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Brief Communication

New fossil assemblages from the Early Ordovician Fezouata Biota

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Abstract. The Fezouata Biota (Morocco) is an exceptionally well-preserved fossil community of Early Ordovician age and although its oldest units are comparable with Burgess Shale-type localities of the Cambrian Explosion, little attention has been paid to the younger units despite potential to reveal the conditions of the Ordovician Radiation. Herein, we describe a new middle to upper Floian Fezouata locality (Taichoute) encompassing an assemblage dominated by large bivalved euarthropods and giant filter-feeding radiodonts, which were transported and preserved in concretions associated with density-flow deposits. Taichoute captures the closing of the taphonomic window that characterizes exceptional fossil preservation during the Cambrian Explosion (i.e., carbonaceous compressions) as well as the faunal transition to assemblages dominated by typical Palaeozoic taxa.

Main text. The Early Ordovician Fezouata Biota of Morocco is an exceptionally-preserved fossil assemblage that contains a combination of soft-bodied extinct organisms that have become synonymous with the Cambrian Explosion, such as radiodonts and marrellomorphs, alongside more derived forms that are representative of typical Palaeozoic faunas, such as horseshoe crabs and cephalopods¹. Much of the research has focused on Fezouata fossils that occur in either upper Tremadocian or middle Floian deposits in the Zagora region² (Fig. 1A), covering the proximal-distal axis of a marine environment³ (Fig. 1B), dominated by wave/storm processes⁴. The exceptionally well-preserved fossils in these units were buried *in situ* by storm-induced deposits close to the storm wave base (SWB)³. Soft-bodied animals in the Fezouata Biota are most commonly preserved as compressions in shales, in a similar fashion to Cambrian BST deposits³. Exceptional preservation within concretions has also been reported from the Fezouata Shale (Fig. 1C), but this mode of fossilization is more restricted compared to shale-hosted macrofossils^{4,5}.

Here, we report a new fossiliferous section of the Fezouata Shale discovered in Taichoute, 80km away from the traditional localities near Zagora (Fig. 1B). Fossils at Taichoute can be categorized into three distinct assemblages based on their diversity and preservation (a1, a2, and a3; Fig. 1A). The lowermost assemblage (a1) is dominated by brachiopods, molluscs (Fig. 2A), echinoderms (Fig. 2B), and graptolites (Fig. 2C). A middle Floian age for assemblage a1 can be inferred by the occurrence of *Baltograptus* gr. *deflexus*⁶ (Fig. 2C). Fossils from this interval are mainly found in concretions (Fig. 1D), in which numerous taxa are well preserved in minute detail with few signs of disarticulation or abrasion (Fig. 2B). The a1 community is comparable to described middle Floian Fezouata assemblages from the Zagora region², where a similar mode of concretion-based preservation has been already documented². Most previously described concretions and those in a1 formed *in situ* while animals were decaying on the seafloor below the SWB⁵ (Fig. 1F). Another type of concretion, preserving unrecognizable bioclasts transported by storm events and formed above the SWB, has also been previously described from the Zagora region⁴, but has not been found in Taichoute (Fig. 1F).

The intermediate interval a2 yields concretions with low taxonomic diversity consisting of large euarthropod pieces (Fig. 2D, E), nautiloid cephalopods, and planktonic graptolites (Fig. 2F). Some of the euarthropods could represent lateral elements of the tripartite carapace of hurdiid radiodonts, such as the filter-feeder *Aegirocassis benmoulai*^{7,8}, based on their shape, size, and the co-occurrence of a block of elongated setose structures arranged in parallel, resembling setal blades⁸ (Fig. 2E). Other large euarthropod carapaces at a2 differ from previously described giant taxa from the Fezouata Shale, and may represent sediment-sifting hurdiid radiodonts or other bivalved euarthropod taxa (e.g., caryocaridids, phyllocarids and hymenocarines; Fig. 2D, E), all of which are generally interpreted as primarily nektonic components of Cambrian and Ordovician ecosystems^{7,8}. The new bivalved carapaces (mean length L=135mm; mean height H=68mm) are considerably larger than some similar taxa described from other sites with soft-tissue preservation in the Cambrian⁹⁻¹⁴ [e.g. *Isoxys* (L=28mm, H=13mm)⁹; *Tuzoia* (L=77mm; H=53mm)¹⁰; *Branchiocaris* (L=43mm; H=33mm)¹¹; *Tokkumia* (L=63mm; H=40mm)¹²]. Some carapaces are covered by meandering traces of varying sizes across their surface, and brachiopod epibionts are found on at least one carapace (Fig. 2D). The dominance of nektonic taxa in a2 suggests that the seafloor was not suitable to sustain a diverse and abundant benthic community. The disarticulated nature of specimens preserved in a2 contrasts with the articulated fossils in a1 (Fig. 1F) and suggests that the nektonic taxa preserved in a2 were deposited upslope, where their carapaces could have acted as nutrient stores for the sparse benthic community and were then transported over a limited distance prior to consolidation in concretions¹⁵.

93 In order to understand the sedimentary processes behind fossil transport in a2, it is essential
94 to look at the uppermost fossiliferous interval a3 (Fig. 1A). Interval a3 is characterized by a large
95 hectometer-scale lobe (Fig. 1A) that consists of coarse mudstone to very fine sandstone displaying
96 dominantly planar lamination, asymmetrical cross-laminations, reactivation surfaces and rare
97 symmetrical cross-lamination. Similar large and laterally tapering sedimentary bodies in the
98 Fezouata Shale (Fig. 1E) are considered as the stratigraphically distal equivalent to the overlying
99 proximal Zini Formation (Fig. 1A). These large lobes are regarded as density-flow deposits in
100 distal-most shelf environments below the SWB¹⁶. The interpretation of Taichoute as the most distal
101 section is in accordance with its position in the basin (Fig. 1B). Fossils (mainly bryozoans and
102 trilobites) are fragmented within this lobe (Fig. 2G-J) confirming the fossil-transport hypothesis in
103 a3 and to some extent in a2 (Fig. 1F). In this sense, a1, a2, and a3 likely represent lateral variations
104 within the same shelf setting (Fig. 1F). The uppermost interval is capped by an accumulation level
105 preserving rhynchonelliform brachiopods and bryozoans in minute details (on planar bedding
106 surfaces, not within concretions) with very little evidence of physical abrasion (Fig. 2K).

107 Exceptional fossil preservation might seem limited in Taichoute (e.g., euarthropod
108 carapaces in a2), particularly when compared to Cambrian sites such as the Chengjiang Biota
109 (China) and the Burgess Shale (Canada) that yielded highly diverse exceptionally-preserved
110 assemblages¹⁷. However, Taichoute fits within the range of preservational patterns seen in the
111 Fezouata Shale, where even localities such as the well-known Bou Izargane (Fig. 1B) yielded very
112 low diversity of exceptionally-preserved fossils (e.g., few marrellomorphs and stylophorans). The
113 discovery of Taichoute supports previous research suggesting that the main characteristic of the
114 Fezouata Biota is its low alpha (raw biodiversity at a particular site), and high beta diversity
115 (variability between sites)¹⁸.

116 Taichoute extends the temporal range of exceptional preservation in the Fezouata Biota
117 into the upper Floian (Fig. 1A), while also expanding the depositional environments preserving
118 fossils to more distal parts of the shelf setting than previously described Fezouata Shale sites (Fig.
119 1F). In some of these environments, soft-bodied fossils are not preserved *in situ*, but were
120 transported and are associated with density-flow deposits (Fig. 1F), which is crucial to consider
121 when attempting to understand assemblage diversity and reconstruct palaeoecological interactions.
122 When examining broad trends through the entire Fezouata Shale, we see that it is transitional both
123 taxonomically and taphonomically. The Fezouata Shale records a taxonomic transition from a
124 mixture of Cambrian and Ordovician taxa co-occurring in upper Tremadocian deposits towards
125 purely Ordovician taxa (e.g., brachiopods and bryozoans) during the upper Floian at the top of the
126 succession in Taichoute. During both the late Tremadocian and middle Floian, exceptional fossil
127 preservation in the Fezouata Shale is dominated by Burgess Shale-type carbonaceous
128 compressions (typical of best-known Cambrian localities such as the Walcott Quarry and the
129 Chengjiang Biota) with only rare occurrences of concretions. By contrast, the middle to upper
130 Floian intervals are dominated by concretion preservation in Taichoute, similar to other Palaeozoic
131 *Lagerstätten* such as the Herefordshire, Mazon Creek and Montceau-les-Mines biotas¹⁹. The
132 Taichoute locality seems to capture the closing of the taphonomic window that characterizes
133 exceptional fossil preservation during the Cambrian Explosion. A table summarizing the overall
134 significance of Taichoute is presented in the *Supplementary Material*. Further fieldwork and
135 palaeontological analyses of this locality will yield new insights into the distribution of BST
136 animals through space and time while completing our understanding of the ecological and
137 evolutionary transition between the Cambrian Explosion and the Ordovician Radiation.

Figure 1. (A) Stratigraphic column for the Lower Ordovician Fezouata Shale and Zini Formation including the Taichoute locality divided into three fossil assemblages. The red arrow in A indicates an accumulation level of brachiopods and bryozoans at the top of the Taichoute section. (B) Taichoute is the most distal site in the depositional environment of the Fezouata Shale. (C) Concretion from the Zagora region. (D) Solatan echinoderm in a small concretion from Taichoute. (E) A large lobe from the Fezouata Shale representative of the upper part of the succession in Taichoute (a3) and interpreted as a density-flow deposit. (F) The numerous types of preservation occurring in the Fezouata Shale along a depositional gradient. SWB: Storm wave base.

Figure 2. Fossils from the Taichoute locality (a1: A-C, a2: D, E, a3: F-J). (A) the gastropod *Lesueurilla prima*. (B) The solutan echinoderm *Plasiacystis mobilis*. (C) The graptolite *Baltograptus* gr. *deflexus*. (D) giant carapace of bivalved euarthropods (yellow arrow). (E) Disarticulated carapaces of soft-bodied euarthropods (yellow arrows indicate large carapaces of bivalved euarthropods, the striated setal blade structure is highlighted with the white arrow). (F) The multiramous graptolite *Holograptus* sp. (G) The calymenid trilobite *Colpocoryphe* cf. *thorali*. (H) The illaenid trilobite *Ectillaenus*? sp. (I) The calymenid trilobite *Neseuretus* cf. *attenuatus* (orange arrow) and Lichidae gen. indet. (left side of the orange arrow). (J) The dalmanitid trilobite *Zeliskellinae* indet. (K) Accumulations of specimens of a new genus of coorthid brachiopod and bryozoans on top of a3. Scale bars = 5mm in A, F, G, H, I, J; 10 mm in B, C and K; 50 mm in D and E.

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Online Material and Methods. In 2017, a field excavation took place in Taichoute (Lower Ordovician, Morocco). Over 300 fossil samples were observed locally, but only 70 samples were transported to the collections of the Cadi Ayyad University in Morocco owing to the heavy weight of the concretions. The following specimens are used in this study (by order from A to J in figure 2): AA.TAI2.OI.9; ML20-259357; AA.TAI3.OI.2; AA.TAI6.OI.1-2; AA.TAI6.OI.6; AA.TAI13.OI.1; AA.TAI13.OI.2; AA.TAI13.OI.3; AA.TAI13.OI.4; AA.TAI14.OI.1. Sampling in Taichoute covers an 84 m sedimentary succession that was logged at a cm-scale.

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Competing interests. The authors declare that they have no competing interests.

Data availability. All data needed to evaluate the conclusions in the paper are present within the *Main Manuscript* and *Supplementary Information*. Additional data related to this paper may be requested from the authors.

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