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New fossil assemblages from the Early Ordovician Fezouata Biota

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ABSTRACT

The Fezouata Biota (Morocco) is a unique Early Ordovician fossil assemblage. The discovery of this biota revolutionized our understanding of Earth's early animal diversifications – the Cambrian Explosion and the Ordovician Radiation – by suggesting an evolutionary continuum between both events. Herein, we describe Taichoute, a new fossil locality from the Fezouata Shale. This locality extends the temporal distribution of fossil preservation from this formation into the upper Floian, while also expanding the range of depositional environments to more distal parts of the shelf. In Taichoute, most animals were transported by density flows, unlike the *in-situ* preservation of animals recovered in previously investigated Fezouata sites. Taichoute is dominated by three-dimensionally preserved, and heavily sclerotized fragments of large euarthropods – possibly representing nekto-benthic/nektoic bivalved taxa and/or radiodonts. Resolving whether this dominance reflects a legitimate aspect of the original ecosystem or a preservational bias requires an in-depth assessment of the environmental conditions at this site. Nevertheless, Taichoute provides novel preservational and palaeontological insights during a key evolutionary transition in the history of life on Earth.

KEYWORDS: Palaeozoic, Morocco, exceptional preservation, taphonomy, arthropods

INTRODUCTION

The Early Ordovician Fezouata Biota of Morocco is an exceptionally-preserved fossil assemblage that contains a combination of non-mineralized extinct organisms that have become synonymous with the Cambrian Explosion, such as radiodonts, halkieriids, lobopodians, nektaspidids, and marrellomorphs, alongside more derived forms that are representative of typical Palaeozoic faunas, such as xiphosurans, cheloniellids, and machaeridians^{1,2}. To date, most palaeobiological research¹⁻²⁵ has focused on Fezouata fossils that occur in either upper Tremadocian or middle Floian deposits in the Zagora region (Fig. 1a, b)²⁶, covering to some extent, the proximal-distal axis of an ancient marine environment (Fig. 1c)^{27, 28}. This environment was dominated by wave/storm processes^{29, 30}. The exceptionally well-preserved fossils in these deposits were buried *in situ* by storm-induced deposits close to the storm wave base (SWB)²⁹⁻³¹. Lightly biomineralized or sclerotized animals in the Fezouata Biota are most commonly preserved in shales as weathered carbonaceous material (compressed to different degrees) and authigenic minerals^{32, 33}. Preservation within concretions has also been reported from this formation (Fig. 1d), but this mode of fossilization is more restricted compared to shale-hosted macrofossils³⁴. Most Fezouata Shale fossil collections are based on discoveries around the Zagora region in Morocco (e.g., Tamegroute, Bou Izargane, and Tinzouline) (Fig. 1b)³²; with little effort spent prospecting fossiliferous localities outside this area. Here, we report a new and continuous fossiliferous section from the Fezouata Shale discovered in Taichoute, 80km away from previously investigated localities (Fig. 1a, c). We discuss the palaeontology, sedimentology, and possible preservational biases operational at this site. Taichoute expands the range of depositional environments yielding non-biomineralized fossils, reveals new modes of preservation for the Fezouata Shale, and expands the occurrence of fossil-bearing strata within this formation.

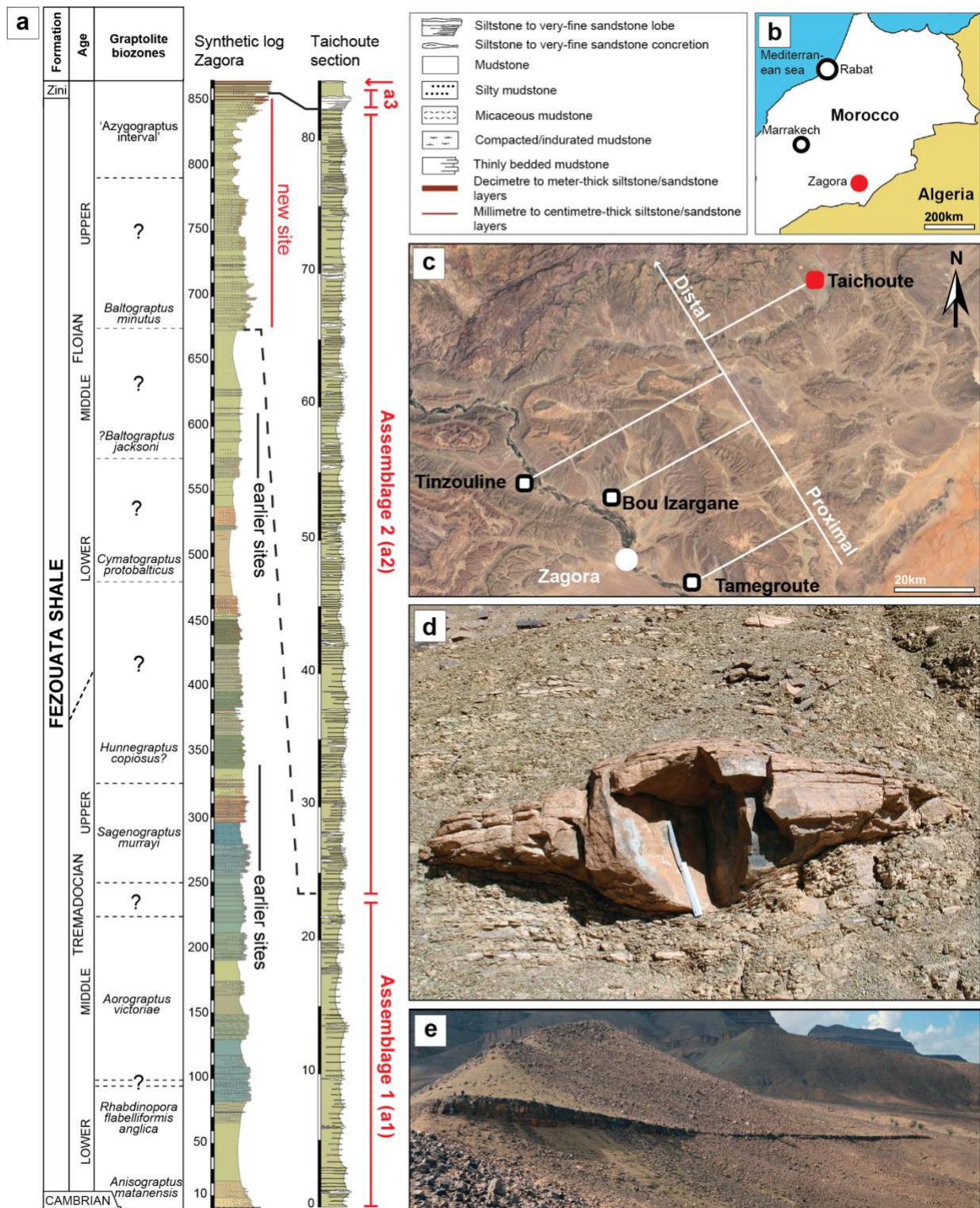


Figure 1. (a) Stratigraphic column for the Lower Ordovician Fezouata Shale and Zini Formation including the Taichoute locality divided into three fossil assemblages. The red arrow in (a) indicates an accumulation level of brachiopods and bryozoans at the top of the Taichoute section. (b) Zoom on the Zagora Region where the Fezouata Shale is discovered. (c) Taichoute is the most distal site in the depositional environment of the Fezouata Shale. (d) Concretion from the Zagora region. (e) A large lobe from the Fezouata Shale at the upper part of the succession (a3) and interpreted as a density-flow deposit.

RESULTS AND DISCUSSION

Faunal content

Euarthropods, brachiopods, echinoderms, and graptolites constitute together most of the preserved biodiversity in the Fezouata Biota³², and this pattern is replicated in the newly described Taichoute locality (Fig. 2). Some animal groups such as sponges, found in some other localities (e.g., Tamegroute and Bou Izargane), remain, so far, absent from Taichoute (Fig. 2).

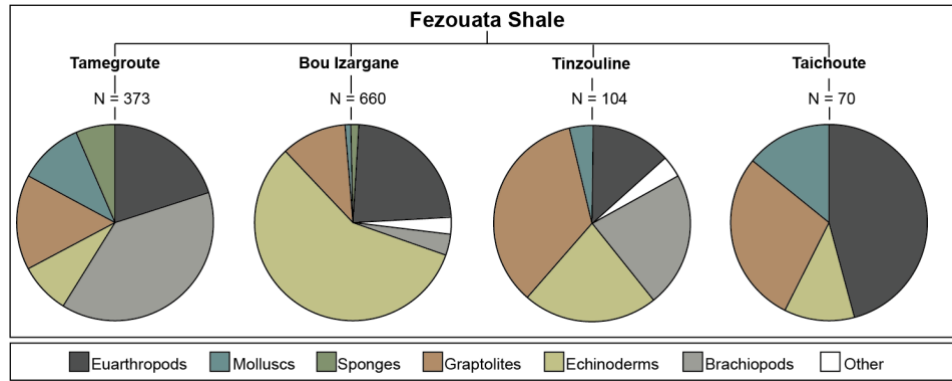
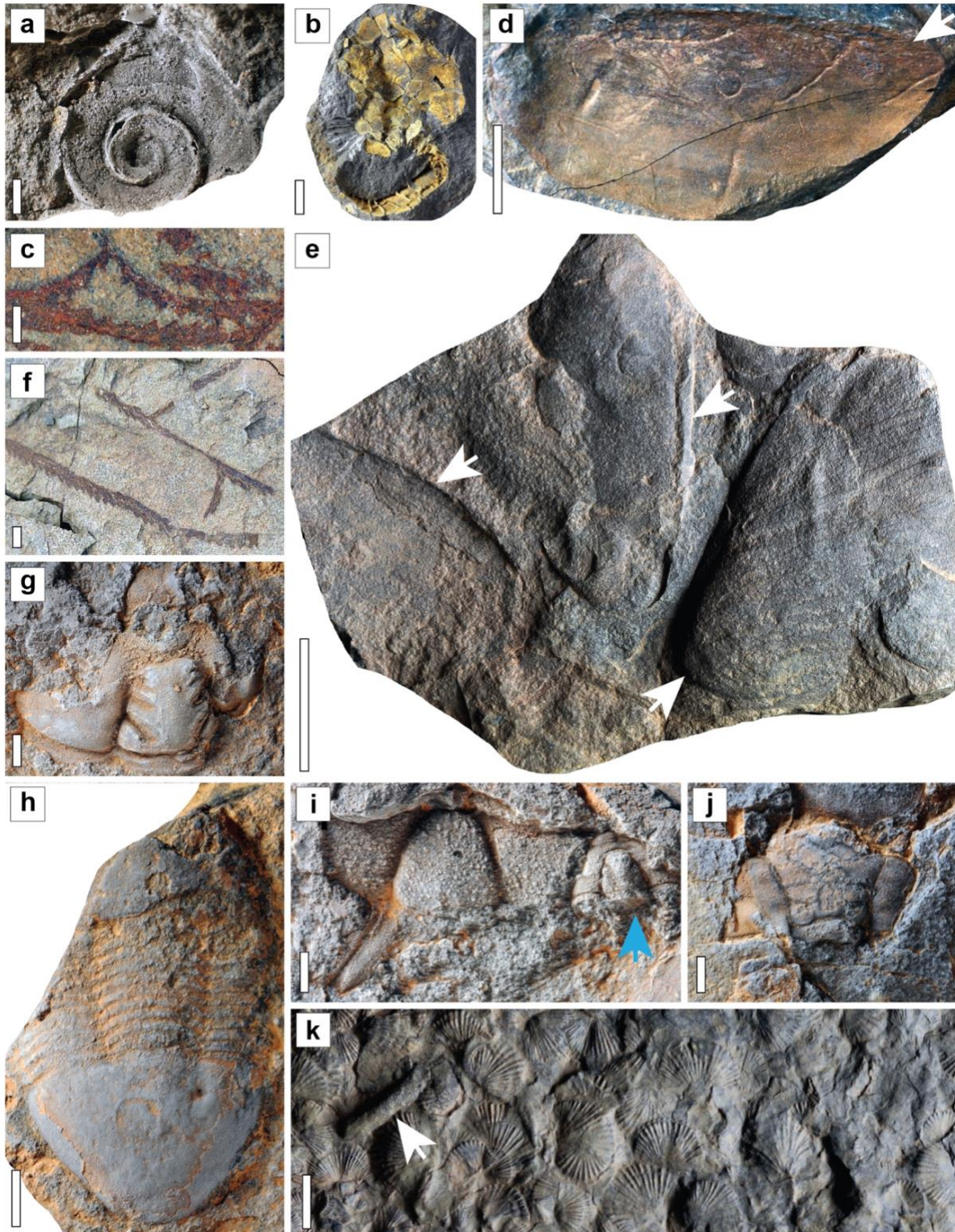


Figure 2. Faunal composition and specimen abundances for each animal group at different Fezouata Shale localities based on the Marrakech Collections of the Cadi Ayyad University (Morocco). Note that the pie chart for Taichoute excludes the accumulation level of brachiopods and bryozoans (above a3, at the top of the succession), as it is impossible to count fossil specimens on this bed. This figure does not account for all specimens recovered/observed at outcrops. For information on how this data was collected and plotted, kindly refer to the Material and Methods section.

Taichoute can be categorized by three distinct assemblages based on their diversity and preservation (a1, a2, and a3; Fig. 1a). The lowermost assemblage (a1) consists of brachiopods, molluscs (Fig. 3a), echinoderms (Fig. 3b), and graptolites (Fig. 3c). A middle Floian age for assemblage a1 can be inferred by the occurrence of *Baltograptus* gr. *deflexus*⁸ (Fig. 3c). Fossils from this interval are mainly found in concretions that typically contain a single specimen (e.g., Fig. 3b). The preservation of minute details, showing various stages of disarticulation and the *in-situ* collapse of echinoderms, with no evidence of abrasion (Fig. 3b), indicate that these animals were not transported, and concretions formed while organisms were decaying on the seafloor below the SWB in a similar way to some previously described concretion-based preservation from the Zagora region². Another type of concretion, preserving unrecognizable bioclasts transported by storm events and formed above the SWB, has also been previously described from the Zagora region²⁹, but has not been found at Taichoute.

The intermediate interval a2 (Fig. 1a) yields concretions with low taxonomic diversity consisting mainly of nautiloid cephalopods, euarthropod fragments (Fig. 3d, e; 4), and graptolites (Fig. 3f). Although there is some variability in their morphology and appearance, the euarthropod carapaces are typically oval-shaped to elongate, and they are preserved with substantial convexity and/or artefacts of previous relief that suggests a heavily sclerotized original constitution (Fig. 3d, e; 4). Coupled with their large size, ranging from ca. 5 to 15cm in length (Fig. 3d, e, 4), and the presence of thickened marginal rims, we tentatively interpret them as corresponding to bivalved euarthropods and possibly elements of radiodonts (Fig. 3d, e, 4). Whilst preliminary, we argue that these affinities are the most plausible for the fragments considering the known diversity of euarthropods during the Early Ordovician, and the fact that giant radiodonts are well known from the Fezouata Shale^{5, 6}. The observed euarthropod carapaces (Fig. 3d, e; 4) from Taichoute are

118 considerably larger than those described from early- and mid-Cambrian sites [e.g., *Balhuticaris*³⁵;
 119 *Isoxys*^{36, 37}; *Tuzoia*^{37, 38}; *Branchiocaris*^{39,40}, and *Tokummia*⁴¹], and are more comparable in size to
 120 stratigraphically younger euarthropods (e.g., phyllocarids) discovered in Silurian and Devonian
 121 taxa^{42, 43}.



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Figure 3. Fossils from the Taichoute locality (a1: A-C, a2: D-F, a3: G-J). (a) The gastropod *Lesueurilla prima*. (b) The solutan echinoderm *Plasiacystis mobilis*. (c) The graptolite *Baltograptus* gr. *deflexus*. (d-e) Giant euarthropod carapaces indicated with white arrows. (d) Carapace likely belonging to previously documented to bivalved arthropods from the Fezouata Biota⁵⁹. (e) Two incomplete but tapering carapaces (left and center) adjacent to a structure that bears possible resemblance to a block of radiodont setal blades (right), consisting of a series of parallel elongated blades a few millimetres wide separated by slight changes in sediment level and/or by intervening sediment, with an overall tapering outline, similar to the setal blade blocks of hurdiids such as *Hurdia* from the Burgess Shale⁶⁰. (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* (blue arrow) and Lichidae gen. indet. (to the left of the blue arrow). (j) The dalmanitid trilobite, subfamily Zeliszskellinae. (k) Accumulations of specimens of a new genus of orthidine brachiopod and bryozoans (white arrow) on top of a3. Scale bars = 5mm in a, f, g, h, i, j; 10 mm in b, c and k; 25 mm in d; 50mm in e. By order from a to j: AA.TAI2.OI.9; ML20-259357; AA.TAI3.OI.2; AA.TAI6.OI.6; AA.TAI13.OI.1; AA.TAI13.OI.2; AA.TAI13.OI.3; AA.TAI13.OI.4; AA.TAI14.OI.6. All specimens are housed at the Marrakech Collections of the Cadi Ayyad University.

Bivalved euarthropods and radiodonts are generally interpreted as primarily nekctic or nektobenthic components of Palaeozoic ecosystems. The dominance of nekctic/nektobenthic euarthropod taxa, nautiloids, and planktonic graptolites in a2 suggests that the seafloor, above which they lived, was not suitable to sustain a diverse and abundant benthic community. However, this environment does not necessarily correspond to Taichoute, mainly because a2 concretions differ from those found in a1 in terms of their quality of fossil preservation. Specimens in a2 are fragmented (Fig. 3d, e, 4). The disarticulated nature of specimens could result from prolonged decay, which may have started in the water column during the bloating and floating stage of initial decomposition, concurrent with processes such as carcass scavenging. Disarticulation may have also resulted from fossil transport, especially that, unlike a1, a2 concretions are generally not formed of a single specimen, and numerous fragments were often trapped within sediments, that were later consolidated in concretions (e.g., Fig. 3e). Some of these carapaces are covered by meandering traces of varying sizes across their surface, and rare brachiopod epibionts are found on some carapaces (Fig. 3d) indicating that they could have acted as nutrient sources for the community and/or as a stable substrate for brachiopods to attach to, following their transport to Taichoute, and prior to their consolidation in concretions in a2⁴⁴.

The upper interval a3 (Fig. 1a) consists of a large sedimentary lobe yielding fragmented bryozoans and trilobites (Fig. 3g-j). These large sedimentary bodies in the Fezouata Shale (Fig. 1e) are considered as the stratigraphically distal equivalent to the overlying proximal Zini Formation (Fig. 1a). Due to the degree of fossil disarticulation and fragmentation within this lobe, it is certain that carcasses were transported prior to their preservation. The uppermost interval, above this lobe shows an accumulation level preserving rhynchonelliform brachiopods and bryozoans in minute detail (on planar bedding surfaces, and not within concretions) with very little evidence of physical abrasion (Fig. 3k).

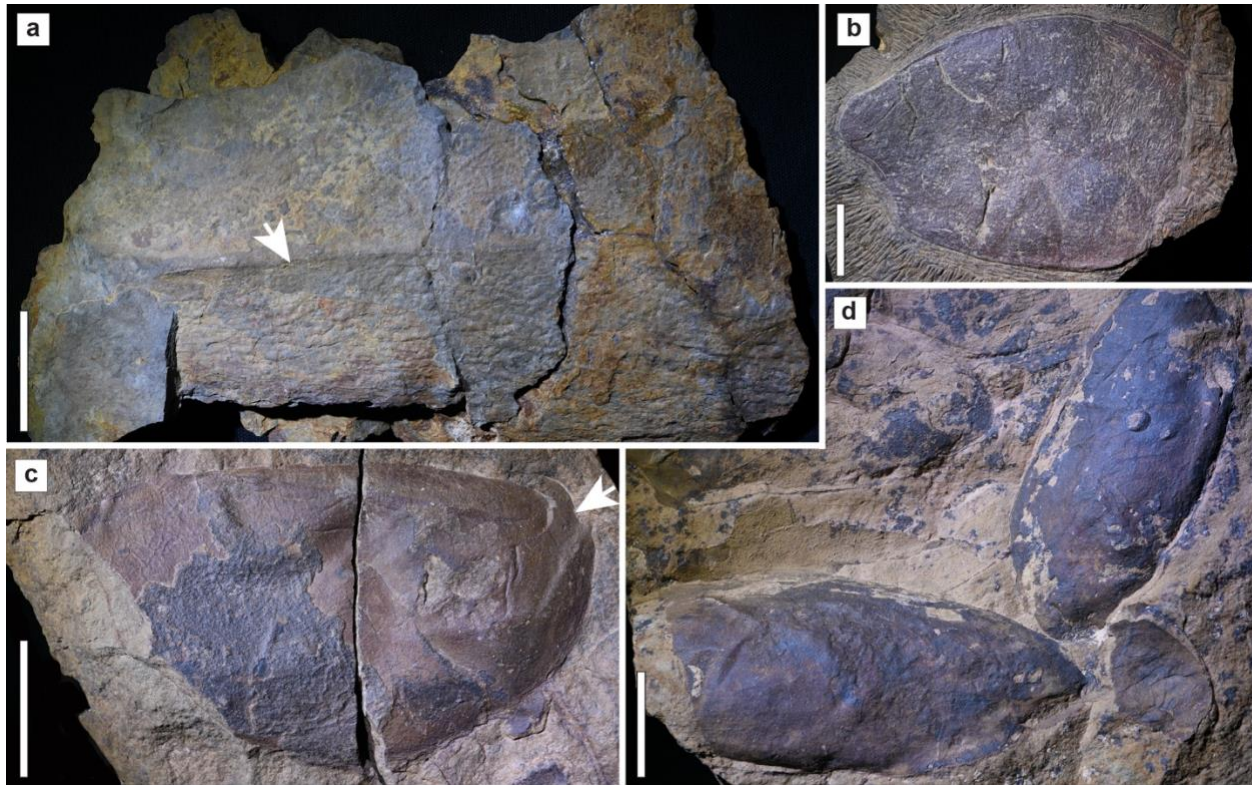


Figure 4. Euarthropod fossils from Taichoute interval a2. (a) Large carapace with central carina (white arrow), similar to that seen in *Aegirocassis* carapace elements⁶. (b) Carapace with an asymmetrically rounded outline with an anterior protrusion similar to that seen in the P-elements of *Hurdia* and other hurdiids⁶⁰. (c) Carapace with an asymmetrically rounded outline with one side bearing a structure similar to the upturned projection (white arrow) described for *Aegirocassis* lateral carapace elements⁶. (d) Assemblage with at least three carapaces together, some of which are elongated and tapering at one end, with a partial outline possibly resembling that of carapace elements of *Aegirocassis*⁶. Scale bars are 4cm in a, and 3cm in b, c, d. By order from a to d: MCZ.TAI001, MCZ.TAI002, MCZ.TAI003, and MCZ.TAI004. All four specimens are housed at the University of Harvard.

Sedimentary environment

The Fezouata Shale sequence shallows upwards, but this is mainly evident in the Zagora area, where it ends with the deposition of the Zini Formation (Fig 1a), interpreted as nearshore sandstones^{30, 45}. However, the entire environment represents a proximal-to-distal gradient from the southeast (in Algeria) to the northwest^{30, 46}. Thus, the shallowing-upwards sequence is not expressed in terms of facies everywhere in the Fezouata Shale. In this formation, the emplacement of large siltstone lobes, similar to the one deposited in a3, reflects an increase in the sediment supply into the basin linked to a lowering of the base level and an increase of erosion in the shallower-water southeastern area. These large hectometric lobes that are siltstone-dominated (Fig. 5a) with minor very fine sandstone components, and displaying dominantly planar lamination, asymmetrical cross-laminations, and reactivation surfaces (Fig. 5b, c), have been described as storm-induced, density-flow deposits in the most distal setting of the Fezouata Shale³⁰. The interpretation of Taichoute as the most distal section is in accordance with its position in the basin and the previously defined proximal-distal axis³⁰ (Fig. 1c). This study is the first to document fossil preservation in association with such settings in the Fezouata Shale, regardless of the fidelity or quality of this preservation. Considering the deposition continuity between a1, a2, and a3 (Fig. 5a), it is likely that all three intervals represent lateral variations of deposition, from normal

sedimentation on the seafloor (a1), passing through lobe fringe (a2) to lobe centre (a3) within the same shelf setting (Fig. 6).

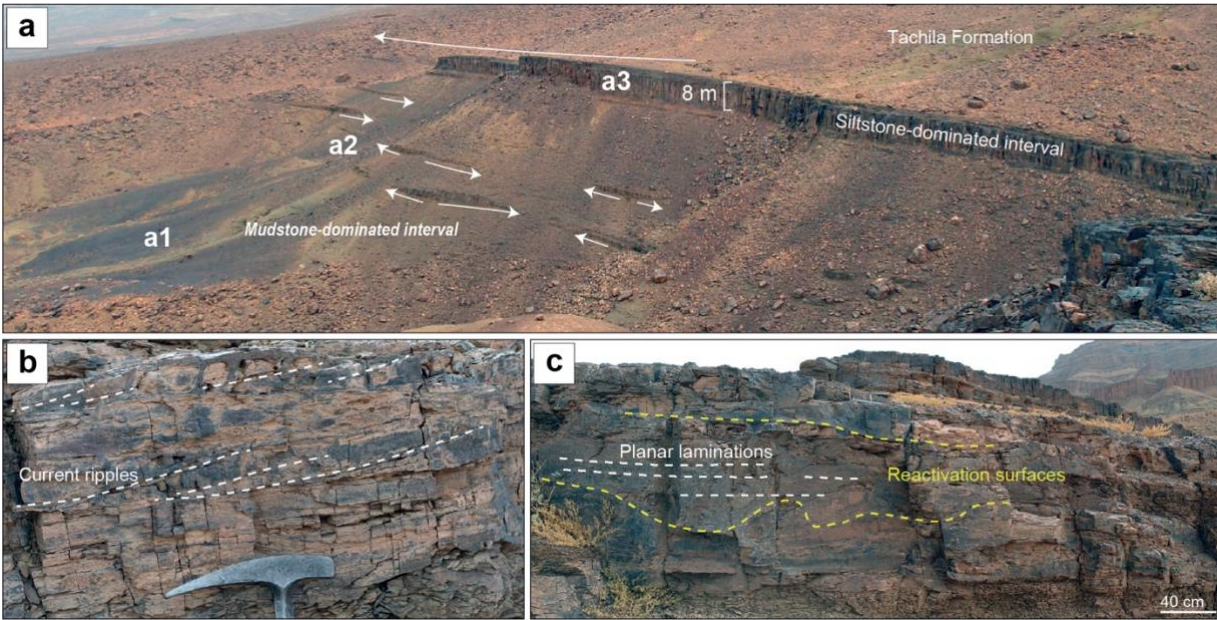


Figure 5. Sedimentary context of Taichoute. (a) Overview of the upper part of the Fezouata Shale displaying a transition between a1, a2, and a3. The large siltstone-lobes of a3 transition upward into the overlying Middle Ordovician Tachilla Formation. The white arrows show the lateral discontinuity, characteristic of the siltstone lobes. (b) The asymmetrical cross-laminations form current ripples displayed in the siltstone lobes. (c) Reactivation surfaces occur frequently in the siltstone lobes, attesting to the turbulence of repeated density flows. These deposits also display planar laminations.

These sedimentological interpretations complement previous studies made on the Fezouata Shale that highlighted a difference in the mechanism of fossil preservation between this Ordovician site and other Cambrian deposits preserving labile anatomies such as the Chengjiang Biota (China) and the Walcott Quarry from the Burgess Shale (Canada). It was suggested that most animals preserved near the Zagora region were preserved *in-situ*^{13, 29, 31} with little to no evidence of transport following death, unlike the aforementioned Cambrian sites where sedimentary flows, particularly turbidity currents, were operational, transporting animals from their living environment to facies favourable for their preservation⁴⁷⁻⁵⁰. The discovery of Taichoute increases the similarity between the Fezouata Shale and some Cambrian sites by showing that carcasses could be transported within the general context of this formation. However, the Fezouata Shale remains a unique formation with various modes of fossilisation including animal preservation (i) in accumulation levels (above a3 in Taichoute) (Fig. 1a) (ii) as bioclasts in concretions deposited above the SWB (present near Zagora); (iii) in shales around the SWB (dominant near Zagora), and (iv) under the SWB: (a) *in-situ*, in concretions of different sizes (similar to a1 in Taichoute and some sites near Zagora), (b) transported, in concretions (similar to a2 in Taichoute), and (c) transported, in large hectometric lobes (similar to a3 in Taichoute) (Fig. 6). This taphonomic variability is likely driven by the wide spatial and temporal distribution of the Fezouata Shale, around 850m of sediments (Fig. 1a) over 900km² in the Draa Valley, spanning ~11 myr. This suggests that the Fezouata Shale is an ideal candidate to further investigate a possible continuum between shale and concretion preservation, and untangle the possible environmental conditions

responsible for the transition between these two modes which preserve most of exceptionally preserved fossils during the Early Palaeozoic.

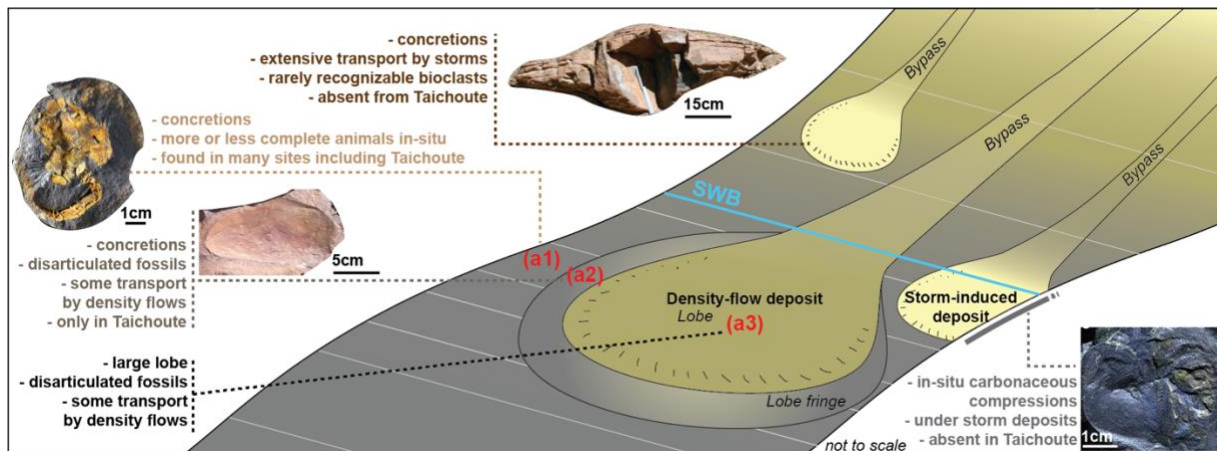


Figure 6. The different modes of preservation within the Fezouata Shale, their distribution, in addition to the sedimentary processes at play for their formation. SWB: Storm Wave Base.

Possible taphonomic biases

Non-biomineralized fossils in Taichoute are restricted to large euarthropod carcasses, consisting of heavily sclerotized material, preserved in substantial three-dimensional relief, to the exclusion of more delicate structures such as body cuticles, cellular sheets in contact with the water column, and internal organs (Fig. 3). As such, it is not possible to exclude a taphonomic filter⁵¹⁻⁵⁴ at play in Taichoute. This filter could result from a prolonged exposure to decay and both biomineralized and heavily sclerotized structures are more resistant to degradation than other tissue-types⁵¹. Furthermore, it was previously shown that big carcasses provide large quantities of decaying organic material favouring concretion growth^{28, 34}. This resulted in the *in situ* preferential preservation of large-bodied remains in concretions in some sites near Zagora^{28, 34}. In Taichoute, large animals were transported and trapped within sediments, that were later consolidated in a2. It is possible, that the organic material generated from these carcasses following their transport, facilitated siltstone (i.e., interpreted as lobe-fringe deposits; Fig. 6) consolidation around large carcasses. The mineralogy of the surrounding matrix might have also played a role controlling what got preserved in Taichoute. Particular mineralogical phases are associated with horizons with soft-tissue preservation in the Fezouata Shale^{55, 56} and in other deposits bearing exceptional preservation around the world^{57, 58}. These minerals replicate soft tissues, provide resistance to decay, and induce damage to bacterial membranes, facilitating the preservation of labile structures in the fossil record. In this sense, the absence of labile tissues and dominance of heavily sclerotized structures could also point to a lack of these favourable mineralogical phases in Taichoute sediments.

CONCLUSION AND PERSPECTIVES

Taichoute is a newly described late Floian fossil site in the Fezouata Shale. This discovery contributes to our understanding of animal preservation in this unique Lower Ordovician formation by showing that some organisms are transported by density flows. Three types of concretion preservation exist in Taichoute, expanding the fossilization modes observed within the Fezouata Shale. The dominant concretion type preserves large euarthropod carcasses, which, based on their morphology and size, might correspond to either bivalved forms and/or possibly radiodonts. Future

mineralogical and geochemical investigations on Taichoute have the potential to produce valuable preservational insights allowing us to resolve whether the aforementioned ecological observations represent legitimate aspects of original ecosystems, or are biased by taphonomic filters. Nevertheless, at this stage, and prior to yielding further investigations on Taichoute, this site remains a significant fossil locality providing novel sedimentary, taphonomic, and paleontological information (Tab. 1) at a key interval in the history of life on Earth – at the transition between the Cambrian Explosion and the Ordovician Radiation.

	Traditional Fezouata Shale sites	This study (Taichoute)
Location	Zagora Region, Morocco	Taichoute, 80km NNE of Zagora, Morocco
Age	late Tremadocian to middle Floian	middle to late Floian
Environment	Dominated by tempestites	Dominated by storm-induced density flows
Transport	Limited, mainly <i>in situ</i>	Pronounced in most of the section
Fossil matrix	Shales (relatively rare concretions)	Concretions of different types and sizes
Preservation fidelity	Biom mineralized, sclerotized, and cuticularized structures, and internal organs	Biom mineralized structures, and heavily sclerotized large euarthropod fragments (new taxa)

Table 1. Comparison between the newly discovered Fezouata Shale locality (Taichoute) and conventional sites.

MATERIAL AND METHODS

In 2017, a field excavation took place in Taichoute (Lower Ordovician, Morocco), 80km away from more traditional Fezouata localities (Fig. 1c). The 85 m-thick sedimentary succession at Taichoute was logged at a dm-scale, taking into account, sedimentary structures, grain size, and bed geometries. Over 300 fossil samples were observed locally, but only 70 samples were transported to the Marrakech Collections of the Cadi Ayyad University in Morocco owing to the heavy weight of the concretions and are accounted for in figure 2. Kindly note that more than 12,000 specimens were transported from Bou Izargane to the Marrakech Collections, but only 660 specimens were identified and inventoried so far, and are as such considered in figure 2. We acknowledge that taxonomic abundances are likely to change following the complete curation of specimens from Bou Izargane and new fossil discoveries at Tamegroute, Tinzouline, and Taichoute, and these abundances are also likely to fluctuate between fossil collections of different institutions (e.g., Cadi Ayyad University, Yale Peabody Museum, University of Lausanne, and Harvard University). For these reasons, abundances are not made central to this manuscript. However, it is important to emphasize that abundance discrepancies between collections and fossiliferous localities do not influence the Taichoute conclusions made within this paper (i.e., location, age, environment, preservation).

REFERENCES

1. Van Roy, P., et al. Ordovician faunas of Burgess Shale type. *Nature*, **465**(7295), 215-218 (2010).
2. Van Roy, P., Briggs, D.E. & Gaines, R.R. The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society*, **172**(5), 541-549 (2015).
3. Vinther, J., Van Roy, P. & Briggs, D.E.G. Machaeridians are Palaeozoic armoured annelids. *Nature*, **451**(7175), 185-188 (2008).
4. Vinther, J., Parry, L., Briggs, D.E.G. & Van Roy, P. Ancestral morphology of crown-group molluscs revealed by a new Ordovician stem aculiferan. *Nature*, **542**(7642), 471-474 (2017).
5. Van Roy, P. & Briggs, D.E.G. A giant Ordovician anomalocaridid. *Nature*, **473**(7348), 510-513 (2011).

6. Van Roy, P., Daley, A.C. & Briggs, D.E., Anomalocaridid trunk limb homology revealed by a giant filter-feeder with paired flaps. *Nature*, **522**(7554), 77-80 (2015).
7. Botting, J.P. Diversity and ecology of sponges in the Early Ordovician Fezouata Biota, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 75-86 (2016).
8. Gutiérrez-Marco, J.C. & Martin, E.L.O. Biostratigraphy and palaeoecology of Lower Ordovician graptolites from the Fezouata Shale (Moroccan Anti-Atlas). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 35-49 (2016).
9. Lehnert, O., et al. Conodonts from the Lower Ordovician of Morocco—Contributions to age and faunal diversity of the Fezouata Lagerstätte and peri-Gondwana biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 50-61 (2016).
10. Lefebvre, B., et al. Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 97-121 (2016).
11. Lefebvre, B., et al. Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. *Geobios*, **52**, 27-36 (2019).
12. Martí Mus, M. A hyolithid with preserved soft parts from the Ordovician Fezouata Konservat-Lagerstätte of Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 122-129 (2016).
13. Martin, E.L., et al. The lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: age, environment and evolutionary perspectives. *Gondwana Research*, **34**, 274-283 (2016).
14. Martin, E.L., et al. Biostratigraphic and palaeoenvironmental controls on the trilobite associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 142-154 (2016).
15. Nowak, H., et al. Palynomorphs of the Fezouata Shale (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 62-74 (2016).
16. Pérez-Peris, F., Laibl, L., Vidal, M. & Daley, A. Systematics, morphology, and appendages of an Early Ordovician pilekiine trilobite *Anacheirurus* from Fezouata Shale and the early diversification of Cheiruridae. *Acta Palaeontologica Polonica*, **66**(4), 857-877 (2021).
17. Pérez-Peris, F., et al. A new nektaspid euarthropod from the Lower Ordovician strata of Morocco. *Geological Magazine*, **158**(3), 509-517 (2016).
18. Polechová, M. The bivalve fauna from the Fezouata Formation (Lower Ordovician) of Morocco and its significance for palaeobiogeography, palaeoecology and early diversification of bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 155-169 (2016).
19. Van Iten, H., et al. Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and Sphenothallus (Medusozoa, Cnidaria), with emphasis on the Fezouata Shale of southeastern Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 170-178 (2016).
20. Saleh, F., Lefebvre, B., Hunter, A.W. & Nohejlová, M. Fossil weathering and preparation mimic soft tissues in eocrinoid and somasteroid echinoderms from the Lower Ordovician of Morocco. *Microscopy today*, **28**(1), 24-28 (2020).
21. Saleh, F., et al. Contrasting Early Ordovician assembly patterns highlight the complex initial stages of the Ordovician Radiation. *Scientific reports*, **12**(1), 1-8 (2022).
22. Allaire, N., Lefebvre, B., Martin, E., Nardin, E., & Vaucher, R. Taphonomy of new *Rhopalocystis* assemblages in the Lower Ordovician of the Zagora area (central Anti-Atlas,

- Morocco). *Progress in Echinoderm Palaeobiology: Cuadernos del Museo Geominero*, **19**, 21-26 (2015).
23. Martin, E., Lefebvre, B., & Vaucher, R. Taphonomy of a stylophoran-dominated assemblage in the Lower Ordovician of Zagora area (central Anti-Atlas, Morocco). *Progress in Echinoderm Palaeobiology: Cuadernos del Museo Geominero*, **19**, 95-100 (2015).
 24. Allaire, N. et al. Morphological disparity and systematic revision of the eocrinoid genus *Rhopalocystis* (Echinodermata, Blastozoa) from the Lower Ordovician of the central Anti-Atlas (Morocco). *Journal of Paleontology*, **91**(4), 685-714 (2017).
 25. Hunter, A.W. & Ortega-Hernández, J. A new somasteroid from the Fezouata Lagerstätte in Morocco and the Early Ordovician origin of Asterozoa. *Biology letters*, **17**(1), 20200809 (2021).
 26. Lefebvre, B., et al. Age calibration of the Lower Ordovician Fezouata Lagerstätte, Morocco. *Lethaia*, **51**(2), 296-311 (2018).
 27. Saleh, F., et al. Storm-induced community dynamics in the Fezouata Biota (Lower Ordovician, Morocco). *Palaios*, **33**(12), 535-541 (2018).
 28. Saleh, F., et al. Large trilobites in a stress-free Early Ordovician environment. *Geological Magazine*, **158**(2), 261-270 (2021).
 29. Vaucher, R., Martin, E.L.O., Hormière, H. & Pittet, B. A genetic link between Konzentrat- and Konservat-Lagerstätten in the Fezouata Shale (lower Ordovician, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **460**, 24-34 (2016).
 30. Vaucher, R., Pittet, B., Hormière, H., Martin, E.L.O. & Lefebvre, B. A wave-dominated, tide-modulated model for the Lower Ordovician of the Anti-Atlas, Morocco. *Sedimentology*, **64**(3), 777-807 (2017).
 31. Saleh, F., et al. 2020. Taphonomic pathway of exceptionally preserved fossils in the Lower Ordovician of Morocco. *Geobios*, **60**, 99-115 (2020).
 32. Saleh, F., et al. Insights into soft-part preservation from the Early Ordovician Fezouata Biota. *Earth-Science Reviews*, **213**, 103464, 1-12 (2021).
 33. Saleh, F., Daley, A.C., Lefebvre, B., Pittet, B. & Perrillat, J.P. Biogenic iron preserves structures during fossilization: a hypothesis. *BioEssays*, **42**(6), 1900243 (2020).
 34. Gaines, R.R., Briggs, D.E.G., Orr, P.J. & Van Roy, P. Preservation of giant anomalocaridids in silica-chlorite concretions from the Early Ordovician of Morocco. *Palaios*, **27**(5), 317-325 (2012).
 35. Izquierdo-López, A. & Caron, J.B. Extreme multisegmentation in a giant bivalved arthropod from the Cambrian Burgess Shale. *iScience*, p.104675 (2022).
 36. Fu, D.J., Zhang, X.L., Budd, G.E., Liu, W. & Pan, X. Ontogeny and dimorphism of *Isoxys auritus* (Arthropoda) from the early Cambrian Chengjiang biota, South China. *Gondwana Research*, **25**(3), 975-982 (2014).
 37. García-Bellido, D.C., et al., The bivalved arthropods *Isoxys* and *Tuzoia* with soft-part preservation from the Lower Cambrian Emu Bay Shale Lagerstätte (Kangaroo Island, Australia). *Palaeontology*, **52**(6), 1221-1241 (2009).
 38. Vannier, J., et al., *Tuzoia*: morphology and lifestyle of a large bivalved arthropod of the Cambrian seas. *Journal of Paleontology*, **81**(3), 445-471 (2007).
 39. Wu, Y., Fu, D.J., Zhang, X.L., Daley, A.C. & Shu, D. Dimorphism of Bivalved Arthropod *Branchiocaris? yunnanensis* from the Early Cambrian Chengjiang Biota, South China. *Acta Geologica Sinica*, **90**(3), 818-826 (2016).

40. Legg, D.A. & Caron, J.B. New Middle Cambrian bivalved arthropods from the Burgess Shale (British Columbia, Canada). *Palaeontology*, **57**(4), 691-711 (2014).
41. Aria, C. & Caron, J.B. Burgess Shale fossils illustrate the origin of the mandibulate body plan. *Nature*, **545**(7652), 89-92 (2017).
42. Briggs, D.E.G., Rolfe, W.I., Butler, P.D., Liston, J.J. & Ingham, J.K. Phyllocarid crustaceans from the Upper Devonian Gogo Formation, Western Australia. *Journal of Systematic Palaeontology*, **9**(3), 399-424 (2011).
43. Jones, W.T., Feldmann, R.M. & Mikulic, D.G. Archaeostracan (Phyllocarida: Archaeostraca) Antennulae and Antennae: Sexual Dimorphism in Early Malacostracans and *Ceratiocaris* as a Possible Stem Eumalacostracan. *Journal of Crustacean Biology*, **35**(2), 191-201 (2015).
44. Mángano, M.G., et al. Nonbiomineralized carapaces in Cambrian seafloor landscapes (Sirius Passet, Greenland): opening a new window into early Phanerozoic benthic ecology. *Geology*, **40**(6), 519-522 (2012).
45. Vaucher, R., et al. Bedforms in a tidally modulated ridge and runnel shoreface (Berck-Plage; North France): implications for the geological record. *Bulletin de la Société Géologique de France*, **189**(1) (2018).
46. Álvaro, J.J., et al. Diachronism in the late Neoproterozoic–Cambrian arc-rift transition of North Gondwana: A comparison of Morocco and the Iberian Ossa-Morena Zone. *Journal of African Earth Sciences*, **98**, 113-132 (2014).
47. Gaines, R.R., Burgess Shale-type preservation and its distribution in space and time. *The Paleontological Society Papers*, **20**, 123-146 (2014).
48. Hammarlund, E.U., et al. Early Cambrian oxygen minimum zone-like conditions at Chengjiang. *Earth and Planetary Science Letters*, **475**, 160-168 (2017).
49. Qi, C., et al. Influence of redox conditions on animal distribution and soft-bodied fossil preservation of the Lower Cambrian Chengjiang Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **507**, 180-187 (2018).
50. Saleh, F., et al. The Chengjiang Biota inhabited a deltaic environment. *Nature communications*, **13**(1), 1-9 (2022).
51. Saleh, F., et al. Taphonomic bias in exceptionally preserved biotas. *Earth and Planetary Science Letters*, **529**, 115873 (2020).
52. Saleh, F., et al. A novel tool to untangle the ecology and fossil preservation knot in exceptionally preserved biotas. *Earth and Planetary Science Letters*, **569**, 117061 (2021).
53. Whitaker, A.F., Schiffbauer, J.D., Briggs, D.E., Leibach, W.W. & Kimmig, J. Preservation and diagenesis of soft-bodied fossils and the occurrence of phosphate-associated rare earth elements in the Cambrian (Wuliuan) Spence Shale Lagerstätte. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **592**, 110909 (2022).
54. Saleh, F., Ma, X., Guenser, P., Mángano, M.G., Buatois, L.A. and Antcliff, J.B. Probability-based preservational variations within the early Cambrian Chengjiang biota (China). *PeerJ*, **10**, p.e13869 (2022).
55. Saleh, F., Pittet, B., Perrillat, J.P. & Lefebvre, B. Orbital control on exceptional fossil preservation. *Geology*, **47**(2), 103-106 (2019).
56. Saleh, F., et al. Iron from continental weathering dictated soft-part preservation during the Early Ordovician. *Terra Nova*, **34**(3), 163-168 (2022).
57. Anderson, R.P., Tosca, N.J., Gaines, R.R., Koch, N.M. and Briggs, D.E.G. A mineralogical signature for Burgess Shale–type fossilization. *Geology*, **46**(4), 347-350 (2018).

58. Anderson, R.P., Tosca, N.J., Saupe, E.E., Wade, J. & Briggs, D.E.G. Early formation and taphonomic significance of kaolinite associated with Burgess Shale fossils. *Geology*, **49**(4), 355-359 (2021).
59. Van Roy, P. Non-trilobite arthropods from the Ordovician of Morocco. Unpublished Ph.D. thesis (2006).
60. Daley, A.C., Budd, G.E. & Caron, J.B. Morphology and systematics of the anomalocaridid arthropod *Hurdia* from the Middle Cambrian of British Columbia and Utah. *Journal of Systematic Palaeontology*, **11**(7), 743-787 (2013).

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