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

INTRODUCTION

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

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

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

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

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

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

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

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

MATERIAL AND METHODS

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

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

RESULTS

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

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

DISCUSSION

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

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

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

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

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

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

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

CONCLUSIONS

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

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

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REFERENCES

- ALLAIRE, N., LEFEBVRE, B., NARDIN, E., MARTIN, E.L.O., VAUCHER, R. and ESCARGUEL, G., 2017, Morphological disparity and systematic revision of the eocrinoid genus *Rhopalocystis* (Echinodermata, Blastozoa) from the Lower Ordovician of the central Anti-Atlas (Morocco): Journal of Paleontology, v. 91, p. 685–714.
- BABIN, C. and DESTOMBES, J., 1990, Les mollusques bivalves et rostroconches ordoviciens de l'Anti-Atlas marocain: intérêt paléogéographique de leur inventaire. Géologie Méditerranéenne, v. 17, p. 243–261.
- BARRANDE, J., 1881, Système Silurien du Centre de la Bohême. Volume 6. Classe des Mollusques, Ordre des Acéphalées: Lemerrier, Paris and Bellman, Prague, 342 p.
- BASSETT, M.G., POPOV, L.E. and HOLMER, L.E., 1999, Organophosphatic brachiopods: patterns of biodiversification and extinction in the Early Palaeozoic: Geobios, v. 32, p. 145–163.
- BOTTING, J.P., 2007, 'Cambrian' demosponges in the Ordovician of Morocco: insights into the early evolutionary history of sponges: Geobios, v. 40, p. 737–748.

298 BOTTING, J.P., 2016, Diversity and ecology of sponges in the Early Ordovician Fezouata Biota,
 299 Morocco: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 460, p. 75–86.

300 BOTTING, J.P., MUIR, L.A. and LEFEBVRE, B., 2013, Echinoderm diversity and environmental
 301 distribution in the Ordovician of the Builth Inlier, Wales: Palaios, v. 28, p. 293–304.

302 BRECHLEY, P.J. and HARPER, D.A.T., 1998, Palaeoecology: Ecosystems, Environments and
 303 Evolution: CRC Press, Taylor and Francis. 402 p.

304 COPE, J.C.W., 1999, Middle Ordovician bivalves from Mid-Wales and the Welsh Borderland.
 305 Palaeontology, v. 42, 467–499.

306 CARTER, J.G., HARRIES, P.J., MALCHUS, N., SARTORI, A.F., ANDERSON, L.C., BIELER, R.,
 307 BOGAN, A.E., COAN, E.V., COPE, J.C., CRAGG, S. and GARCIA-MARCH, J., 2012, Illustrated
 308 glossary of the Bivalvia: Treatise Online, p. 1-209.

309 DESTOMBES, J., HOLLARD, H. and WILLEFERT, S., 1985, Lower Palaeozoic rocks of Morocco.
 310 in Holland, C.H., (ed.), Lower Palaeozoic of North-Western and West Central Africa: New
 311 York, Wiley, p. 91–336.

312 EBBESTAD, J.O.R., 2016, Gastropoda, Tergomya and Paragastropoda (Mollusca) from the
 313 Lower Ordovician Fezouata Formation, Morocco: Palaeogeography, Palaeoclimatology,
 314 Palaeoecology, v. 460, p. 87–96.

315 EMIG, C., 1997, Ecology of inarticulated brachiopods in Kaesler, R.L. (ed.), Treatise on
 316 Invertebrate Paleontology, Part H, Brachiopoda 1 (Revised): Geological Society of America,
 317 Boulder, Colorado and The University of Kansas, Lawrence, Kansas, p. 473–495.

318 FREEMAN, R.L., DATTILO, B.F., MORSE, A., BLAIR, M., FELTON, S. and POJETA, Jr, J., 2013,
 319 The “curse of *Rafinesquina*:” negative taphonomic feedback exerted by strophomenid shells
 320 on storm-buried lingulids in the Cincinnati Series (Katian, Ordovician) of Ohio: Palaios,
 321 v. 28, p. 359–372.

322 GUTIERREZ-MARCO, J.C. and MARTIN, E.L.O., 2016, Biostratigraphy and palaeoecology of
 323 Lower Ordovician graptolites from the Fezouata Shale: Palaeogeography,
 324 Palaeoclimatology, Palaeoecology, v. 460, p. 35–49.

325 HAMMER, Ø., HARPER, D.A.T. and RYAN, P.D., 2001, PAST - Paleontological Statistics
 326 software: Package for Education and data Analysis: Palaeontologia Electronica, v. 4, p. 9.

327 HAMMOND, L.S., 1983, Experimental studies of salinity tolerance, burrowing behavior and
 328 pedicle regeneration in *Lingula anatina* (Brachiopoda, Inarticulata): Journal of
 329 Paleontology, v. 57, p. 1311–1316.

330 HARPER, D.A.T., 2006, The Ordovician biodiversification: Setting an agenda for marine life:
 331 Palaeogeography, Palaeoclimatology, Palaeoecology, v. 232, p. 148–166.

332 HAVLÍČEK, V., 1971, Brachiopodes de l'Ordovicien du Maroc: Notes et Mémoires du Service
 333 géologique du Maroc, v. 230, p. 1–135.

334 HE, W.H., TWITCHETT, R.J., ZHANG, Y., SHI, G.R., FENG, Q.L., YU, J.X., WU, S.B. and PENG,
 335 X.F., 2010, Controls on body size during the Late Permian mass extinction event:
 336 Geobiology, v. 8, p. 391–402.

337 HE, W., SHI, G.R., XIAO, Y., ZHANG, K., YANG, T., WU, H., ZHANG, Y., CHEN, B., YUE, M.,
 338 SHEN, J., WANG, Y., YANG, H. and WU, S., 2017, Body-size changes of latest Permian
 339 brachiopods in varied palaeogeographic settings in South China and implications for
 340 controls on animal miniaturization in a highly stressed marine ecosystem: Palaeogeography,
 341 Palaeoclimatology, Palaeoecology, v. 486, p. 33–45.

342 HUTCHINSON, Z.L., HENDRICK, V.J., BURROWS, M.T., WILSON, B. and LAST, K.S., 2016,
 343 Buried alive: the behavioural response of the mussels *Modiolus modiolus* and *Mytilus edulis*
 344 to sudden burial by sediment: PLoS ONE, v. 11(3), doi:e0151471.doi:10.1371/
 345 journal.pone.0151471

346 HUANG, B., HARPER, D.A.T., RENBIN, Z. and JIAYU, R., 2010, Can the Lilliput Effect be
 347 detected in the brachiopod faunas of South China following the terminal Ordovician mass
 348 extinction? *Palaeogeography, Palaeoclimate, Palaeoecology*, v. 285, p. 277–286.

349 JABLONSKI, D., 1996, Body size and macroevolution, *in* Jablonski, D., Erwin D.H., and Lipps,
 350 J.H. (eds.): *Evolutionary Paleobiology*. University of Chicago Press, Chicago, p. 256–289.

351 KIDWELL, S., 1991, Taphonomy: Releasing the data locked in the fossil record: Topics in
 352 *Geobiology*, v. 9, p. 211–290.

353 KRÖGER, B. and LEFEBVRE, B., 2012, Palaeogeography and palaeoecology of early Floian
 354 (Lower Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco:
 355 *Fossil Record*, v. 15, p. 61–75.

356 LEFEBVRE, B. and BOTTING, J.P., 2007, First report of the mitrate *Peltocystis cornuta* Thoral
 357 (Echinodermata, Stylophora) in the Lower Ordovician of central Anti-Atlas (Morocco):
 358 *Annales de Paléontologie*, v. 93, p. 183–198.

359 LEFEBVRE, B., EL HARIRI, K., LEROSSEY-AUBRIL, R., SERVAIS, T. and VAN ROY, P., 2016a, The
 360 Fezouata Shale (Lower Ordovician, Anti-Atlas, Morocco): a historical review:
 361 *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 7–23.

362 LEFEBVRE, B., ALLAIRE, N., GUENSBURG, T.E., HUNTER, A.W., KOURAISS, K., MARTIN,
 363 E.L.O., NARDIN, E., NOAILLES, F., PITTET, B., SUMRALL, C.D. and ZAMORA, S., 2016b,
 364 Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of
 365 central Anti-Atlas, Morocco: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460,
 366 p. 97–121.

367 LEFEBVRE, B., GUTIERREZ-MARCO, J.C., LEHNERT, O., MARTIN, E.L.O., NOWAK, H., AKODAD,
 368 M., EL HARIRI, K. and SERVAIS, T., 2018, Age calibration of the Lower Ordovician Fezouata
 369 Lagerstätte, Morocco: *Lethaia*, v. 51, p. 296–311.

370 LEGG, D.A., 2016, An acerrostracan marrellomorph (Euarthropoda) from the Lower
 371 Ordovician of Morocco: *The Science of Nature*, v. 103 (21).

372 LEHNERT, O., NOWAK, H., SARMIENTO, G.N., GUTIERREZ-MARCO, J.C., AKODAD, M. and
 373 SERVAIS, T., 2016, Conodonts from the Lower Ordovician of Morocco – contributions to
 374 age and faunal diversity of the Fezouata Lagerstätte and peri-Gondwana biogeography:
 375 *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 50–61.

376 MARTIN, E.L.O., 2016, Communautés animales du début de l'Ordovicien (env. 480 Ma): études
 377 qualitatives et quantitatives à partir des sites à préservation exceptionnelle des Fezouata,
 378 Maroc: Unpublished PhD Thesis, Lyon 1 University, France, 483 p.

379 MARTIN, E.L.O., LEFEBVRE, B. and VAUCHER, R., 2015, Taphonomy of a stylophoran-
 380 dominated assemblage in the Lower Ordovician of Zagora area (central Anti-Atlas,
 381 Morocco), in Zamora, S., and Rabano, I. (eds.), *Progress in Echinoderm Palaeobiology:*
 382 *Cuadernos del Museo Geominero*, v. 19, p. 95–100.

383 MARTIN, E.L.O., PITTET, B., GUTIERREZ-MARCO, J.C., VANNIER, J., EL HARIRI, K., LEROSEY-
 384 AUBRIL, R., MASROUR, M., NOWAK, H., SERVAIS, T., VANDENBROUCKE, T.R.A., VAN ROY,
 385 P., VAUCHER, R. and LEFEBVRE, B., 2016a, The Lower Ordovician Fezouata Konservat-
 386 Lagerstätte: age, environment and evolutionary perspectives: *Gondwana Research*, v. 34, p.
 387 274–283.

388 MARTIN, E.L.O., VIDAL, M., VIZCAINO, D., VAUCHER, R., SANJOFRE, P., LEFEBVRE, B. and
 389 DESTOMBES, J., 2016b, Biostratigraphic and palaeoenvironmental controls on the trilobite
 390 associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco:
 391 *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 142–154.

392 MCALESTER, A.L., 1965, Systematics, affinities, and life habits of *Babinka*, a transitional
 393 Ordovician lucinoid bivalve. *Palaeontology*, v. 8, p. 231–246.

394 MERGL, M., 1981, The genus *Orbithele* (Brachiopoda, Inarticulata) from the Lower Ordovician
395 of Bohemia and Morocco: Věstník Ústředního ústavu geologického, v. 56, p. 287–292.

396 MERGL, M., 2002, Linguliformean and craniiformean brachiopods of the Ordovician (Třenice
397 to Dobrotivá formations) of the Barrandian, Bohemia: Sborník Národního muzea v Praze,
398 B, Přírodní vědy, v. 58, p. 1–82.

399 MERGL, M. and KORDULE, V., 2008, New Middle Cambrian lingulate brachiopods from the
400 Skryje-Týřovice area (Central Bohemia, Czech Republic): Bulletin of Geosciences, v. 83, p.
401 11–22.

402 NOWAK, H., SERVAIS, T., PITTET, B., VAUCHER, R., AKODAD, M., GAINES, R.R., and
403 VANDENBROUCKE, T.R.A., 2016, Palynomorphs of the Fezouata Shale (Lower Ordovician,
404 Morocco): age and environmental constraints of the Fezouata Biota: Palaeogeography,
405 Palaeoclimatology, Palaeoecology, v. 460, p. 62–74.

406 ORTEGA-HERNANDEZ, J., VAN ROY, P. and LEROSEY-AUBRIL, R., 2016, A new aglaspidid
407 euarthropod with a six-segmented trunk from the Lower Ordovician Fezouata Konservat-
408 Lagerstätte, Morocco: Geological Magazine, v. 153, p. 524–536.

409 PAYNE, J.L. and CLAPHAM, M.E., 2012, End-Permian Mass Extinction in the Oceans: An
410 ancient analog for the Twenty-First Century? Annual Review of Earth and Planetary
411 Sciences, v. 40, p. 89–111.

412 PETTERSSON STOLK, S., HOLMER, L.E. and CARON, J.-B., 2010, First record of the brachiopod
413 *Lingulella waptaensis* with pedicle from the Middle Cambrian Burgess Shale: Acta
414 Zoologica, v. 91, p. 150–162.

415 POLECHOVÁ, M., 2013, Bivalves from the Middle Ordovician Šarka Formation (Prague Basin,
416 Czech Republic): Bulletin of Geosciences, v. 88, p. 427–461.

417 POLECHOVÁ, M., 2016, The bivalve fauna from the Fezouata Formation (Lower Ordovician) of
418 Morocco and its significance for palaeobiogeography, palaeoecology and early

419 diversification of bivalves: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p.
 420 155–169.

421 POPOV, L.E., HOLMER, L.E., BASSETT, M.G., GHOBADI POUR, M. and PERCIVAL, I.G. 2013.
 422 Biogeography of Ordovician linguliform and craniiform brachiopods. In Harper, D.A.T. and
 423 Servais, T. (eds), *Early Palaeozoic Biogeography and Palaeogeography*. Geological
 424 Society, London, Memoirs, **38**, 117–126.

425 READING, H.G., 1996, *Sedimentary Environments: Processes, Facies and Stratigraphy*, 3rd
 426 edition. Blackwell Science, Oxford, 688p.

427 SÁNCHEZ, T.M., 2008, The early bivalve radiation in the Ordovician Gondwanan basins of
 428 Argentina: *Alcheringa*, v. 32 (3), p. 223–246.

429 SÁNCHEZ, T.M. and BENEDETTO, J.L., 2007, The earliest known estuarine bivalve assemblage,
 430 Lower Ordovician of northwestern Argentina. *Geobios*, v. 40, p. 523–533.

431 SAVRDA, C.E. and BOTTJER, D.J., 1986, Trace-fossil model for reconstruction of paleo-
 432 oxygenation in bottom waters: *Geology*, v. 14, p. 3–6.

433 SERVAIS, T. and HARPER, D.A.T., 2018, The Great Ordovician Biodiversification Event
 434 (GOBE): definition, concept and duration: *Lethaia*, v. 51, p. 151–164.

435 TASCH, P., 1953, Causes and paleontological significance of dwarfed fossil marine
 436 invertebrates: *Journal of Paleontology*, v. 27, p. 356–444.

437 THAYER, C.W. and STEELE-PETROVIC, H.M., 1975, Burrowing of the lingulid brachiopod
 438 *Glottidia pyramidata*: its ecologic and paleoecologic significance: *Lethaia*, v. 8, p. 209–221.

439 TORVSIK, T.H. and COCKS, L.R.M., 2011, The Palaeozoic palaeogeography of central
 440 Gondwana: Geological Society, London, Special Publications, v. 357, p. 137–166.

441 TORVSIK, T.H. and COCKS, L.R.M., 2013, Gondwana from top to base in space and time:
 442 *Gondwana Research*, v. 24, p. 999–1030.

443 TWITCHETT, R.J., 2007, The Lilliput Effect in the aftermath of the end-Permian extinction
 444 event: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 252, p. 132–144.
 445 URLICHS, M., 2012, Stunting in some invertebrates from the Cassian Formation (Late Triassic,
 446 Carnian) of the Dolomites (Italy): *Neues Jahrbuch für Geologie und Paläontologie*
 447 *Abhandlungen*, v. 265, p. 1–25.
 448 VAN ITEN, H., MUIR, L., SIMOES, M. G., LEME, J. M., MARQUES, A. C. and YODER, N., 2016,
 449 *Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and*
 450 *Sphenothallus (Meduzoa, Cnidaria), with emphasis on the Fezouata Shale of southeastern*
 451 *Morocco: Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 460, p. 170–178.
 452 VAN ROY, P., 2006, *Non-Trilobite Arthropods from the Ordovician of Morocco: Unpublished*
 453 *PhD thesis, Ghent University. Belgium, 230 p.*
 454 VAN ROY, P., and BRIGGS, D.E.G., 2011, A giant Ordovician anomalocaridid: *Nature*, v. 473,
 455 p. 510–513.
 456 VAN ROY, P. and TETLIE, O.E., 2006, A spinose appendage fragment of a problematic arthropod
 457 from the Early Ordovician of Morocco: *Acta Palaeontologica Polonica*, v. 51, p. 239–246.
 458 VAN ROY, P., ORR, P.J., BOTTING, J.P., MUIR, L.A., VINTHER, J., LEFEBVRE, B., EL HARIRI, K.
 459 and BRIGGS, D.E.G., 2010, Ordovician faunas of Burgess Shale type: *Nature*, v. 465, p. 215–
 460 218.
 461 VAN ROY, P., BRIGGS, D.E.G. and GAINES, R.R., 2015a, The Fezouata fossils of Morocco; an
 462 extraordinary record of marine life in the Early Ordovician: *Journal of the Geological*
 463 *Society*, v. 172, p. 541–549.
 464 VAN ROY, P., DALEY, A.C. and BRIGGS, D.E.G., 2015b, Anomalocaridid trunk limb homology
 465 revealed by a giant filter-feeder with paired flaps: *Nature*, v. 522, p. 77–80.

466 VAUCHER, R., MARTIN, E.L.O., HORMIERE, H. and PITTET, B., 2016, A genetic link between
 467 Konzentrat- and Konservat-Lagerstätten in the Fezouata Shale (Lower Ordovician,
 468 Morocco): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 460, p. 24–34.

469 VAUCHER, R., PITTET, B., HORMIERE, H., MARTIN, E.L.O. and LEFEBVRE, B., 2017, A wave-
 470 dominated, tide-modulated model for the Lower Ordovician of the Anti-Atlas, Morocco:
 471 Sedimentology, v. 64, p. 777–807.

472 VERMEIJ, G., 2016, Gigantism and its implications for the history of life: PLoS ONE, v. 11 (1).
 473 doi: e0146092.

474 VIDAL, M., 1998, Trilobites (Asaphidae et Raphiophoridae) de l'Ordovicien inférieur de l'Anti-
 475 Atlas, Maroc: Palaeontographica Abteilung A, v. 251, p. 39–77.

476

477 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.

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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).

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