The Fezouata Biota: an exceptional window on the Cambro-Ordovician faunal transition

Fossil-Lagerstätten were initially defined as ‘bodies of rock unusually rich in palaeontological information’ (Seilacher, 1985). In the case of the Konservat-Fossil-Lagerstätten (simplified as Lagerstätten thereafter; singular, Lagerstätte), this palaeontological significance resides in the quality of preservation, such deposits yielding remains of entirely soft-bodied organisms. As first pointed out by Allison and Briggs (1993), the Cambrian is unusually rich in Lagerstätten compared to other periods of the Palaeozoic Era. This is particularly fortunate, for these remarkable strata provide unparalleled insights into one of the most critical events of the history of life: the Cambrian Explosion. Virtually every palaeontologist, most geologists, and a significant part of the scientific community, but also many people simply having an interest in natural sciences have heard of the Burgess Shale in the Canadian Rocky Mountains or Chengjiang in South China. Over the last three decades, however, numerous other localities yielding Early Palaeozoic soft-bodied assemblages have been discovered around the world. All are from lower to middle Cambrian rocks, except for a few notable exceptions (e.g.; Briggs et al., 1991, 2015; Aldridge et al., 2001; Leroosey-Aubril et al., 2014), and none really compete with Chengjiang or the Burgess Shale in terms of diversity and abundance (Gaines, 2014). However, with a fauna comprising more than 160 genera – half of them representing soft-bodied organisms (Van Roy et al., 2015a) – the Lower Ordovician Fezouata Shale (undifferentiated Lower and Upper Fezouata formations) of Morocco might well join in a near future these two illustrious localities in the pantheon of Early Palaeozoic Lagerstätten.

The discovery of this extremely diverse, exceptional biota was so sensational that its report made the cover of the prestigious journal *Nature* (Van Roy et al., 2010). This finding demonstrated for the first time that a notable proportion of the taxa as-yet regarded as emblematic of the Cambrian Explosion were still major components of marine communities in the Early Ordovician. Moreover, some surprisingly advanced taxa were found to co-occur with these typical Burgess Shale-type organisms, indicating that the diversification of a number of non-biomineralised post-Cambrian clades started much earlier than hitherto assumed. The view of a complete restructuring of these communities, supposedly occurring in-between the Cambrian Explosion (early to middle Cambrian) and the Great Ordovician Biodiversification Event (GOBE; Middle to Late Ordovician), was seriously questioned. This discovery also illustrated that the taphonomic window opened in the early Cambrian remained agape well after the middle Cambrian, where facies favourable to the preservation of (mostly) carbonaceous remains persisted.

This is the case in two main stratigraphic intervals of the Fezouata Shale, which are now known to be of late Tremadocian and middle Floian ages (Gutiérrez-Marco and Martin, this issue; Lehnert et al., this issue; Nowak et al., this issue). These beds preserve typical organisms of the Cambrian Explosion, together with classical fossils of the GOBE (Van Roy et al., 2010, 2015a). If more such ‘windows’ of similar magnitude can be found in the late Cambrian to Late Ordovician time interval, our view on the early evolution of marine ecosystems may change forever, and the concepts of Cambrian explosion and GOBE may need to be revised.

Although geological and palaeontological investigations in the Anti-Atlas (Morocco) started in the first part of the 20th century (Neltner, 1929; Bigot and Dubois, 1931; Choubert, 1942; Choubert et al., 1955; Destombes, 1962; Destombes et al., 1985), the first exceptionally preserved fossils from the Ordovician strata of the Zagora area were only found in late 1999,

possibly early 2000 by a local fossil collector, Mohamed ‘Ou Saïd’ Ben Moula. In the months that followed, Belgian, French, and British palaeontologists were given access to some of these recently discovered fossils, including arthropods (Peter Van Roy), echinoderms (Bertrand Lefebvre) and sponges (Joseph Botting), which led to the independently launches of the first scientific field campaigns (for a detailed account of this early investigations, see Lefebvre et al., this issue a).

In December 2003, at the Annual Meeting of the Palaeontological Association in Leicester, England, the three palaeontologists shared their discoveries and started an informal collaboration. An official French-Moroccan exchange programme was launched in 2002, with field campaigns in the years 2003 and 2004, while the Belgian-Moroccan exchange intensified separately, with teams visiting sites in 2002, 2003, 2006, and 2008. In September 2008, a successful application to the Research and Exploration grant program of the National Geographic Society allowed more extensive fieldwork in the area. Another project funded between 2009–2012 promoted scientific exchanges through field work and collections between Moroccan and (mostly) European researchers and students, and largely contributed to the development of the palaeontological collections of Cadi-Ayyad University in Marrakesh. Later, two large-scale projects on the Fezouata Biota were funded. One of these projects, financed by the National Science Foundation (NSF) in the U.S.A., involved researchers from Yale University and Pomona College, and was entitled ‘The exceptionally preserved Fezouata Biota from the Lower Ordovician of Morocco: a unique window into the Cambro-Ordovician faunal transition’ (2011-2016). The second one, financed by the French Agence Nationale de la Recherche (ANR) and entitled ‘The Rise of Animal Life (Cambrian-Ordovician) - organization and tempo: evidence from exceptionally preserved biotas’, was established between working groups from the Universities of Lyon 1 and Lille 1 (2011–2015).

The researchers of the different groups working on the Fezouata Biota informally met at the Annual Meetings of the Palaeontological Association in 2010 (Ghent, Belgium), 2011 (Plymouth, England), 2012 (Dublin, Ireland), and 2013 (Zürich, Switzerland), before attending a workshop organized in March 2014 at the University of Lille, France. This workshop was the occasion for scientists from Belgium, France, Morocco, Spain, and the United States to present their results and discuss further initiatives. It was also decided to produce a first compilation of articles, summarizing the recent advances of the Fezouata research made by the different groups (financed by the NSF, the ANR, and other sources). The editors of the journal *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* were approached and decided to support this project of a special issue dedicated to the Fezouata Lagerstätte. The present volume is thus the fruit of the joint efforts of the different research teams over the last decade.

Since the original discovery by Mohamed 'Ou Saïd' Ben Moula in the early 2000s, studies have primarily focused on systematic descriptions of some components of the Fezouata Biota (Van Roy and Tetlie, 2006; Botting, 2007; Lefebvre and Botting, 2007; Vinther et al., 2008; Fortey, 2009, 2011, 2012; Sumrall and Zamora, 2011; Van Roy and Briggs, 2011; Kröger and Lefebvre, 2012; Valent et al., 2013; Ebbestad and Lefebvre, 2015; Valent and Corbacho, 2015; Van Roy et al., 2015b; Ortega-Hernandez et al., 2016; Legg, 2016). Otherwise a few works addressed the question of its taphonomy (Gaines et al., 2012; Allaire et al., 2015; Martin et al., 2015), while others substantially clarified the biostratigraphical and palaeoenvironmental context of the Fezouata Shale (Nowak et al., 2015; Martin et al., 2016).

Contents

The aim of this special issue is to significantly improve our understanding of the Fezouata Shale and its exceptionally preserved biota. Using palaeontological data from various groups,

101 complemented by sedimentological data, this collection of contributions provides a far more
102 detailed picture of the biostratigraphical, palaeoecological, palaeogeographic, and
103 palaeoenvironmental contexts associated with the deposition of this unique Lower Ordovician
104 Lagerstätte and the preservation of its remarkable biota than hitherto available. Still, the
105 resulting picture is little more than a sketch so the task is great, but it is our deepest hope that
106 it will provide a firm ground for future investigations of all or part of the biota, as well as a
107 source of hypotheses to be tested in the light of newly collected data.

108 The volume begins with a historical review of the investigations on the geology of the
109 Anti-Atlas, and more specifically the palaeontology of the Lower Ordovician strata exposed
110 in the Zagora area. This review is followed by a reconstruction of the depositional context of
111 the Fezouata Shale, with a special emphasis on the sedimentological characteristics of the
112 intervals yielding exceptionally preserved fossils. Subsequent contributions focus on one,
113 rarely two particular fossil groups, namely: acritarchs and chitinozoans, bivalves, cnidarians,
114 conodonts, echinoderms, gastropods (and relatives), graptolites, hyolithids, palaeoscoleids,
115 sponges, and trilobites. As varied as they are, all these studies have a similar objective: using
116 the information provided by a fossil group to enlighten general aspects of the Fezouata Biota.
117 Some fossil groups, such as acritarchs and chitinozoans, conodonts, and especially graptolites,
118 proved particularly useful for constraining the ages of the Lower Ordovician strata
119 outcropping in the Zagora area, and especially the intervals associated with exceptional
120 preservation. The others provide valuable insights into the palaeobiogeographic affinities of
121 the Fezouata Biota and their evolution through time, the palaeoenvironment(s) it lived in,
122 and/or its ecological structure. The main outcomes of each of these studies can be
123 summarized as follows.

124 Over a century of geological investigations in the Lower Ordovician of the Central Anti-
125 Atlas (Morocco) is reviewed by Lefebvre et al. (this issue a), with a special emphasis on the

critical contributions of Georges Choubert and Jacques Destombes. This thorough review put current research on the Fezouata Biota in its historical context, and provides the first detailed account of the discovery of the Lagerstätte and its subsequent scientific investigation over the last 15 years.

Vaucher et al. (this issue) propose a depositional model for the Fezouata Shale, which recognizes two main types of fossiliferous beds, both related to storm activity, but at different bathymetries. Shell beds are interpreted as time-averaged, storm-generated local accumulations in proximal settings. Horizons with exceptional preservation are regarded as resulting from the sudden burial of autochthonous communities by distal tempestites in deeper, more inhospitable environments.

A detailed, graptolite-based biostratigraphic framework for the whole Fezouata Shale is defined by Gutiérrez-Marco and Martin (this issue), which allows correlations with the Algerian Sahara. Graptolite biochronology suggests that in the Fezouata Shale, exceptional preservation occurs in two distinct intervals that can be dated as late Tremadocian and middle Floian, respectively. Mass occurrences of mesopelagic graptolites in the lower part of the succession are regarded as suggestive of relatively deep, outer shelf depositional conditions.

A low diversity conodont assemblage is described for the first time in the Lower Ordovician of the Anti-Atlas by Lehnert et al. (this issue), and compared with the rare, but similar faunas documented from other regions of the 'subpolar faunal domain' (high-latitude, siliciclastic peri-Gondwanan shelves). In the Fezouata Shale, the strongly recrystallized conodont elements retrieved from the stratigraphically lower interval with exceptional preservation suggest a late Tremadocian–early Floian age.

Abundant and diverse palynomorph assemblages typical of open shelf environments in high-latitude, peri-Gondwanan regions are documented by Nowak et al. (this issue) in the Lower Ordovician of the Anti-Atlas. Acritarchs extracted from the lower interval with

151 exceptional preservation support the late Tremadocian age inferred from the study of
152 graptolites and conodonts. The younger (Floian) age suggested by the chitinozoans from this
153 interval stresses the need for a revision of chitinozoan biozones.

154 In the lower part of the Fezouata Shale, sponges form a significant component of benthic
155 communities. Their palaeoecology and unusual distribution pattern are extensively discussed
156 by Botting (this issue). Monospecific dense aggregations, usually known from a single
157 bedding plane, are interpreted as opportunistic colonisations of relatively hostile
158 environments by r-strategists. By contrast, other taxa are known from various levels, but
159 never form crowded assemblages; these are considered as K-strategists adapted to more stable
160 settings.

161 Gastropods and related molluscs (tergomyans and paragastropods) represent a small
162 component of the Fezouata Biota. Their palaeoecology, systematics, and biostratigraphic
163 distribution are reviewed by Ebbestad (this issue) based on abundant new material.
164 Comparison with other Early Ordovician assemblages reveals that the Fezouata gastropods
165 (and related taxa) show strong affinities (at species level) with those from the Montagne Noire
166 (France) and, to a lesser extent, with those from Argentina and Bohemia.

167 Echinoderms are particularly abundant and diverse in benthic communities of the Fezouata
168 Shale. Their palaeoecology, palaeobiogeographic affinities and evolutionary significance are
169 investigated by Lefebvre et al. (this issue b). Late Tremadocian low-diversity mass-
170 occurrences of dwarfed echinoderms are interpreted as evidence for opportunistic
171 colonization of inhospitable settings by cosmopolitan, Cambrian-like taxa at that time. Higher
172 diversity assemblages dominated by peri-Gondwanan, post-Cambrian taxa are associated with
173 more stable environments.

174 The description of preserved soft parts in a hyolithid from the lower part of the Fezouata
175 Shale gives the opportunity to Martí Mus (this issue) to critically discuss the palaeoecology,

taphonomy and systematic affinities of these extinct organisms. A sediment-like infill in part of the gut is interpreted as diagenetic in origin, rather than evidence for specialized deposit feeding habits. Soft parts protruding beyond the conch aperture are described for the first time in hyolithids and support lophotrochozoan affinities.

Palaeoscolecoid worms occur in the lower part of the Fezouata Shale, sometimes in great abundance. The material, composed of long body fragments and almost complete individuals, is described by Martin et al. (this issue a). An epibenthic lifestyle and deposit feeding habits (to some degree) are deduced based on anatomical, ichnological, and sedimentological data. Comparison with other Ordovician palaeoscolecoid occurrences indicate great faunal affinities with Bohemia.

Trilobites are a major component of both regular ('shelly') and exceptionally preserved assemblages in the Fezouata Shale. Their palaeoecology, biostratigraphy and palaeogeographic affinities are analysed in detail by Martin et al. (this issue b). Trilobite assemblages suggest the occurrence of relatively restricted environmental conditions in the lower part of the Fezouata Shale, while preliminary geochemical analyses suggest temporary dysoxic conditions in the lower interval with exceptional preservation.

The palaeobiogeographic affinities and palaeoecology of the abundant bivalve assemblages occurring in the upper part of the Fezouata Shale are discussed by Polechová (this issue). The composition of these assemblages shows striking similarities with that of the faunas documented in other Ordovician peri-Gondwanan localities, similarly associated with siliciclastic shelf settings. The occurrence of two distinct, complex muscular systems in the Fezouata bivalves indicates that they were active infaunal burrowers. This illustrates the rapid ecological diversification of these molluscs during the Early Ordovician.

Lastly, the Fezouata Shale has yielded a low-diversity assemblage of cnidarians, comprising both scyphozoans (conulariids) and probable medusozoans (*Sphenothallus*). Their

palaeogeographic affinities and palaeoecology are investigated by Van Iten et al. (this issue). The Moroccan conulariid fauna is more similar to a contemporaneous fauna from Wales. In the Fezouata Shale, conulariids typically occur in low-diversity, high-abundance assemblages, some individuals being attached to larger conulariids or to linguliform brachiopods.

Dedication

This volume is dedicated to Mohamed ‘Ou Saïd’ Ben Moula, the discoverer of the Fezouata Biota (Fig. 1). It is not an exaggeration to state that without him, and his eagerness to support scientific research, this volume would not exist, and no-one would ever have known about this major exceptionally preserved fauna.

Mohammed Ben Moula was born in 1952 in Alnif, as the son of Saïd ben Hammou and Aïcha bent Daoud. Alnif, being in the middle of an area of extensive outcrops of Cambrian, Ordovician and Devonian ages, belongs to the classical heartland of Moroccan palaeontology and so, not before long, Mohamed became involved with fossil collecting. With time, his collecting trips led him farther afield, until he started focussing on the area to the north of Zagora, some 200 km south-east of his home town. At the time, this was virtually virgin territory, with little or no collecting activity going on. First, he went there to collect classical ‘shelly’ fossils – mainly trilobites and echinoderms. However, around the turn of the century, some of his digs started turning up other, more unusual creatures. Other collectors likely would have discarded these unfamiliar fossils – but not Ou Saïd: he knew he was onto something special. In 2000, one of the very first of these remarkable fossils, a specimen of *Tremaglaspis*, made its way into the hands of Brahim Tahiri, an international collector and fossil dealer from Erfoud. Two more years would elapse before Mohamed started large-scale excavations targeting the Fezouata Biota. From there, as the saying goes, the rest is history.

The success of the Fezouata project can entirely be traced back to Mohamed Ben Moula and his family. Not only did Mohamed discover the Fezouata Biota and recognised its interest – crucially, he has also always been very open and supportive of scientific research on any of the fossils discovered by him. Last but not least, he is an absolutely remarkable collector, recovering mm-sized fossils that are almost invisible to the naked eye. Although he never received any formal palaeontological training, he displays an amazing insight into the fossils he discovers - to the extent that it would put many ‘professional’ palaeontologists to shame! His understanding of the local geology translates into an uncanny ability to pinpoint sites in the desert for excavation, with a remarkable degree of success. Without Mohamed’s kind help, collaboration and understanding of the fossils, the Fezouata research would quite simply not exist.

While recently, as a result of this success, some other collectors have also started to take an interest in the Fezouata fossils, Mohamed Ben Moula undoubtedly remains the master of this remarkable biota. Nowadays, he is joined in the field by his sons Lahcen, Brahim and Yusuf, who exhibit the same talent and enthusiasm for the subject as their father, ensuring decades of exciting discoveries to come.

Reconstruction of the Fezouata sea floor

Exceptionally preserved biotas not only provide increased insight into the systematic aspects of the groups that are preserved; they also offer a much more complete understanding of the composition and functioning of ancient ecosystems than would ever be possible from normal fossils faunas preserving only biomineralized taxa alone. This is conferred in the stunning rendition of the Fezouata sea floor by Marguerite Lardanchet (Fig. 2), which is centred on a fresh carcass of the giant filter-feeding anomalocaridid *Aegirocassis benmoulai*

that has come to grief in a meadow of *Rhopalocystis* eocrinoids. The decaying giant has started to attract a varied assemblage of scavengers who have come to feast on the remains. While, as is almost inevitably the case with this kind of reconstructions, the assemblage depicted may seem unrealistically dense and diverse, it needs pointing out that some sites in the Fezouata Shale have yielded multiple specimens belonging to a couple dozen different taxa from an excavation area less than the size of an average bill board. The animals depicted in the reconstruction are only a small sample of the total diversity of the Fezouata Biota (see Van Roy *et al.* 2015a for a provisional, and incomplete faunal list); in fact, most Fezouata fossils still await formal description. The taxa depicted in the scene are as follows:

1. The anomalocaridid *Aegirocassis benmoulai*
2. The oldest known horseshoe crab
3. A basal chelicerate
4. The oldest known cheloniellid arthropod
5. *Brachyaglaspis singularis*, an atypical aglaspidid
6. *Tremaglaspis* sp., a possible aglaspidid
7. A marrellid arthropod
8. *Platypeltoides magrebiensis*, a nileid trilobite
9. *Anacheirurus* sp., a cheirurid trilobite
10. *Plumulites bengtsoni*, a machaeridian annelid
11. *Palaeoscolex? tenensis*, a palaeoscolecoid worm
12. *Eoconularia* sp., a conulariid
13. *Hamptonia christi*, a protomonaxonid sponge
14. *Pirania auraeum*, another protomonaxonid sponge
15. *Elegantilites* sp., a hyolithid
16. *Orbithele* sp., an inarticulate brachiopod

- 276 17. *Araneograptus murrayi*, a dendroid graptolite
277 18. The eocrinoid *Rhopalocystis destombesi*
278 19. *Thoralicystis* sp., a cornute stylophoran
279 20. *Anatifopsis trapeziiformis*, a mitrate stylophoran
280 21. A new somasteroid
281 22. A chaetocladid alga

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Figure captions

498 Fig. 1. Mohamed ‘Ou Said’ Ben Moula and his sons Lahcen and Brahim, photographed in the
499 field in January 2014 while extracting material from a small excavation at Bou Izargane,
500 about 20 km N. of Zagora, central Anti-Atlas, Morocco.

501 Fig. 2. Reconstruction of the Fezouata Biota. (A) Original drawing. (B) Keys to the
502 identification of the taxa represented in (A) and listed in the text.

503

Figure 1

Figure 2

Figure Caption of Figure 2