

## The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician

Peter Van Roy<sup>1</sup>, Derek E. G. Briggs<sup>1\*</sup> & Robert R. Gaines<sup>2</sup>

<sup>1</sup> Department of Geology and Geophysics and Yale Peabody Museum of Natural History, Yale University, PO Box 208109, New Haven, CT 06520-8109, USA

<sup>2</sup> Geology Department, Pomona College, 185 E. Sixth St., Claremont, CA 91711, USA

\*Correspondence: derek.briggs@yale.edu

**Abstract:** The discovery of the Fezouata biota in the latest Tremadocian of southeastern Morocco has significantly changed our understanding of the early Phanerozoic radiation. The shelly fossil record shows a well-recognized pattern of macroevolutionary stasis between the Cambrian Explosion and the Great Ordovician Biodiversification Event, but the rich soft-bodied Fezouata biota paints a different evolutionary picture. The Fezouata assemblage includes a considerable component of Cambrian holdovers alongside a surprising number of crown group taxa previously unknown to have evolved by the Early Ordovician. Study of the Fezouata biota is in its early stages, and future discoveries will continue to enrich our view of the dynamics of the early Phanerozoic radiation and of the nature of the fossil record.

**Supplementary material:** A complete faunal list is available at <http://www.geolsoc.org.uk/SUP18843>.

**Received** 18 February 2015; **revised** 29 April 2015; **accepted** 1 May 2015

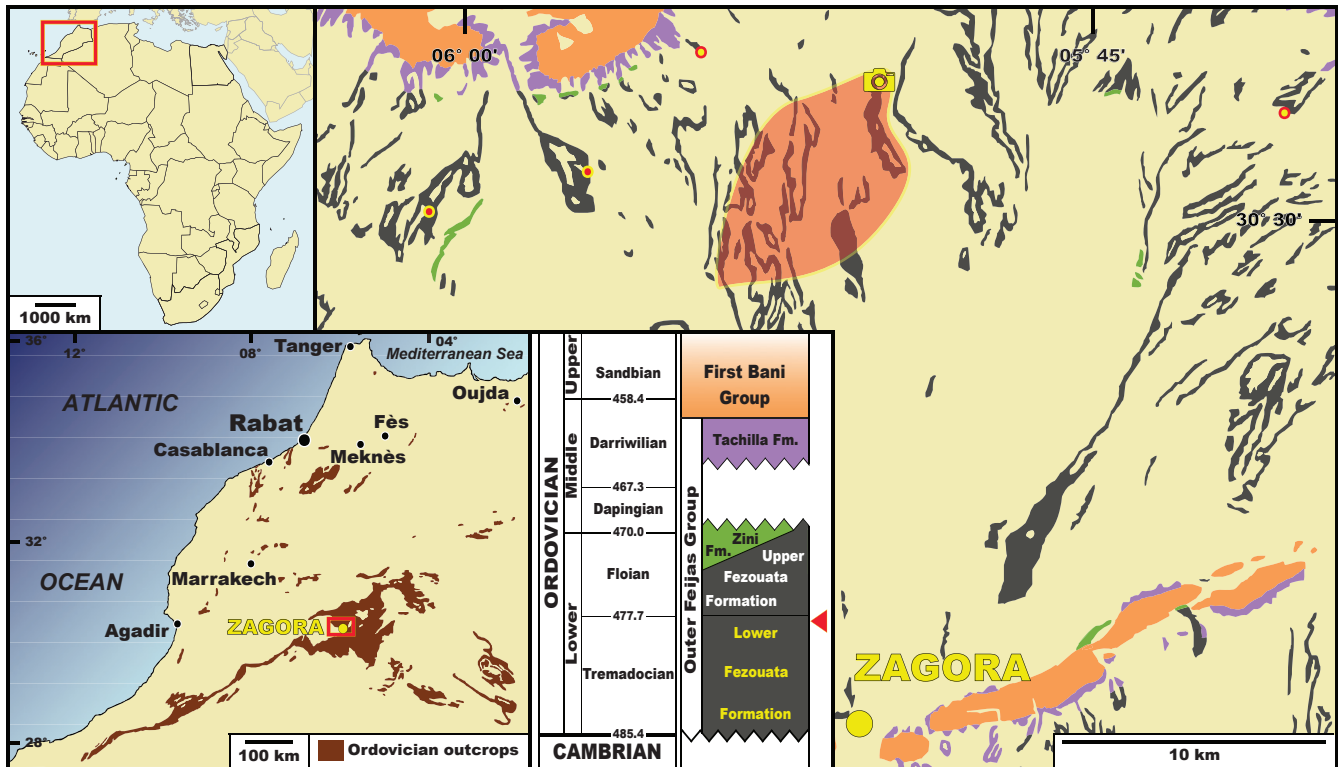
The Lower Ordovician Fezouata formations of Morocco hit the headlines in 2010 when they were reported to yield a diverse fauna of Burgess Shale-type fossils (Van Roy *et al.* 2010). Exceeding 1000 m in combined thickness, the Lower and Upper Fezouata formations are extensive units that crop out over a wide area in the Anti-Atlas region of southeastern Morocco, extending some 200 km south of the town of Alnif, and a similar distance to the west of Zagora, where the Fezouata biota was first discovered (Figs 1 and 2). Although abundant and diverse open-marine shelly faunas had been reported from these fine-grained siliciclastic deposits since the 1950s (e.g. Choubert *et al.* 1955; Destombes & Willefert 1959; Destombes 1962, 1972; Chauvel 1966, 1978; Havlíček 1971; Destombes *et al.* 1985), the first exceptionally preserved fossils were discovered only in the early 2000s by Mohamed 'Ou Said' Ben Moula, a local collector (Van Roy 2006; Van Roy & Tetlie 2006). He first shared information about his localities with Peter Van Roy in 2002, initiating a collaboration between a Moroccan collector and Belgian researcher that continues to this day.

The similarities between the Ordovician Fezouata and Cambrian Burgess Shale biotas came as a surprise. A number of Fezouata animals would not look out of place in Walcott's Burgess Shale Quarry in British Columbia (Fig. 3), and the biota appears to have followed a preservational pathway similar to that of the Burgess Shale, one that was widely believed to have been lost after the mid-Cambrian. Part of the importance of the Fezouata Konservat-Lagerstätte is the extension of the stratigraphic record of these 'Cambrian' animals into the Ordovician, but it is also remarkable in preserving the earliest representatives of groups such as horseshoe crabs, significantly extending the origins of several typical post-Cambrian clades back in time (Fig. 4). Burgess Shale-type preservation was defined by Butterfield (1995, 2003) as exceptional preservation of non-biomineralizing organisms as carbonaceous compressions in marine shales. Butterfield (1995, 2003) originally identified this type of preservation as characteristic of the early Neoproterozoic and early to mid-Cambrian. The primary agent responsible for Burgess Shale-type preservation of

soft-bodied fossils is the survival of carbonaceous films (Gaines *et al.* 2008). In some cases the carbonaceous film is associated with authigenic minerals, such as apatite in the gut (Briggs 1981; Butterfield 2002), or pyrite in limbs (Gabbott *et al.* 2004), and this may be the case for Fezouata fossils, although extensive weathering has affected their appearance. Such weathering resulted in degradation of the carbonaceous remains and also liberated iron from the oxidation of pyrite, staining the specimens and giving them their characteristic red–orange appearance (Figs 3 and 4). Although the appearance of the Fezouata fossils is generally more similar to the weathered fossils of the early Cambrian Chengjiang biotas of China (Hou *et al.* 2004) than to those of the original Burgess Shale itself, detailed understanding of taphonomy at the specimen level is still in progress, and careful analysis is required to peel back the effects of weathering upon the original taphonomic mode.

Prior to the discovery of the Fezouata fossils, the kinds of Cambrian animals that populate the Burgess Shale largely seemed to disappear from the fossil record after the mid-Cambrian (Conway Morris 1989). Although a literal reading of the fossil record would suggest that many of these taxa became extinct, as observed for some components of the shelly fauna during the late Cambrian (e.g. Saltzman *et al.* 2000), the absence of these animals is more likely to reflect a lack of suitable environments for their preservation. The general paucity of outer-shelf muddy environments favourable to Burgess Shale-type preservation in late Cambrian and Early Ordovician strata has made this assertion difficult to test. The rifting of Avalonia from the western margin of Gondwana, however, provided an ideal setting for the deposition of fine-grained clastic sediments during the Early Ordovician (Destombes *et al.* 1985; Cocks & Torsvik 2006). The thick succession of offshore marine mudstones making up the Fezouata formations crops out over an area of several hundred square kilometres in a desert landscape replete with exposures and, as such, offers a perfect target for prospecting for exceptionally preserved fossils.

The occurrence of a large number of Burgess Shale-type Konservat-Lagerstätten in the Cambrian, coincident with the



**Fig. 1.** Ordovician outcrop map of the area north of Zagora, southeastern Morocco. Areas that yield exceptionally preserved fossils are indicated in colour: red areas with yellow trim belong to the *Araneograptus murrayi* biozone; yellow areas with red trim fall in the *Hunnegraptus copiosus* zone. A few additional sites considerably farther to the west and north fall outside the area covered by the map. The camera icon indicates the position of the photograph in Figure 2. Insets show the position of the map below in Africa, the study area within Morocco, and the stratigraphic context. The red arrow indicates the stratigraphic position of the Fezouata biota.

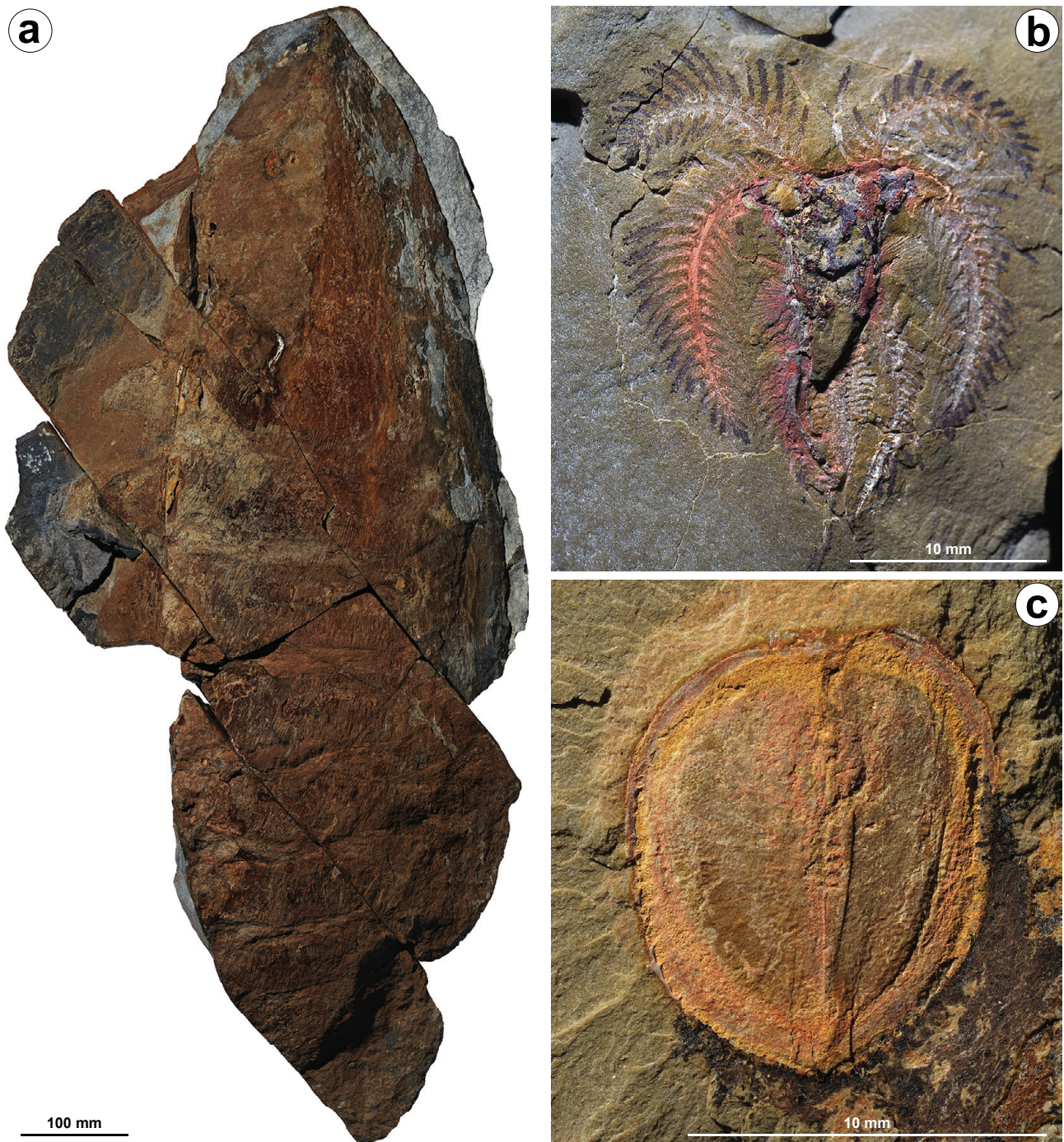


**Fig. 2.** View towards the north from Tigzigzaouine Hill, west of Oued Ezegzaou, c. 25 km north of the town of Zagora. The position where the photograph was taken is indicated by the camera icon on the outcrop map in Figure 1. The Lower Ordovician Lower Fezouata Formation crops out in the hills in the foreground; it is here that the complete anomalocaridid specimens were collected. The low hills in the middle distance are a Cambrian inlier, whereas the mountains on the horizon represent the shales of the Middle Ordovician Tachilla Formation overlain by the sandstone-shale successions of the Middle to lower Upper Ordovician First Bani Group.

explosion of animal diversity, has attracted a number of explanations. Popular for a time was the idea that infaunal animals had not evolved sufficient penetrating power to burrow to the depths required to destroy carcasses buried by sedimentation events (Allison & Briggs 1993). Gaines *et al.* (2012b), however, showed that a number of important Cambrian Lagerstätten were deposited under persistent anoxic conditions and were not susceptible to bioturbation. In addition, where settings similar to those in the Cambrian occur in the later Phanerozoic rock record, they lack exceptional preservation; hence, another mechanism must account for Burgess Shale-type occurrences. The Cambrian oceans were relatively low in sulphates and high in alkalis, two features of seawater chemistry that affect preservation (Gaines *et al.* 2012c). Low levels of sulphate may have inhibited sulphate-reducing bacteria, the primary degraders in marine sediments. Alkaline seas, working in concert, appear to

have greatly amplified this effect through early sealing of the seafloor sediment by carbonate cement, inhibiting diffusion from the overlying seawater and thus indirectly inhibiting decay. Such considerations (Gaines *et al.* 2012c) are based on analyses of samples covering a significant stratigraphic range through the Cambrian. Extension of a comprehensive sample suite into the Early Ordovician is under way and preliminary results indicate that the Fezouata sediments were subject to similar chemical conditions to those of the Cambrian.

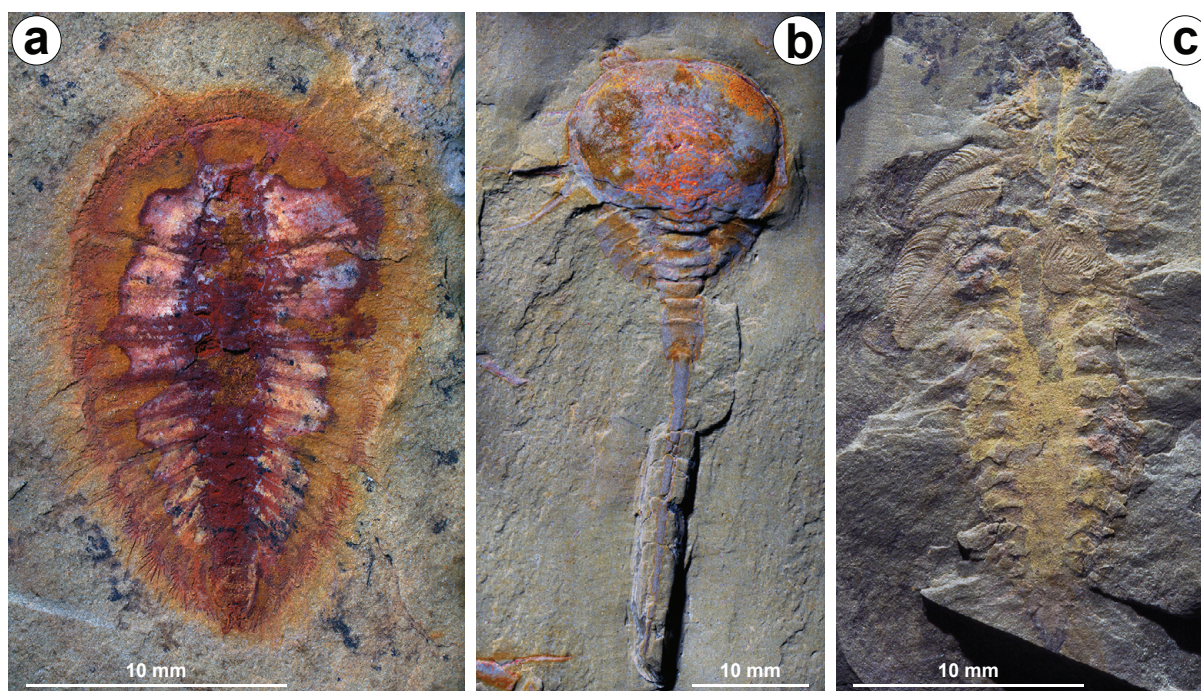
The Fezouata biota opens up a window of Burgess Shale-type preservation in the Early Ordovician. But it is a particularly valuable Konservat-Lagerstätte because, in contrast to most other Ordovician examples (see Box 1), the fauna represents a fully marine biota, with a complete range of shelly and non-biomineralized taxa (see Box 2; Table 1). In this respect it contrasts with other Ordovician Konservat-Lagerstätten such as Winneshiek (Darriwilian; Liu *et al.*



**Fig. 3.** Typical Burgess Shale-type animals from the Fezouata biota. (a) *Aegirocassis benmoulai*, a giant filter-feeding anomalocaridid preserved in three dimensions within a concretion. Two sets of swimming flaps are evident on the left side of the trunk. (YPM (Yale Peabody Museum) 237172.) (b) A marrellomorph arthropod, probably belonging to the genus *Furca*. (MHNT (Natural History Museum of Toulouse) PAL.2007.39.80.1.) (c) Different type of marrellomorph showing similarities to *Skania* and *Vachonisia*. (YPM 226539.) The body and appendages are concealed by the carapace. All specimens are from the uppermost Tremadocian *Araneograptus murrayi* biozone.

2006), Beecher's Trilobite Bed (Katian: Briggs *et al.* 1991; Farrell *et al.* 2009), William Lake and Airport Cove, Manitoba (Katian: Young *et al.* 2007), and the Soom Shale (Hirnantian or even earliest Silurian: Aldridge *et al.* 1994, 2001; Vandenbroucke *et al.* 2009), all of which yield restricted assemblages from marginal environments. However, a marrellomorph resembling *Furca*, a signature taxon of the Fezouata biota, was recently reported from the early Ordovician Floresta Formation of Argentina (Aris & Palomo 2014), raising the possibility that other normal, fully marine exceptional faunas of this age may be present elsewhere (see Box 1). Exceptional preservation was originally believed to occur from the top of the Lower Fezouata Formation throughout the Upper Fezouata Formation, based on

collections from numerous small exposures (e.g. Van Roy *et al.* 2010). However, Martin *et al.* (2015) used constraints from graptolites and acritarchs to show that only two intervals, c. 25 and 15 m thick, yield exceptionally preserved fossils. Both intervals are situated near the top of the Lower Fezouata Formation and are of latest Tremadocian age (*Araneograptus murrayi* and *Hunnegraptus copiosus* biozones respectively). Martin *et al.* (2015) interpreted the fossil-bearing sediments as deposited just above storm wave base and argued that storms buried the fauna essentially *in situ* in upper offshore to lower shore-face settings. Significant variation in the extent of bioturbation suggests that unstable oxygen conditions at the sea floor periodically favoured the development of benthic communities.



**Fig. 4.** Typical post-Cambrian animals from the Fezouata biota. (a) The oldest representative of the cheloniellid arthropods, which range to the Devonian. (NMS (National Museums of Scotland) G 2004.2.1.) (b) The oldest horseshoe crab, a subadult specimen showing the fused segments at the rear characteristic of living horseshoe crabs (YPM 227586). (c) The first specimen of a machaeridian (*Plumulites bengtsoni*) with preserved soft tissues, which finally revealed its affinities 150 years after isolated trunk plates were first described: it is a polychaete annelid. (YPM 221134.) (a) is from the *Hunnegraptus copiosus* biozone, (b) and (c) are from the *Aranograptus murrayi* biozone, all uppermost Tremadocian.

### Extending temporal ranges

Description and analysis of the fauna and its palaeoenvironment are continuing but a number of exciting discoveries have already been made. Fezouata is a new taphonomic window representing a time when exceptional preservation was essentially unknown and, as we might anticipate, extends the ranges of a number of rarely preserved taxa: unusual Cambrian stem group forms up into the Tremadocian, and crown group taxa back into the Early Ordovician (Box 2).

One group of charismatic Cambrian stem organisms whose range is extended into the Ordovician by the Fezouata biota are armoured lobopodians, which are very diverse in the Cambrian but largely unknown in later marine biotas. These are of particular importance as they provide crucial information about the early stages of panarthropod and onychophoran evolution (Smith & Ortega-Hernández 2014). A second iconic Cambrian clade represented in the Fezouata biota is the anomalocaridids (Fig. 3a): the Fezouata biota includes at least five forms, some of substantial size (Van Roy & Briggs 2011; Van Roy *et al.* 2014, 2015; Box 2; Table 1).

The potential for discovering anomalocaridids in suitable facies in the Ordovician was hinted by the discovery of *Schinderhannes bartelsi* in the Devonian Hunsrück Slate. Represented by just one specimen, *Schinderhannes bartelsi* (Kühl *et al.* 2009) was described as a euarthropod retaining the raptorial appendages, large eyes and radial mouth characteristic of anomalocaridids. The unusual pair of large swimming appendages behind the head have recently found an analogy in the pair of hypertrophied post-cephalic flaps in the Chengjiang anomalocaridid *Lyrarapax unguispinus* (Cong *et al.* 2014).

The Fezouata biota also extends the range of more modern animals back to the Early Ordovician and is host to a surprising diversity of advanced chelicerates, including horseshoe crabs (Van Roy *et al.* 2010; Box 2; Table 1). This diversity suggests a Gondwanan origin for Chelicerata, an idea that is also supported by the recent discovery of a eurypteroid in the Late Ordovician of SE Turkey (Lamsdell *et al.* 2013). The Fezouata horseshoe crabs are among the most abundant fossils in the fauna and are remarkably modern

in aspect, with the segments that make up the posterior division of the body partially fused in a step towards the morphology of modern *Limulus* (Fig. 4b). They extend the range of this group back some 25 Ma. Their presence suggests an even earlier evolutionary history of the group, back into the Cambrian, an extension further supported by the presence of chasmataspidid trace fossils in the late Cambrian of Texas (Dunlop *et al.* 2004). Apart from extending the range of the group downwards, the Moroccan horseshoe crabs also provide important new insights into the way the fused trunk of modern horseshoe crabs evolved.

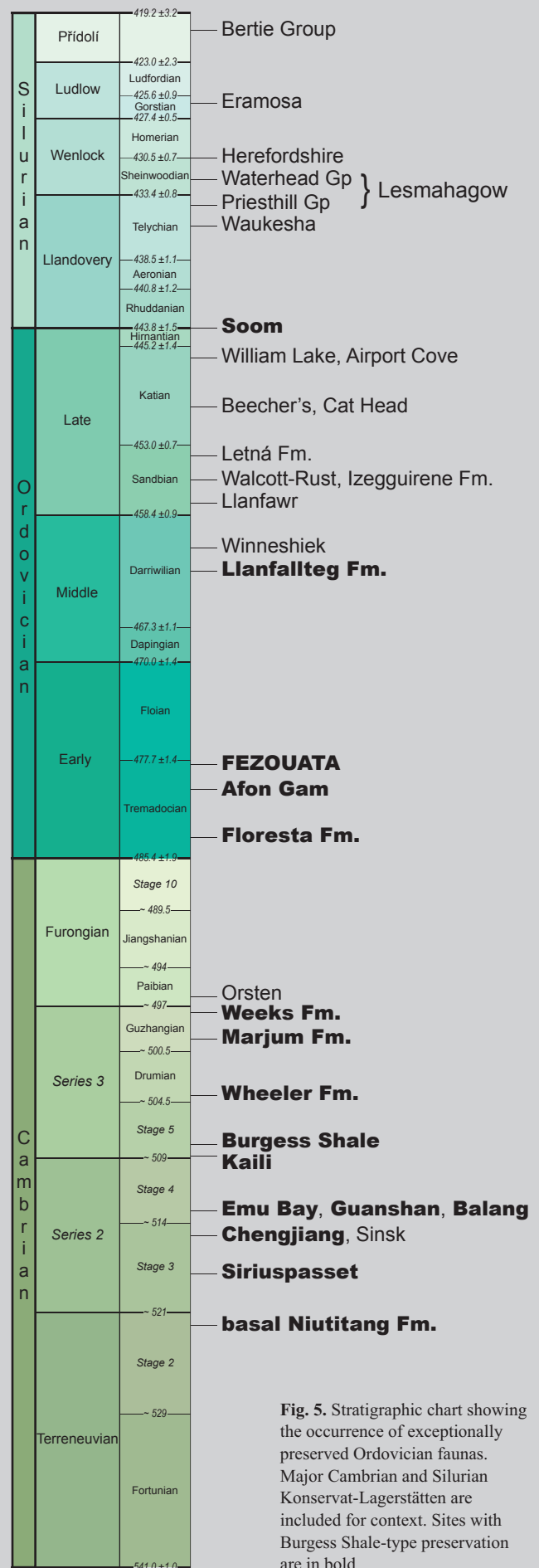
### New morphological information

Exceptionally preserved fossil occurrences are important not only because they reveal organisms that are not otherwise represented in the fossil record, but also because they flesh out creatures otherwise incompletely known through their mineralized hard parts. Machaeridians were first described in 1857 and are known from a diversity of shelly plates, which range in age from Early Ordovician to Carboniferous. Hypotheses of their relationships had ranged from barnacles through echinoderms, molluscs and annelids. The complete armour was known, but had not resolved the question of machaeridian affinity. As living annelids with a calcite armour are unknown and mineralized annelid jaws are rare, an annelid assignment appeared least likely. A Fezouata specimen of the previously described genus *Plumulites*, preserving soft parts (Fig. 4c), finally provided the answer. The segmented soft body beneath the armour carries paired parapodia with bundles of bristles or setae (Vinther *et al.* 2008) showing that the animal is a polychaete annelid. This discovery has parallels in the classic example of conodonts. Conodont elements were first described in 1856, a year before machaeridian plates. Complete apparatuses preserved on bedding planes did not resolve their affinities. The soft parts were not discovered until the 1980s when specimens turned up in the Lower Carboniferous of Edinburgh (Briggs *et al.* 1983); the evidence of a handful of specimens showed them to be vertebrates.

**Box 1: Fezouata: filling the gap**

The Cambrian is host to an exceptionally large number of Konservat-Lagerstätten (Conway Morris 1989) only the most important of which are included in the accompanying chart. These Lagerstätten have provided major new insights into the Cambrian Explosion and early metazoan ecosystems. In dramatic contrast, only a handful of Ordovician exceptionally preserved faunas are known (Allison & Briggs 1993) and most of these represent low-diversity assemblages from marginal environments, rather than typical marine communities. As a consequence, these sites have had little impact on our understanding of the Great Ordovician Biodiversification Event (GOBE), which has been documented almost exclusively from shelly faunas, providing a very incomplete view of the ecosystems they represent (e.g. Dorjes 1972; Driscoll & Swanson 1973). The Fezouata biota is the only major, diverse exceptionally preserved fauna from an open-marine environment to fill the *c.* 70 Ma interval between the last Cambrian (Weeks Formation, Guzhangian; Lerosey-Aubril *et al.* 2014) and first Silurian (Herefordshire, Wenlock; Briggs *et al.* 1996, 2008) examples from normal marine settings.

Few other Ordovician normal open-marine deposits have yielded exceptionally preserved fossils in any numbers. Exceptional preservation in the Walcott–Rust Quarry (Sandbian) is limited to trilobite appendages (Brett *et al.* 1999). The fauna of the Llanfawr mudstones (Sandbian) (Botting *et al.* 2011) is less well preserved and is dominated by a few rapidly dispersing taxa, suggesting that it may represent a short-lived biota from an unstable, tectonically and volcanically active environment. Exceptional preservation in the deeper water deposits of the Llanfallteg Formation (Darriwilian) is rare, but the fauna does include a few Burgess Shale-type taxa (Whittington 1993; Legg & Hearing 2015). The slightly older early late Tremadocian Afon Gam fauna (Botting *et al.* 2015) is from a comparable water depth and palaeolatitude to the Fezouata biota (*c.* 60°S for Afon Gam, versus *c.* 65°S for Fezouata; Martin *et al.* 2015). However, the Afon Gam fauna is dominated by algae and Burgess Shale sponge taxa, with other groups being of minor importance. The generally poor quality of soft tissue preservation suggests that the composition of the Afon Gam biota may be due in part to taphonomic bias. It seems probable, however, that Afon Gam, like the younger Llanfawr biota from the same basin, is a less representative fauna adapted to an unstable, tectonically and volcanically active environment. The recently discovered biota of the Floresta Formation of Argentina (Aris & Palomo 2014) is most exciting: given its early Tremadocian age and geographical position, it has the potential to provide a comparison with the Fezouata biota. However, so far only two non-biom mineralized arthropods, one of uncertain affinity and a possible example of the genus *Furca*, have been reported. Thus, only the Fezouata biota has the capacity to reveal that the sudden replacement of typical Cambrian shelly taxa by those of the Palaeozoic Evolutionary Fauna during the GOBE is not matched by a similar turnover among soft-bodied and lightly sclerotized organisms. The association of advanced, typically post-Cambrian non-biom mineralized taxa with Burgess Shale-type elements in the Fezouata biota implies that the GOBE was more advanced at this time than has been appreciated; rather than being discrete events, the Cambrian and Ordovician radiations may represent successive stages within the same large-scale diversity dynamic (Droser & Finnegan 2003; Van Roy *et al.* 2010).



**Fig. 5.** Stratigraphic chart showing the occurrence of exceptionally preserved Ordovician faunas. Major Cambrian and Silurian Konservat-Lagerstätten are included for context. Sites with Burgess Shale-type preservation are in bold.

**Box 2: The faunas**

The Fezouata biota is exceptionally rich and diverse (Table 1): although most of the fauna is still under investigation, over 160 genera have been documented. The shelly fauna accounts for about 50% of the recorded taxa, and is typical for a normal, open-marine environment in the Early Ordovician; the diversity of trilobites, and the size attained by several of them, is remarkable (Fortey 2009, 2011, 2012; Corbacho & Vela 2010; Corbacho & López-Soriano 2012). A significant proportion of the biota (*c.* 30 taxa) consists of non-biomineralized organisms similar to those from Cambrian Burgess Shale-type Lagerstätten, and at least 10 other non-biomineralized taxa represent first occurrences of typical post-Cambrian groups: Burgess Shale-type and post-Cambrian taxa occur in association, as members of the same communities. As in other normal marine faunas, panarthropods dominate, being represented by over 60 taxa. Most of the Fezouata organisms are benthic, as they were more easily engulfed by storm-generated sediment gravity flows than nektonic

animals. A striking feature of the Fezouata biota is the differences in faunal composition between approximately coeval excavations. Many taxa commonly occur throughout the area, but some of them are markedly more abundant at one site than others (e.g. *Aegirocassis benmoulaei*, ‘synziphosurines’, xiphosurids, *Cothurnocystis*, *Thoralicystis*). Other fossils are abundant at one or a few sites, sometimes almost to the exclusion of other taxa, but are virtually absent elsewhere (e.g. *Thelxiope* sp.). Some rare taxa are known from several localities (e.g. the cheloniellid), but others are represented by only one or a few specimens from a single site. These preliminary observations suggest ecological–environmental variation between different communities occupying different parts of the sea floor. Differences have also been observed between faunas from the two successive intervals. Part of this variability may also be ecological, but given the temporal range of up to 2 Ma within the Fezouata biota, some is likely to be evolutionary. Hence, the Fezouata biota offers an unparalleled opportunity to study the interplay between ecology, environment and evolution in Ordovician communities.

**Table 1.** *The faunas***Algae**

**Sponges:** including *Pirania*, *Hamptonia*, *Choaia*, leptomitids, wapkiiids, other demosponges and hexactinellids

**Cnidarians:** including *Plumalina*-like form, several conulariids, *Sphenothallus*

**Brachiopods:** *Ranorthis fasciata*, lingulid and other taxa

**Bryozoans**

**Molluscs:** wiwaxiid, halkieriid, helcionelloid, hyolithoids, *Babinka*, *Coxiconcha*, *Redonia*, *Ribeiria*, *Carcasonella*, *Deshoylites*, *Lesueurilla*, *Thoralispira*, *Bactroceras*, *Bathmoceras australe*, *Bathmoceras taichoutense*, *Destombesiceras zagorense*, *Polymeres*, *Protocryptendoceras longicameratum*, *Rioceras*

**Annelids:** including the machaeridian *Plumulites bengtsoni*, other polychaetes, scolecodonts

**Priapulids:** also including palaeoscolecid

**Lobopodians:** five undescribed taxa including armoured forms

**Anomalocaridids:** including *Aegirocassis benmoulaei*, and four undescribed taxa

**Trilobites:** including *Asaphellus stubbsi*, *Asaphellus cuervoae*, *Asaphellus fezouataensis*, *Asaphopsis*, *Basilicus*, *Kierarges morrisoni*, *Platypeltoides*, *Symphysurus*, *Apatokephalus*, *Dikelocephalina brenchleyi*, *Orometopus*, *Cnemidopyge*, *Lichakephalus stubbsi*, *Parvilichas marochii*, *Selenopeltis*, *Harpides*, *Foulonia*, *Lehua adserai*, *Lehua corbachoi*, *Lehua tahirii*, *Lehua velai*, *Parapilekia*, *Toletanaspis*, *Bathycheilus*, *Bavarilla*, *Colpocoryphe*, *Pharostomina*, *Prionocheilus*, *Agerina*, *Euloma*, *Geragnostus*

**Other arthropods:** including a canadaspidid, *Furca*, acerostracan, leanchoiliid, possible retificiid, *Thelxiope*, *Mollisonia*, naraoid, liwiid, aglaspidid, *Tremaglaspis*, ‘synziphosurine’, xiphosurid, chasmatspidid, eurypterids, cheloniellid, *Pseudoangustidontus duplospineus*, phyllocarid, ostracod, lepadomorph barnacle

**Echinoderms:** including a somasteroid, *Balantiocystis*, *Rhopalocystis*, *Macrocystella*, *Aristocystites*, *Palaeosphaeronites*, *Plasiacystis*, *Ramseyocrinus*, *Argodiscus espilezorom*, *Anedriophus moroccoensis*, rhenopyrgid, *Anatifopsis*, *Chauvelicystis*, *Phyllocystis*, *Thoralicystis*, cothurnocystid, hanusiid, *Peltocystis cornuta*

**Graptolites:** including *Clonograptus rigidus*, *Didymograptus*, *Hunnegraptus copiosus*, ‘*Kiaerograptus*’ *supremus*, *Koremagraptus*, *Paradelograptus norvegicus*, *Paradelograptus tenuis*, *Paratemnograptus magnificus*, ‘*Tetragraptus*’ *bulmani*, *Araneograptus murrayi*, *Dictyonema*, tuboid

**Chordates:** dermal plates, several conodonts

**Problematic metazoans****Chitinozoans****Acritarchs**

A second example is provided by the marrellomorph *Furca* (Van Roy 2006; Van Roy *et al.* 2010; Rak *et al.* 2012). This non-biomineralized taxon was first described by Fritsch (1908*a,b*) on the basis of isolated head shields from the Sandbian of the Letná Formation in the Czech Republic. Fritsch (1908*a,b*) interpreted the fossils as crinoid larvae, but later Perner (1919) suggested a marrellomorph affinity for the fossils, a view also followed by Chlupáč (1999*a,b*). However, in the absence of the rest of the body, lingering doubts over the affinities of *Furca* remained (Chlupáč 1999*a,b*), until exquisitely preserved complete specimens were discovered in the Fezouata biota (Van Roy 2006; Van Roy *et al.* 2010). *Furca* shares the head shield morphology of marrellids, with three pairs of curved projections bearing marginal spines. These marginal spines are more pronounced than in the middle Cambrian *Marrella splendens* from the Burgess Shale, and closer in size to those of the Early Devonian

genus *Mimetaster hexagonalis*. The appendages show similarities to those of both *M. splendens* and *M. hexagonalis*. *Mimetaster hexagonalis* and *Marrella* have long been regarded as closely related (Stürmer & Bergström 1976; Bartels *et al.* 1998; Kühl & Rust 2010).

The Fezouata specimens of the anomalocaridid *Aegirocassis benmoulaei* (Fig. 3a) also revealed important new morphological information. It is the first anomalocaridid to show definitive evidence of both dorsal and ventral flaps. Anomalocaridids are potentially critical to understanding the origin of the arthropod biramous limb, sitting, as they do, stemward of the euarthropods but above lobopodians (Budd 1996; Zhang & Briggs 2007; Daley *et al.* 2009; Kühl *et al.* 2009; Cong *et al.* 2014; Vinther *et al.* 2014; Ortega-Hernández 2015; Van Roy *et al.* 2015). Prior to the discovery of *A. benmoulaei*, anomalocaridids had been reconstructed with just one row of flaps along each side of the trunk (e.g. Whittington & Briggs 1985; Daley *et al.* 2009).

*A. benmoulai* reveals an additional dorsal set of flaps to which setal blades, which probably functioned as gills, are attached (equivalent to the exite or outer branch of the Cambrian biramous limb: Wolff & Scholtz 2008). Although the flaps of the anomalocaridid trunk are very different from modern arthropod limbs, even inserting at different places on the body wall rather than branching from the same limb base, it is clear that they are equivalent to the two branches typical of living aquatic arthropods. *A. benmoulai* shows a stage prior to fusion of the limb branches to form the biramous limb (Van Roy *et al.* 2015).

The ecology of *Aegirocassis benmoulai* is equally remarkable. The animal, which is preserved near complete in three dimensions in giant concretions and reached a size in excess of 2 m, has the paired anterior appendages characteristic of anomalocaridids. Unlike the head limbs of the great majority of anomalocaridids, however, which are clearly for grasping large animals, those of *A. benmoulai* are equipped for filter feeding on small prey in the plankton (Van Roy *et al.* 2015). The only other anomalocaridid known to be similarly equipped is *Tamisiocaris borealis* from the lower Cambrian Sirius Passet locality of Greenland (Vinther *et al.* 2014) but to date it is known only from its anterior appendages. The filter-feeding appendage of *Aegirocassis* is considerably more complex and sophisticated than that of *Tamisiocaris* and may herald a shift in the Early Ordovician to large-scale filter feeding in the oceans, associated with a massive plankton radiation at the start of the Great Ordovician Biodiversification Event (GOBE) (Servais *et al.* 2010). *Aegirocassis benmoulai* foreshadows the much later appearance of giant filter-feeding bony fishes, sharks and whales (Friedman *et al.* 2010; Marx & Uhen 2010), and provides an early example of the origin of massive filter-feeders within a macro-predatory clade at a time of large-scale diversification in the plankton.

### Faunal composition and ecology

In addition to lobopodians, marrellomorphs and anomalocaridids (Fig. 3), the Fezouata biota includes a wide range of other exceptionally preserved typical 'Cambrian' taxa such as great appendage arthropods like *Leanchoilia*, other arthropods and halwaxiid molluscs (Van Roy *et al.* 2010; Box 2; Table 1). As well as machaeridian annelids and horseshoe crabs (Fig. 4b and c), examples of exceptionally preserved typical post-Cambrian taxa include the oldest cheloniellid arthropod (Fig. 4a) and probable lepadomorph barnacles (Van Roy *et al.* 2010; Box 2; Table 1).

Co-occurring with the non-biomineralized taxa is a typical diverse Ordovician shelly fauna (Box 2; Table 1). The shelly fossils include a diversity of sponges, predominantly demosponges of Cambrian aspect (Botting 2007; Van Roy *et al.* 2010), trilobites (asaphids, harpetids, lichids, odontopleurids, phacopids, corynexochids, ptychopariids and agnostids; e.g. Fortey 2009, 2011, 2012; Corbacho & Vela 2010, 2011; Van Roy *et al.* 2010; Corbacho & López-Soriano 2012), echinoderms (stylophorans, asterozoans, blastozoans, edrioasteroids and some of the earliest crinoids: Lefebvre & Fatka 2003; Lefebvre & Botting 2007; Van Roy *et al.* 2010; Sumrall & Zamora 2011); and molluscs (hyolithoids, helcionelloids, rostroconchs, bivalves, gastropods and cephalopods: Van Roy *et al.* 2010; Kröger & Lefebvre 2012), conulariids and *Sphenothallus*, nonarticulate and articulate brachiopods, and occasional bryozoans. Both benthic and planktic graptolites are also present (Van Roy *et al.* 2010). Several of the trilobite taxa show preserved appendages and digestive structures, and preserved soft tissues may be present in some brachiopods, a tuboid graptolite and potentially also in hyoliths and conulariids. The shelly fauna is typical of a normal, open-marine Early Ordovician biota, and it would be unremarkable were it not for the high degree of articulation of fragile multi-element skeletons, and the preservation of soft tissues in some taxa.

The composition of different assemblages within the Fezouata biota has yet to be analysed in detail (Box 3) but it is clear that there

is variability, no doubt partly ecological, but perhaps to a degree reflecting stratigraphic level. In the 25 m thick interval with exceptional preservation that falls in the *Araneograptus murrayi* biozone, the same taxa occur at different sites, but their relative abundance often shows wide variation. These sites presumably represent different communities occupying different parts of the sea floor. Exposures in the *Hunnegraptus copiosus* zone, the higher interval with exceptional preservation, are much rarer. Differences between these assemblages and those in the older horizon may reflect evolutionary change. The recent description of a new Burgess Shale locality from Marble Canyon (Caron *et al.* 2014), some 40 km distant and stratigraphically younger than Walcott's original mid Cambrian locality, provides an illuminating parallel to the Fezouata discoveries. Marble Canyon has yielded spectacularly preserved taxa such as the primitive fish *Metaspriggina* (Conway Morris & Caron 2014), a large proportion of which are not represented in the original Walcott Quarry including some otherwise only known from the early Cambrian. By sampling a new part of the sea floor this new discovery emphasizes the variability of marine assemblages on and in different parts of the Cambrian sea bed. The Marble Canyon assemblage, however, is less than 1 Ma younger than other Burgess Shale localities in the region (it extends Burgess Shale occurrences from the *Bathyriscus–Elrathina* biozone to the *Ehmaniella* trilobite biozone within Cambrian Stage 5). As such it highlights the significance of the Fezouata deposits, which are 25 Ma younger and crop out over a huge area, providing the potential to investigate the different marine communities that populated the Ordovician sea floor (Box 3).

### Box 3: Outstanding questions

- (1) Which dynamics govern the differences in faunal composition between sites in the Fezouata biota?
- (2) How do the Fezouata faunas change over time?
- (3) How were the Fezouata communities structured?
- (4) What ecological changes occur over the Cambro-Ordovician interval, as documented by the Fezouata and earlier biotas?
- (5) Are the Cambrian Explosion and the Great Ordovician Biodiversification Event separate episodes, or are they phases within the same large-scale diversity dynamic?
- (6) What are the specific taphonomic pathways leading to the preservation of the Fezouata communities?
- (7) How does this taphonomic understanding influence our appreciation of the observed community structure?

### Taphonomy

The Fezouata formations are remarkable in that exceptional preservation occurs in two distinct modes. Although most of the soft-bodied fossil assemblages are preserved as 2D Burgess Shale-type compressions in mudstones, as described above, some of the larger Fezouata fossils, including anomalocaridids and some trilobites, are preserved three-dimensionally in concretions (Fig. 3a). Some of those containing anomalocaridids exceed 1 m in maximum length, and concretions containing trilobite clusters may exceed 2 m. The 3D preservation of soft-bodied animals indicates that vigorous decay (including the activity of sulphate reducers) set up strong geochemical gradients leading to rapid precipitation of a silica–chlorite–calcite mineral matrix around the carcasses. Although many other instances of soft-bodied preservation are known from concretions, the mineralogical composition of the Fezouata concretions is apparently unique, and is best explained by contributions from the dissolution of volcanic ash in the sediments (Gaines *et al.* 2012a). Volcanic ash is present regionally in the Fezouata formations (Destombes *et al.* 1985; Piqué & Michard 1989), but has not been documented where concretions occur.

Most Fezouata localities preserve diverse assemblages that include both *in situ* and locally transported animals. A few small, localized lenses are almost monospecific and show clear evidence of transport, presumably representing groups of gregarious animals caught up in mud flows. Understanding the processes that led to particular accumulations will be important to a more detailed understanding of the community ecology of the Fezouata assemblages, a topic scheduled for future study (Box 3).

### A note on nomenclature

When the giant filter-feeding anomalocaridid from the Fezouata biota was formally described (Van Roy *et al.* 2015), it was named *Aegirocassis benmoulae*, using the female genitive ending *-ae* for the specific name. This was done erroneously because the surname on which the specific name is based, Ben Moula, ends in an *-a*. It has been pointed out to us that the male genitive ending *-i* should have been used, as the taxon is named after Mr Mohamed Ben Moula (ICZN article 31.1.2; International Commission on Zoological Nomenclature 1999). Therefore, the name of this taxon is here formally corrected to *Aegirocassis benmoulai*.

### Conclusion

The term, Great Ordovician Biodiversification Event, is used to characterize the steep increase in diversity during the Ordovician and to distinguish it from the Cambrian Explosion. Whereas the Cambrian Explosion established the major body plans (the phyla), the GOBE witnessed diversification at lower levels in the taxonomic hierarchy. The classic papers of Sepkoski (1979, 1984) reflect this shift, and the change in the dominant shelly taxa, by defining a Cambrian Evolutionary Fauna versus a Palaeozoic Evolutionary Fauna. The concept of ‘evolutionary faunas’ was based on shelly taxa, and although these taxa in Sepkoski’s ‘evolutionary faunas’ are typical of the intervals of time in question, elements of the Cambrian fauna range into the later Palaeozoic. The evidence of the soft-bodied taxa in the Fezouata Formation emphasizes this, and shows that the turnover between the Cambrian and post-Cambrian faunas was a much more protracted affair than previously thought. At the same time, the presence of particularly advanced forms in the fauna suggests that considerable diversification had already taken place by the late Tremadocian. This shows that, at least among non-biomineralized taxa, the GOBE took off much earlier than generally assumed. The Fezouata discoveries reveal the complexity of a prolonged event like the GOBE, which unfolded over at least 25 Ma and shows considerable taxonomic and geographical variation (Webby *et al.* 2004; Harper 2006). The evidence of the fossils supports the view that the Cambrian Explosion and the GOBE, rather than two separate events, are subsequent phases within the same large-scale diversity dynamic (Droser & Finnegan 2003; Van Roy *et al.* 2010) (Box 3). The Fezouata biota underscores the unparalleled importance of exceptionally preserved faunas to our understanding of major evolutionary and ecological turnovers in deep time.

### Acknowledgements and Funding

M. Ben Moula, L. Ben Moula and B. Tahiri provided field support and practical assistance. S. Butts and J. Utrup facilitated access to the collections at the Yale Peabody Museum, and G. Fleury provided access to the material of the Natural History Museum of Toulouse. D. Hunt and D. Harper pointed out the nomenclatorial error, and the required correction to *A. benmoulai*. Over the years, S. Beardmore, J. and L. Botting-Muir, W. and D. De Winter, D. Field, A. Little, B. McGabhann, P. Orr, R. Racicot, R. and V. Reboul-Baron, O. E. Tetlie, C. Upton, B. Van Bocxlaer, D. and K. Van Damme, T. Vandenbroucke and J. Vinther assisted with field work, and P. Bommel, D. Broussy, P. Cato, F. Escuillié and L. Lacombe provided access to specimens in their collections. D. Vandeveld, P. and O. Van Roy-Lassaut and M. Wagenaar provided financial support. The research was supported by NSF Grant EAR-1053247 and by the Division of Invertebrate Paleontology, Yale Peabody Museum of Natural History. We are grateful for the collaboration of our colleagues involved in the Agence Nationale de la Recherche research project entitled ‘The Rise of Animal

Life (Cambrian–Ordovician): organization and tempo’ (RALI 197) led by J. Vannier, B. Lefebvre and T. Servais. G. Edgecombe and an anonymous reviewer commented on the submitted paper. D.E.G.B.’s contribution was written while he was a sabbatical visitor at Stanford University.

*Scientific editing by Philip Donoghue*

### References

- Aldridge, R.J., Theron, J.N. & Gabbott, S.E. 1994. The Soom Shale: A unique Ordovician fossil horizon in South Africa. *Geology Today*, **10**, 218–221.
- Aldridge, R.J., Gabbott, S.E. & Theron, J.N. 2001. The Soom Shale. In: Briggs, D.E.G. & Crowther, P.R. (eds) *Palaeobiology II*. Blackwell Science, Oxford, 340–342.
- Allison, P.A. & Briggs, D.E.G. 1993. Exceptional fossil record: Distribution of soft-tissue preservation through the Phanerozoic. *Geology*, **21**, 527–530.
- Aris, M.J. & Palomo, M. 2014. Primer registro de una fauna Ordovícica ‘tipo Burgess Shale’ en Argentina y Sudamérica. *XIX Congreso Geológico Argentino, Córdoba*. Junio 2014, Asociación Geológica Argentina, Buenos Aires, Abstracts, S2–S4.
- Bartels, C., Briggs, D.E.G. & Brassel, G. 1998. *Fossils of the Hunsrück Slate—Marine Life in the Devonian*. Cambridge University Press, New York.
- Botting, J.P. 2007. ‘Cambrian’ demosponges in the Ordovician of Morocco: Insights into the early evolutionary history of sponges. *Geobios*, **40**, 737–748.
- Botting, J.P., Muir, L.A., Sutton, M.D. & Barnie, T. 2011. Welsh gold: A new exceptionally preserved pyritized Ordovician biota. *Geology*, **39**, 879–882.
- Botting, J.P., Muir, L.A., Jordan, N. & Upton, C. 2015. An Ordovician variation on Burgess Shale-type biotas. *Scientific Reports*, **5**, 9947, <http://dx.doi.org/10.1038/srep09947>.
- Brett, C.E., Whiteley, T.E., Allison, P.A. & Yochelson, E.L. 1999. The Walcott–Rust quarry: Middle Ordovician trilobite Konservat-Lagerstätten. *Journal of Paleontology*, **73**, 288–305.
- Briggs, D.E.G. 1981. The arthropod *Odaraia alata* Walcott, Middle Cambrian, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, Series B*, **291**, 541–584.
- Briggs, D.E.G., Clarkson, E.N.K. & Aldridge, R.J. 1983. The conodont animal. *Lethaia*, **16**, 1–14.
- Briggs, D.E.G., Bottrell, S.H. & Raiswell, R. 1991. Pyritization of soft-bodied fossils: Beecher’s Trilobite Bed, Upper Ordovician, New York State. *Geology*, **19**, 1221–1224.
- Briggs, D.E.G., Siveter, D.J. & Siveter, D.J. 1996. Soft-bodied fossils from a Silurian volcanoclastic deposit. *Nature*, **382**, 248–250.
- Briggs, D.E.G., Siveter, D.J., Siveter, D.J. & Sutton, M.D. 2008. Virtual fossils from 425 million-year-old volcanic ash. *American Scientist*, **96**, 474–481.
- Budd, G.E. 1996. The morphology of *Opabinia regalis* and the reconstruction of the arthropod stem-group. *Lethaia*, **29**, 1–14.
- Butterfield, N.J. 1995. Secular distribution of Burgess Shale-type preservation. *Lethaia*, **28**, 1–13.
- Butterfield, N.J. 2002. *Leaenchoilia* guts and the interpretation of three dimensional structures in Burgess Shale-type fossils. *Paleobiology*, **28**, 154–170.
- Butterfield, N.J. 2003. Exceptional fossil preservation and the Cambrian explosion. *Integrative and Comparative Biology*, **43**, 166–177.
- Caron, J.-B., Gaines, R.R., Aria, C., Gabriela Mángano, M. & Streng, M. 2014. A new phyllopod bed-like assemblage from the Burgess Shale of the Canadian Rockies. *Nature Communications*, **5**, 1–6.
- Chauvel, J. 1966. Echinodermes de l’Ordovicien du Maroc. *Cahiers de Paléontologie*. CNRS, Paris.
- Chauvel, J. 1978. Compléments sur les échinodermes du Paléozoïque marocain (diploporites, éocrinoides, édréoastéroïdes). *Notes du Service Géologique du Maroc*, **39**, 27–78.
- Chlupáč, I. 1999a. Some problematical arthropods from the Upper Ordovician Letná Formation of Bohemia. *Journal of the Czech Geological Society*, **44**, 79–92.
- Chlupáč, I. 1999b. Unusual arthropods from the Bohemian Ordovician—A review. *Acta Universitatis Carolinae—Geologica*, **43**, 393–396.
- Choubert, G., Hindermeier, J. & Hupé, P. 1955. Découverte du Trémadoc dans l’Anti-Atlas (Maroc). *Comptes Rendus de l’Académie des Sciences*, **241**, 1592.
- Cocks, L.R.M. & Torsvik, T.H. 2006. Major terranes in the Ordovician. In: Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 61–67.
- Cong, P., Ma, X., Hou, X.-G., Edgecombe, G.D. & Strausfeld, N.J. 2014. Brain structure resolves the segmental affinity of anomalocaridid appendages. *Nature*, **513**, 538–542.
- Conway Morris, S. 1989. The persistence of Burgess Shale-type faunas: Implications for the evolution of deeper-water faunas. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **80**, 271–283.
- Conway Morris, S. & Caron, J.-B. 2014. A primitive fish from the Cambrian of North America. *Nature*, **512**, 419–422.
- Corbacho, J. & López-Soriano, F.J. 2012. A new asaphid trilobite from the Lower Ordovician (Arenig) of Morocco. *Batalleria*, **17**, 2–10.
- Corbacho, J. & Vela, J.A. 2010. Giant trilobites from Lower Ordovician of Morocco. *Batalleria*, **15**, 3–32.
- Corbacho, J. & Vela, J.A. 2011. Revisión de las especies de *Lehua* de la región de Zagora, Marruecos. *Batalleria*, **16**, 46–49.



## The Fezouata fossils of Morocco

- Daley, A.C., Budd, G.E., Caron, J.-B., Edgecombe, G.D. & Collins, D. 2009. The Burgess Shale anomalocaridid *Hurdia* and its significance for early euarthropod evolution. *Science*, **323**, 1597–1600.
- Destombes, J. 1962. Stratigraphie et paléogéographie de l'Ordovicien de l'Anti-Atlas (Maroc). Un essai de synthèse. *Bulletin de la Société Géologique de France*, **7**, 453–460.
- Destombes, J. 1972. Les trilobites du sous-ordre des Phacopina de l'Ordovicien de l'Anti-Atlas (Maroc). *Notes et Mémoires du Service Géologique de Maroc*, **240**, 1–113.
- Destombes, J. & Willefert, S. 1959. Sur la présence de *Dictyonema* dans le Trémadoc de l'Anti-Atlas (Maroc). *Comptes Rendus de l'Académie des Sciences*, **249**, 1246.
- Destombes, J., Hollard, H. & Willefert, S. 1985. Lower Paleozoic rocks of Morocco. In: Hollard, C.H. (ed.) *Lower Paleozoic of North-Western and West-Central Africa*. Wiley, New York, 91–336.
- Dorjes, J. 1972. Distribution and zonation of macrobenthic animals. *Senckenbergiana Maritima*, **4**, 183–216.
- Driscoll, E.G. & Swanson, R.A. 1973. Diversity and structure of epifaunal communities on mollusk valves, Buzzard Bay, Massachusetts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **14**, 229–247.
- Droser, M.L. & Finnegan, S. 2003. The Ordovician radiation: A follow-up to the Cambrian explosion? *Integrative and Comparative Biology*, **43**, 178–184.
- Dunlop, J.A., Anderson, L.I. & Braddy, S.J. 2004. A redescription of *Chasmataspis laurencii* Caster & Brooks, 1956 (Chelicerata: Chasmataspidida) from the Middle Ordovician of Tennessee, USA, with remarks on chasmataspid phylogeny. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **94**, 207–225.
- Farrell, Ú.C., Martin, M.J., Hagadorn, J.W., Whiteley, T. & Briggs, D.E.G. 2009. Beyond Beecher's Trilobite Bed: Widespread pyritization of soft-tissues in the Late Ordovician Taconic Foreland Basin. *Geology*, **37**, 907–910.
- Fortey, R.A. 2009. A new giant asaphid trilobite from the Lower Ordovician of Morocco. *Memoirs of the Association of Australasian Palaeontologists*, **37**, 9–16.
- Fortey, R.A. 2011. Trilobites of the genus *Dikelocephalina* from Ordovician Gondwana and Avalonia. *Geological Journal*, **46**, 405–415.
- Fortey, R.A. 2012. The first known complete lichakephalid trilobite, Lower Ordovician of Morocco. *Memoirs of the Association of Australasian Palaeontologists*, **42**, 1–7.
- Friedman, M., Shimada, K., Martin, D.L., Everhart, M.J., Liston, J., Maltese, A. & Triebold, M. 2010. 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. *Science*, **327**, 990–993.
- Fritsch, A. 1908a. Problematica Silurica. In: Barrande, J. (ed.) *Système Silurien du centre de la Bohême*. Bellman, Prague, 1–28.
- Fritsch, A. 1908b. Über eine Echinodermenlarve aus dem Untersilur Böhmens. *Zoologische Anzeiger*, **33**, 797–798.
- Gabbott, S.E., Hou, X.G., Norry, M.J. & Siveter, D.J. 2004. Preservation of Early Cambrian animals of the Chengjiang biota. *Geology*, **32**, 901–904.
- Gaines, R.R., Briggs, D.E.G. & Zhao, Y.-L. 2008. Cambrian Burgess Shale-type deposits share a common mode of fossilization. *Geology*, **36**, 755–758.
- Gaines, R.R., Briggs, D.E.G., Orr, P.J. & Van Roy, P. 2012a. Preservation of giant anomalocaridids in silica-chlorite concretions from the early Ordovician of Morocco. *Palaio*, **27**, 317–325.
- Gaines, R.R., Droser, M.L., Orr, P.J., Garson, D., Hammarlund, E.U., Qi, C.-S. & Canfield, D.E. 2012b. Burgess Shale-type biotas were not entirely burrowed away. *Geology*, **40**, 283–286.
- Gaines, R.R., Hammarlund, E.U. et al. 2012c. Mechanism for Burgess Shale-type preservation. *Proceedings of the National Academy of Sciences of the USA*, **109**, 5180–5184.
- Harper, D.A.T. 2006. The Ordovician biodiversification: Setting an agenda for marine life. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **232**, 148–166.
- Havlíček, V. 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Mémoires du Service Géologique du Maroc*, **230**, 1–135.
- Hou, X.-G., Aldridge, R.J., Bergström, J., Siveter, D.J., Siveter, D.J. & Feng, X.-H. 2004. *The Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life*. Blackwell Science, Oxford.
- International Commission on Zoological Nomenclature. 1999. *International Code of Zoological Nomenclature*, 4th edn. International Trust for Zoological Nomenclature, London.
- Kröger, B. & Lefebvre, B. 2012. Palaeogeography and palaeoecology of early Floian (Early Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco. *Fossil Record*, **15**, 61–75.
- Kühl, G. & Rust, J. 2010. Re-investigation of *Mimetaster hexagonalis*: A marrellomorph arthropod from the Lower Devonian Hunsrück Slate (Germany). *Paläontologische Zeitschrift*, **84**, 397–411.
- Kühl, G., Briggs, D.E.G. & Rust, J. 2009. A great appendage arthropod with a radial mouth from the Lower Devonian Hunsrück Slate, Germany. *Science*, **323**, 771–773.
- Lamsdell, J.C., Hoşgör, İ. & Selden, P.A. 2013. A new Ordovician eurypterid (Arthropoda: Chelicerata) from southeast Turkey: Evidence for a cryptic Ordovician record of Eurypterida. *Gondwana Research*, **23**, 354–366.
- Lefebvre, B. & Botting, J.P. 2007. First report of the mitrate *Peltocystis cornuta* Thoral (Echinodermata, Stylophora) in the Lower Ordovician of central Anti-Atlas (Morocco). *Annales de Paléontologie*, **93**, 183–198.
- Lefebvre, B. & Fatka, O. 2003. Palaeogeographical and palaeoecological aspects of the Cambro-Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **195**, 73–97.
- Legg, D.A. & Hearing, T.W. 2015. A late surviving xenopod (Arthropoda) from the Ordovician Period, Wales. *Geological Magazine*, <http://dx.doi.org/10.1017/S001675681400065X>.
- Lerosey-Aubril, R., Hegna, T.A., Babcock, L., Bonino, E. & Kier, C. 2014. Arthropod appendages from the Weeks Formation Konservat-Lagerstätte: New occurrences of anomalocaridids in the Cambrian of Utah, USA. *Bulletin of Geosciences*, **89**, 269–282.
- Liu, H., McKay, R.M., Young, J.N., Witzke, B.J., McVey, K.J. & Liu, X. 2006. A new Lagerstätte from the Middle Ordovician St. Peter Formation in north-east Iowa, USA. *Geology*, **34**, 969–972.
- Martin, E.L.O., Pittet, B. et al. 2015. The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: Age, environment and evolutionary perspectives. *Gondwana Research*. First published online 5 May 2015, <http://doi.org/10.1016/j.gr.2015.03.009>.
- Marx, F.G. & Uhen, M.D. 2010. Climate, critters, and cetaceans: Cenozoic drivers of the evolution of modern whales. *Science*, **327**, 993–996.
- Ortega-Hernández, J. 2015. Making sense of 'lower' and 'upper' stem-group Euarthropoda, with comments on the strict use of the name Arthropoda von Siebold, 1848. *Biological Reviews*. <http://dx.doi.org/10.1111/brv.12168>.
- Perner, J. 1919. *Furca bohémica*—zástupce nové čeledi koryšů v českém siluru. *Časopis Musea Království českého*, **93**, 32–33.
- Piqué, A. & Michard, M. 1989. The Moroccan hercynides: A synopsis. The Paleozoic sedimentary and tectonic evolution at the northern margin of West Africa. *American Journal of Science*, **289**, 286–330.
- Rak, Š., Ortega-Hernandez, J. & Legg, D.A. 2012. A revision of the Late Ordovician marrellomorph arthropod *Furca bohémica* from Czech Republic. *Acta Palaeontologica Polonica*, **58**, 615–628.
- Saltzman, M.R., Ripperdan, R.L. et al. 2000. A global carbon isotope excursion (SPICE) during the Late Cambrian: Relation to trilobite extinctions, organic-matter burial and sea level. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **163**, 211–223.
- Sepkoski, J.J. 1979. A kinetic model of Phanerozoic taxonomic diversity II. Early Phanerozoic families and multiple equilibria. *Paleobiology*, **5**, 222–251.
- Sepkoski, J.J. 1984. A kinetic model of Phanerozoic taxonomic diversity III. Post-Paleozoic families and mass extinctions. *Paleobiology*, **10**, 246–267.
- Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B. & Munnecke, A. 2010. The Great Ordovician Biodiversification Event (GOBE): The palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **294**, 99–119.
- Smith, M.R. & Ortega-Hernández, J. 2014. *Hallucigenia*'s onychophoran-like claws and the case for Tactopoda. *Nature*, **514**, 363–366.
- Stürmer, W. & Bergström, J. 1976. The arthropods *Mimetaster* and *Vachonisia* from the Devonian Hunsrück Shale. *Paläontologische Zeitschrift*, **50**, 78–111.
- Sumrall, C.D. & Zamora, S. 2011. Ordovician edrioasteroids from Morocco: Faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology*, **9**, 425–454.
- Vandenbroucke, T.R.A., Gabbott, S.E., Paris, F., Aldridge, R.J. & Theron, J.N. 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. *Journal of Micropalaeontology*, **28**, 53–66.
- Van Roy, P. 2006. *Non-trilobite arthropods from the Ordovician of Morocco*. PhD dissertation, Ghent University.
- Van Roy, P. & Briggs, D.E.G. 2011. A giant Ordovician anomalocaridid. *Nature*, **473**, 510–513.
- Van Roy, P. & Tetlie, O.E. 2006. A spinose appendage fragment of a problematic arthropod from the Early Ordovician of Morocco. *Acta Palaeontologica Polonica*, **51**, 239–246.
- Van Roy, P., Orr, P.J. et al. 2010. Ordovician faunas of Burgess Shale type. *Nature*, **465**, 215–218.
- Van Roy, P., Daley, A.C. & Briggs, D.E.G. 2014. Anomalocaridid diversity in the Early Ordovician Fezouata Biota of southeastern Morocco. In: *4th International Palaeontological Congress, Mendoza, Argentina, 2014. The History of Life: A View from the Southern Hemisphere*, International Palaeontological Association, and CONICET, Mendoza, Abstracts Volume, 398.
- Van Roy, P., Daley, A.C. & Briggs, D.E.G. 2015. Anomalocaridid trunk limb homology revealed by a giant Ordovician filter-feeder with paired lateral flaps. *Nature*, **522**, 77–80. <http://dx.doi.org/10.1038/nature14256>.
- Vinther, J., Van Roy, P. & Briggs, D.E.G. 2008. Machaeridians are Palaeozoic armoured annelids. *Nature*, **451**, 185–188.
- Vinther, J., Stein, M., Longrich, N.R. & Harper, D.A.T. 2014. A suspension-feeding anomalocarid from the Early Cambrian. *Nature*, **507**, 496–499.
- Webby, B.D., Paris, F., Droser, M.L., & Percival, I.G. (eds) 2004. *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.
- Whittington, H.B. 1993. Anatomy of the Ordovician trilobite *Placoparia*. *Philosophical Transactions of the Royal Society of London, Series B*, **339**, 109–118.
- Whittington, H.B. & Briggs, D.E.G. 1985. The largest Cambrian animal, *Anomalocaris*, Burgess Shale, British Columbia. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 569–609.
- Wolff, C. & Scholtz, G. 2008. The clonal composition of biramous and uniramous arthropod limbs. *Proceedings of the Royal Society of London, Series B*, **275**, 1023–1028.
- Young, G.A., Rudkin, D.M., Dobrzanski, E.P., Robson, S.P. & Nowlan, G.S. 2007. Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology*, **35**, 883–886.
- Zhang, X.-L. & Briggs, D.E.G. 2007. The nature and significance of the appendages of *Opabinia* from the Middle Cambrian Burgess Shale. *Lethaia*, **40**, 161–173.