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Preface

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 et al., 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; Lerosey-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-biomineralized 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, 2016-in this issue; Lehnert et al., 2016-in this issue; Nowak et al., 2016-in 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 independent launches of the first scientific field campaigns (for a detailed account of these early investigations, see Lefebvre et al., 2016a-in 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 and 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-

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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-Hernández 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).

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

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

Over a century of geological investigations in the Lower Ordovician of the Central Anti-Atlas (Morocco) is reviewed by Lefebvre et al. (2016a-in 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. (2016-in 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 (2016-in 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. (2016-in 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. (2016-in this issue) in the Lower Ordovician of the Anti-Atlas. Acritarchs extracted from the lower interval with exceptional preservation support the late Tremadocian age inferred from the study of graptolites and conodonts. The younger (Floian) age suggested by the chitinozoans from this interval stresses the need for a revision of chitinozoan biozones.

In the lower part of the Fezouata Shale, sponges form a significant component of benthic communities. Their palaeoecology and unusual distribution pattern are extensively discussed by Botting (2016-in this issue). Monospecific dense aggregations, usually known from a single bedding plane, are interpreted as opportunistic colonizations of relatively hostile environments by r-strategists. By contrast, other taxa are known from various levels, but never form crowded assemblages; these are considered as K-strategists adapted to more stable settings.

Gastropods and related molluscs (tergomyans and paragastropods) represent a small component of the Fezouata Biota. Their palaeoecology, systematics, and biostratigraphic distribution are reviewed by Ebbestad (2016-in this issue) based on abundant new material. Comparison with other Early Ordovician assemblages reveals that the Fezouata gastropods (and related taxa) show strong affinities (at species level) with those from the Montagne Noire (France) and, to a lesser extent, with those from Argentina and Bohemia.

Echinoderms are particularly abundant and diverse in benthic communities of the Fezouata Shale. Their palaeoecology, palaeobiogeographic affinities and evolutionary significance are investigated by Lefebvre et al. (2016b-in this issue b). Late Tremadocian low-diversity mass-occurrences of dwarfed echinoderms are interpreted as evidence for opportunistic colonization of inhospitable settings by cosmopolitan, Cambrian-like taxa at that time. Higher diversity assemblages dominated by peri-Gondwanan, post-Cambrian taxa are associated with more stable environments.

The description of preserved soft parts in a hyolithid from the lower part of the Fezouata Shale gives the opportunity to Martí Mus (2016-in this issue) to critically discuss the palaeoecology, taphonomy and