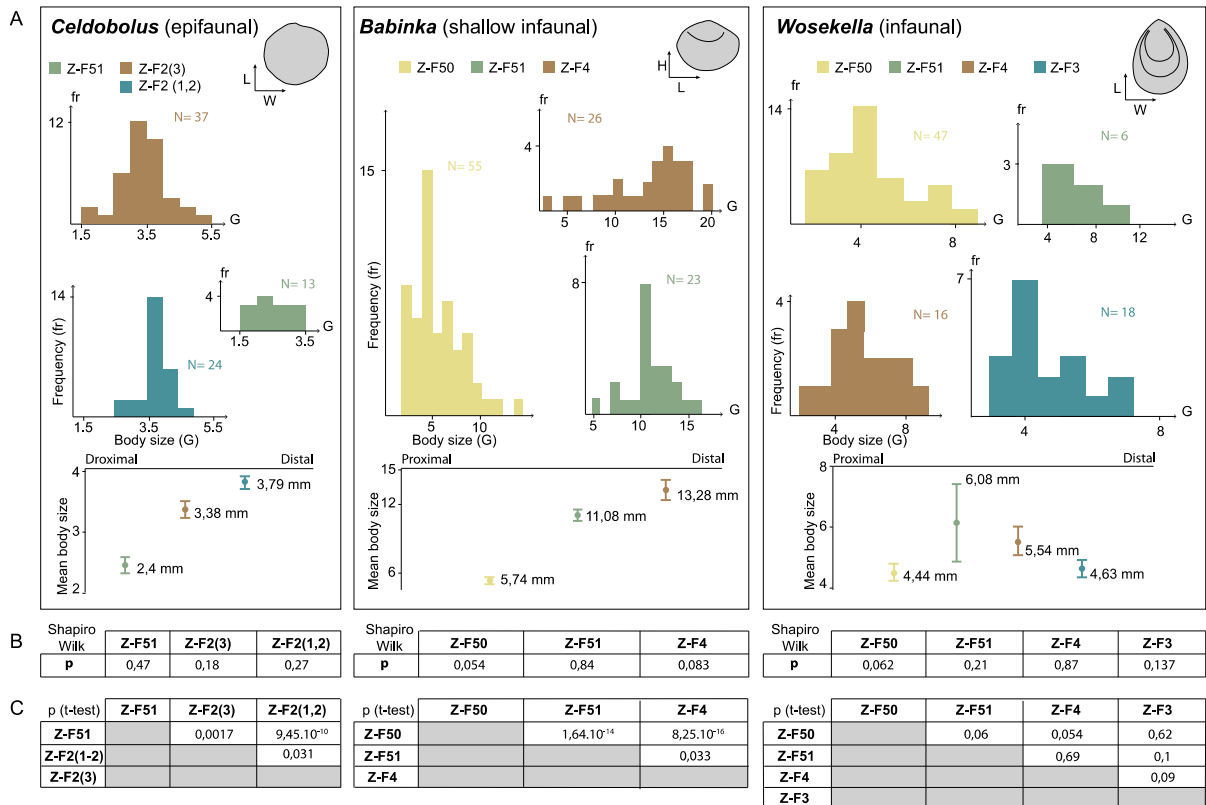
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