

# Ordovician faunas of Burgess Shale type

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**The renowned soft-bodied faunas of the Cambrian period, which include the Burgess Shale, disappear from the fossil record in the late Middle Cambrian, after which the Palaeozoic fauna<sup>1</sup> dominates. The disappearance of faunas of Burgess Shale type curtails the stratigraphic record of a number of iconic Cambrian taxa. One possible explanation for this loss is a major extinction<sup>2,3</sup>, but more probably it reflects the absence of preservation of similar soft-bodied faunas in later periods<sup>4</sup>. Here we report the discovery of numerous diverse soft-bodied assemblages in the Lower and Upper Fezouata Formations (Lower Ordovician) of Morocco, which include a range of remarkable stem-group morphologies normally considered characteristic of the Cambrian. It is clear that biotas of Burgess Shale type persisted after the Cambrian and are preserved where suitable facies occur. The Fezouata biota provides a link between the Burgess Shale communities and the early stages of the Great Ordovician Biodiversification Event.**

The large number of Burgess Shale-type occurrences in the Cambrian<sup>2</sup> provide a remarkable record of the results of the initial radiation of metazoan marine life. In contrast, exceptional preservation is rare in Ordovician strata: the few previously reported examples<sup>5–8</sup> are low diversity assemblages from environmentally restricted settings and do not represent a normal, open marine ecosystem. Consequently our understanding of the Great Ordovician Biodiversification Event, which is one of the most dramatic episodes in the history of marine life<sup>9–12</sup>, is based almost exclusively on the shelly fossil record.

During this event, most marine higher taxa diversified at a faster rate than at any other time in the Phanerozoic. Biodiversity increased twofold at the ordinal level, about three times at the family level, and nearly four times at the level of genus<sup>9–11</sup>. This major radiation resulted in the replacement of the Cambrian Evolutionary Fauna by the Palaeozoic Evolutionary Fauna that dominated the marine realm until the end-Permian mass extinction<sup>1</sup>. It was accompanied by a major increase in ecological complexity<sup>12</sup>. Until now, however, no exceptionally preserved biotas recording the critical early stages of the Ordovician radiation were known. Beecher's Trilobite Bed<sup>5</sup> of New York, and the Soom Shale of South Africa<sup>6</sup>, are late Ordovician (Sandbian and latest Hirnantian to earliest Rhuddanian<sup>13</sup>, respectively) in age. The former represents a low-oxygen environment with a low diversity fauna including the olenid trilobite *Triarthrus eatoni*<sup>5</sup>, and the latter is dominated by nektonic organisms and probably accumulated in an euxinic environment. Other examples from the Middle and Upper Ordovician<sup>7,8</sup> are low diversity assemblages from near-shore marginal environments.

A complex of recently discovered exceptionally preserved faunal assemblages occurs in muddy bottom open marine settings in the Lower Ordovician of southeastern Morocco. These assemblages record

considerable diversity, including a number of taxa characteristic of Early to Middle Cambrian Burgess Shale-type faunas, previously thought to have become extinct during the Cambrian, which occur here in association with elements typical of later biotas. About 1,500 soft-bodied fossil specimens representing at least 50 different taxa have been collected to date from approximately 40 excavations spread out over an area of about 500 km<sup>2</sup> in the Draa Valley, north of Zagora in southeastern Morocco (Supplementary Fig. 1). All these localities fall in the Lower Fezouata Formation (Tremadocian) or the conformably overlying Upper Fezouata Formation (Floian) which reach a combined thickness of 1,100 m (ref. 14) in the area north of Zagora. The largely transgressive sequence crops out over a wide area in the Anti-Atlas and consists mainly of mudstone and siltstone. Although sediments become coarser near the top of the sequence, implying slightly shallower and more energetic conditions, our observations indicate that the depositional setting for all localities is a deeper-water, low-energy environment. Although generally below storm wave base, the infrequent occurrence of thin, laterally discontinuous hummocky cross-stratified sandstones and shell pavements shows that occasional heavy storms influenced deposition in the area. The majority of fossiliferous horizons represent sediment mobilized by storms or other events that was re-deposited rapidly, entombing locally transported and *in situ* elements within and below event beds.

Horizons of exceptional preservation range from the top of the Lower Fezouata Formation through to the top of the Upper Fezouata Formation. The fossils are distributed in distinct lenses or as more laterally continuous horizons. The strata containing exceptionally preserved specimens vary from greenish silty mudstones to sandy siltstones rich in detrital mica. Bioturbation associated with the soft-bodied fossils is dominated by low diversity, small diameter (1–3 mm) burrows parallel or inclined to bedding. Although high sedimentation rates may have limited the infauna, the low diversity and consistently small diameter of burrows suggest that low-oxygen conditions may have prevailed. The simplicity, small size and occurrence of the burrows is reminiscent of bioturbation reported from the exceptionally preserved Cambrian faunas of Sirius Passet, Chengjiang and Kaili<sup>15</sup>.

The exceptionally preserved fossils are usually flattened. Various worms, presumed to be annelids, however, are preserved with some three-dimensionality. Most non-biomineralized arthropods and some of the trilobites preserve evidence of their appendages. Preserved soft tissues are typically bright reddish-brown to yellow in colour, resulting from the oxidation of pyrite that precipitated on the surface<sup>16</sup>. Framboidal and polyhedral pyrite morphologies, now iron oxide pseudomorphs, vary consistently between different tissues, the form of pyrite probably reflecting the decay-susceptibility of the original material<sup>17</sup>. The preservation, and consequently appearance, of

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the fossils is remarkably similar to that of the Early Cambrian Chengjiang fauna from China<sup>17</sup>, reflecting similar sedimentation and diagenetic pathways.

The Fezouata assemblages are dominated by benthic organisms. There is pronounced spatial and stratigraphic variation in taxonomic composition and relative abundance, suggesting ecological variation

and/or evolutionary change between assemblages at different stratigraphic levels. The shelly fossils include conulariids, a diversity of trilobites (asaphids, harpetids, odontopleurids, phacopids, proetids, ptychopariids and agnostids), articulated hyolithoids and other molluscs (helcionelloids, bivalves, gastropods, nautiloids), brachiopods, occasional bryozoans, and echinoderms (homalozoans, asterozoans,



**Figure 1 | Exceptionally preserved Burgess Shale-type organisms from the Early Ordovician Fezouata biota.** **a**, Demosponge *Pirania auraeum*<sup>19</sup>, top of Lower Fezouata Formation (CAMSM X 50156.1a). **b**, Choiid demosponge, top of Lower Fezouata Formation (YPM 226567). **c**, Annelid worm, top of Lower Fezouata Formation (YPM 226538). **d**, Organism showing possible similarities to halkieriids, Upper Fezouata Formation (YPM 227515). **e**, Possible armoured lobopod, Upper Fezouata Formation (YPM 227516).

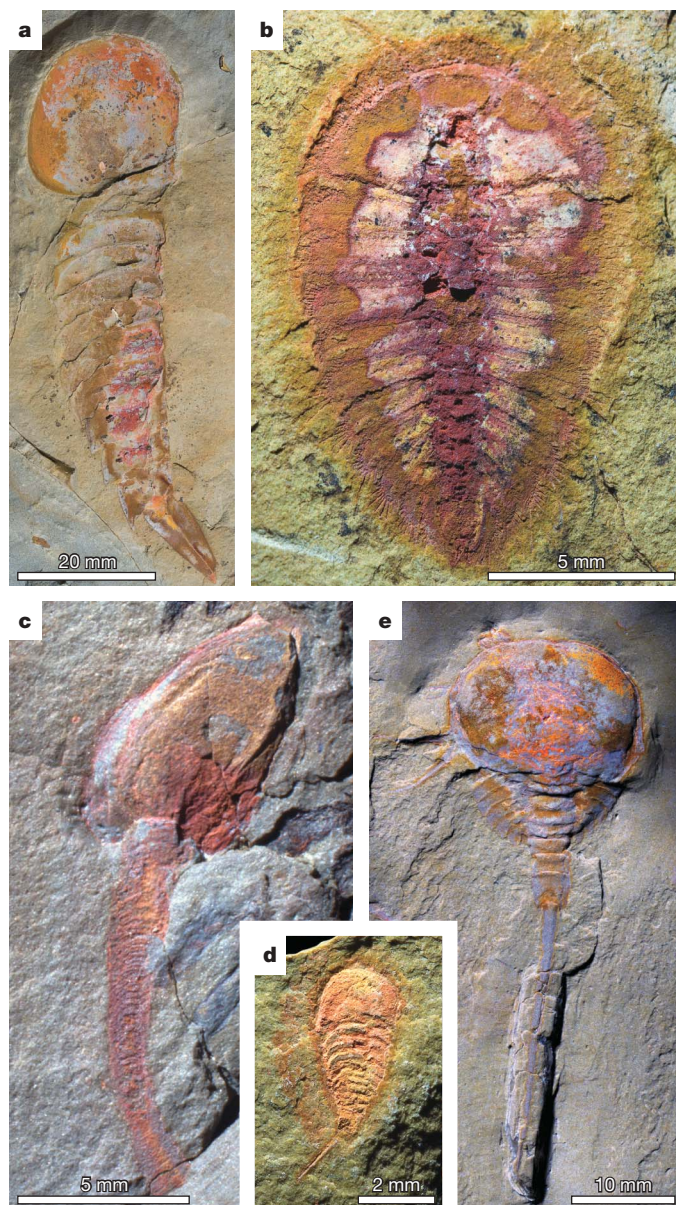
**f**, *Thelxiopelike* arthropod, Upper Fezouata Formation (YPM 226544). **g**, Marrellomorph arthropod, probably belonging to the genus *Furca*, Upper Fezouata Formation (MHNT.PAL.2007.39.80.1). **h**, Skaniid arthropod, Upper Fezouata Formation (YPM 226539). **i**, Spinose arthropod appendage apparatus consisting of six overlapping elements, top of Lower Fezouata Formation (YPM 226559).

various eocrinoids, cystoids, rare crinoids); planktic and benthic graptolites are also present (Supplementary Fig. 2). Most of these elements are typical of normal open-marine shelly Ordovician faunas, with many taxa representative of the Palaeozoic Evolutionary Fauna<sup>1</sup>; they are exceptional only in the high degree of articulation of multi-element skeletons in trilobites and echinoderms. In contrast to Chengjiang<sup>18</sup>, a diverse echinoderm fauna is present, indicating normal salinities. The consistently high faunal diversity and comparable sedimentology indicate that the environmental setting, which was not subject to large variations in temperature or salinity, was similar at all Moroccan sites.

The shelly taxa are supplemented by at least 50 non-biomineralized taxa, which dominate the biota, representing at least two-thirds of all specimens collected. Many of these non-biomineralized forms are recorded from the Ordovician for the first time. A striking feature is the high number of organisms archetypal of Cambrian Burgess Shale-type faunas, including various demosponges (*Pirania*, *Hamptonia*, *Choiia*<sup>19</sup>, wapkiiids, and other undescribed forms; Fig. 1a, b), annelid worms (Fig. 1c, Supplementary Fig. 3a–c), an organism with possible similarities to halkieriids (Fig. 1d, Supplementary Fig. 3d, e), palaeoscoleoids, possible armoured lobe-pods and other stem arthropods (Fig. 1e, Supplementary Fig. 3f), a *Thelxiope*-like arthropod (Fig. 1f), marrellomorphs (Fig. 1g), skaniids (Fig. 1h), a naraoiid, and arthropods of uncertain affinity (Fig. 1i). The Burgess Shale-type organisms co-occur with several taxa characteristic of later biotas, such as machaeridians<sup>16</sup>, other worms including tube-dwelling forms, *Tremaglaspis* (Fig. 2a), a cheloniellid (Fig. 2b, Supplementary Fig. 3g), a possible stalked barnacle (Fig. 2c, Supplementary Fig. 3h) and two new xiphosuran genera (Fig. 2d, e, Supplementary Fig. 3i). The cheloniellids and horseshoe crab fossils mark the oldest unequivocal examples of these groups, pushing their likely origins back into the Cambrian. The horseshoe crabs are the most abundant arthropods; several hundreds of specimens of the two taxa are known. One of these new xiphosurans is a small, basal form retaining a fully segmented opisthosoma (Fig. 2d). The other, in contrast, is highly derived, with a fused preabdomen and appendages very similar to those of extant horseshoe crabs (Fig. 2e, Supplementary Fig. 3i). The horseshoe crabs, and several other arthropods, are represented by successive instars. Some 20 to 30 other exceptionally preserved invertebrates await study, mainly arthropods, but also problematica; no chordates have been discovered to date. Two different algae are also represented.

These Moroccan discoveries show that Burgess Shale-type faunas flourished at least until the Floian. The rarity of Burgess Shale-type taxa in post-Middle Cambrian rocks elsewhere probably results from a lack of preservation<sup>2,4</sup> rather than the extinction and replacement of these faunas during the later Cambrian. A number of explanations have been offered for the closure of this taphonomic window, including a change in clay chemistry<sup>20</sup>, greater depth of bioturbation<sup>21,22</sup>, and increased behavioural complexity and ecospace occupation by burrowing organisms<sup>23</sup>. The scarcity of bioturbation at most localities in the Fezouata formations implies that direct scavenging was limited; more importantly, it shows that environmental conditions hostile to an infauna, for example, low-oxygen conditions, as indicated by consistently small burrow diameters and low ichnological diversity, prevailed. Whereas Cambrian Burgess Shale-type faunas occur at relatively low palaeolatitudes<sup>24</sup>, the Moroccan sites were situated very close to the Ordovician South Pole; Burgess Shale-type biotas clearly persisted globally in cold, deep marine settings<sup>2</sup>.

The new discoveries in the Fezouata formations indicate that Burgess Shale-type taxa continued to have an important role in the diversity and ecological structure of deeper marine communities well after the Middle Cambrian, and prompt a reassessment of the structure of post-Cambrian Palaeozoic communities. Several typical Burgess Shale taxa were present in the early Ordovician, while naraoiids extend to the Silurian<sup>25</sup> and some groups, for example, marrellomorphs<sup>26</sup>, great appendage arthropods<sup>27</sup> and eldonioids<sup>28</sup> survived at least into the Devonian (eldonioids have also been recorded from the Upper



**Figure 2 | Exceptionally preserved post-Cambrian elements of the Fezouata biota.** **a**, Aglaspidid arthropod *Tremaglaspis*, Upper Fezouata Formation (MHNT.PAL.2007.39.92.1). **b**, Cheloniellid arthropod, Upper Fezouata Formation (NMS G 2004.2.1). **c**, Possible stalked barnacle, Upper Fezouata Formation (YPM 227519). **d**, Xiphosuran with fully segmented opisthosoma, top of Lower Fezouata Formation (MHNT.PAL.2007.39.43.2). **e**, Xiphosurid with fused preabdomen, Upper Fezouata Formation (YPM 227586).

Ordovician of Morocco<sup>29,30</sup>). The continued importance of Burgess Shale-type organisms through the Lower Palaeozoic reduces the distinction between Cambrian and subsequent faunas and warrants re-investigation of the dramatic turnover between the Cambrian and Palaeozoic evolutionary faunas in the light of new discoveries of soft-bodied fossils. At the same time, the presence of post-Cambrian taxa (for example, machaeridian<sup>16</sup> and tube-dwelling annelids, horseshoe crabs, cheloniellids, phacopids, asterozoans and crinoids) alongside Burgess Shale-type elements in the Fezouata biota indicates that significant diversification occurred before the Tremadocian.

## METHODS SUMMARY

All figured specimens are housed in the collections of the Yale Peabody Museum of Natural History, Lyon 1 University, the Natural History Museum of Lyon, the Natural History Museum of Marseille, the Natural History Museum of

Toulouse, the National Museums of Scotland and the Sedgwick Museum, as indicated by their accession numbers. Locality details for all specimens are kept at these institutions, and can be provided by the authors upon request. Specimens were prepared with scalpels and fine needles under high magnification using Nikon SMZ800 and 1500 stereomicroscopes and, when necessary, repaired using cyanoacrylate glue. Interpretative drawings were made with a camera lucida attached to Leica MZ6, Nikon SMZ1500 and Wild M5 stereomicroscopes. Photographs were made with Canon EOS 350D, Nikon D80 and Nikon D200 digital reflex cameras, Leica MZ16 and MZ6 stereomicroscopes with a Leica DFC 425 digital camera, and a Leica MZ16FA with an Olympus ColourView III digital camera. With the exception of the images in Fig. 1a, e, Fig. 2c, Supplementary Figs 2c–i and 3d, photographs were taken with crossed polarizers. Digital photographs were processed in Adobe Photoshop CS2 and CS3, and composite images (Fig. 1b, c, f, h, i; Fig. 2c, e; Supplementary Figs 2a, b, 3a) were stitched together using Adobe Photoshop CS3 and Microsoft ICE.

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