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An introduction to the Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco

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Abstract:

The exquisitely preserved, diverse and abundant fossil assemblages yielded by the ‘echinoderm meadows’ of the Tafilalt region of the eastern Anti-Atlas represent a new Konservat-Lagerstätte, one of the few exceptionally preserved Late Ordovician open marine faunas found globally, giving us an insight into the radiation of life during the later phases of the Great Ordovician Biodiversification Event (GOBE) in high-latitude peri-Gondwana. The GOBE saw most phyla increase exponentially in diversity, at the fastest rate of the entire Phanerozoic and represents one of the most significant events in the evolution of the marine biosphere, preceding the end-Ordovician mass extinction. This volume is the culmination of over 20 years of research by several international teams that integrates sedimentology, palaeobiology and palaeobiogeographic approaches. Nine different phyla and several soft-bodied problematica are represented in the Tafilalt, including several notable echinoderm

Lagerstätten. This volume brings together a series of contributions that look at diverse aspects of the biota, including the stratigraphic distribution of the faunas, systematic palaeontology, preservation and palaeobiogeographic features and the nature and impact of the international fossil trade on these exceptionally preserved fossil faunas.

The Tafilalt Biota represents a series of highly significant fossil assemblages found within the Tafilalt area of the Moroccan Anti-Atlas, centered around the Ziz River. The region, and in particular the town of Erfoud, are noted for their local fossil industry. The Tafilalt assemblages vary from those that consist of exceptionally preserved fossil remains, some with soft tissue preservation (**Budil & Fatka 2020; Lefebvre *et al.* In-review**), to those that are rich in shelly fossil remains, including a series of echinoderm Lagerstätten or starfish beds that have yielded exceptionally preserved articulated specimens showing delicate structures such as arms, brachioles, and theca (**Botting 2018; Zamora *et al.* 2019; Nohejlová & Lefebvre 2021; Lefebvre *et al.* 2022a, 2022b**). For more than 20 years, these fossils have been exploited for their commercial value within the international fossil trade leading to important scientific discoveries (**Gutiérrez-Marco & García-Bellido 2018**). As these fossils are widely available for sale commercially, it was a key aim of the volume to describe these fossil faunas and to bring together as many geological and palaeontological aspects as possible. The Tafilalt Biota dates from the Late Ordovician, approximately 458 to 443 million years ago, and represents a critical point in the development and diversification of invertebrate communities during the Great Ordovician Biodiversification Event or GOBE (**Álvaro *et al.* 2022**). The GOBE is one of the major evolutionary radiations in the history of animal life; based on the shelly fossil record, is classically considered to start approximately 40 million years after the Cambrian Explosion. In comparison with the Cambrian Explosion, about twice as much biodiversity was added at the ordinal level during the GOBE, about three times at the family level, and nearly four times at the genus level; during this time, the distinctive Cambrian Evolutionary Fauna is replaced by the Palaeozoic Evolutionary Fauna, dominated by suspension feeders. The Early Ordovician Fezouata Biota, from the Anti-Atlas region close to Zagora, documents the onset of diversification of the GOBE (**Lefebvre *et al.* in review**). In contrast, the Late Ordovician Tafilalt Biota provides a snapshot of peak diversity during the closing stages of the GOBE.

In early to mid-Palaeozoic times, Morocco was situated on the margin of Gondwana at a high latitude; as a consequence, the Tafilalt Biota provides a significant high latitude perspective on the GOBE (**Lefebvre *et al.* in review**). These faunas demonstrate diverse

affinities to neighbouring peri-Gondwanan regions, predominantly with other regions of the Mediterranean Province, and in particular with Bohemia (Czech Republic) (**Gutiérrez-Marco *et al.* 2019**), while brachiopods are largely endemic (**Colmenar *et al.* 2018**). Being high latitude, the faunas also show evidence of gigantism induced by cold, nutrient-rich waters, as observed in bryozoans and the conulariid *Archaeoconularia* (**Van Iten *et al.* 2018**; **Ernst 2019**).

This volume brings together twenty contributions that explore different aspects of the Tafilalt Biota, including the geological setting and stratigraphic distribution of the fauna (**Álvaro *et al.* 2022**), followed by an account of the international fossil trade (**Gutiérrez-Marco & García-Bellido 2018**), and finally a series of detailed systematic contributions that look at several systematic groups describing many new taxa and trace fossils (**Muir *et al.* 2018**). The main achievement of this volume is to bring together stratigraphic and faunal features of the Tafilalt Biota integrated within a single book volume, which represents a significant advance in the understanding of the biota and its significance to the GOBE.

Geological and faunal context

The volume begins with an overview of the fauna (**Lefebvre *et al.* in review**), where all the different faunal elements, as well as trace fossils, are described. This is followed by a detailed analysis of the Ordovician stratigraphy of the eastern Anti-Atlas, Morocco, and a global overview of faunal changes in benthic communities (**Álvaro *et al.* 2022**).

International fossil trade

One of the more high-profile and novel contributions within this volume looks at the international fossil trade from the Palaeozoic of the Anti-Atlas, Morocco (**Gutiérrez-Marco & García-Bellido 2018**). The annual turnover of the fossil trade from southern Morocco was estimated at around US\$ 40 million, being the primary source of income to more than 50,000 people, generating a true 'fossil industry' (**Gutiérrez-Marco & García-Bellido 2018**). This study looks into the fossil hunting economy of diggers, miners, artisans, and those that prepare and restore fossils. It follows the Moroccan wholesalers, who annually attend the fossil fairs across the world. They detail the ongoing threat to the palaeontological sites while discussing proposed measures for sustainable development to protect this geological heritage while maintaining a vital part of the local economy (**Gutiérrez-Marco & García-Bellido 2018**).

Early Palaeozoic faunas from the Anti-Atlas

Trilobites are one of the most iconic elements of the Tafilalt Biota; we present two contributions that look at different aspects of this fossil group. The significance of trilobites from the Bou Nemrou assemblage (**Gutiérrez-Marco et al. 2019**) describes 11 species belonging to ten genera with strong Bohemian affinities. In contrast, **Budil & Fatka (2020)** document the preservation of trilobite soft parts. **Colmenar et al. (2018)** provide a synopsis of the low diversity, mostly endemic Late Ordovician brachiopod faunas in the Anti-Atlas. **Villas & Colmenar (2018)** describe brachiopods from the Upper Ordovician of the Erfoud area and their stratigraphic correlation to the bryozoan-rich Khabt-el-Hajar Formation, with strong Mediterranean affinities. The volume includes a detailed analysis of a diverse range of early Palaeozoic invertebrates, including conulariids from the Katian Upper Tiouririne Formation (**Van Iten et al. 2018**), bryozoans (**Ernst 2019**), benthic graptolites and a possible hydroid (**Gutiérrez-Marco et al. 2020**), and molluscs (**Ebbestad et al. 2019**). The latter describes 30 species of tergomyans, gastropods, bivalves, and cephalopods. The conulariids are assigned to *Archaeoconularia* with their large size suggestive of gigantism induced by cold, nutrient-rich waters; that is also observed in the bryozoans (**Ernst 2019**). Finally, **Muir et al. (2018)** describe the early Cambrian-type agglutinated tube *Onuphionella corusca*. This is the first report of *Onuphionella* from Ordovician rocks and the first from Gondwana.

Echinoderm Lagerstätten

The ‘starfish beds’ of the Tafilalt Biota represent a series of exceptionally preserved echinoderm assemblages. Despite the name ‘starfish beds’, asterozoans (ophiuroids and asteroids) represent a relatively minor component of the fauna, with other echinoderms such as mitrate stylophorans (**Lefebvre et al. 2022a**) and solutans (**Nohejlová & Lefebvre 2021**) being far more significant. The contribution from **Lefebvre et al. (2022b)** presents a new and diverse fauna of Middle to Late Ordovician cornute stylophorans from the Tafilalt. Other exceptionally preserved echinoderms have been described along with their mode of preservation and their paleobiogeographic distribution, including crinoids (**Botting, 2018**), edrioasteroids (**Sumrall & Zamora 2018**), *Hexedriocystis*, (**Zamora & Sumrall 2019**), rhombiferans (**Zamora et al. 2019**) and the coronate *Mespilocystites sp.* (**Zamora & Sumrall 2018**), the latter representing the first report from Africa. **Botting (2018)** describes a crinoid assemblage of at least ten species from the biota. While *Hexedriocystis* is presented as an enigmatic echinoderm with a combination of isorophid, edrioasteroid and blastozoan characteristics (**Zamora & Sumrall 2019**). Exceptionally preserved edrioasteroids

Moroccopyrgus matacarros and *Euryeschatia reboulorum* are found only attached to rhombiferans and conulariids, suggesting a commensal relationship between these fossil groups (Sumrall & Zamora 2018).

The style of preservation of these echinoderms, combined with observed sedimentary structures, indicates a mixture of autochthonous and para-autochthonous assemblages. At Bou Nemrou, the preservation of soft tissues in trilobites (Gutiérrez-Marco *et al.* 2019, Budil & Fatka 2020) and the exceptional preservation of articulated echinoderms (Lefebvre *et al.* 2022b) suggest these are autochthonous assemblages, while the other echinoderm Lagerstätten are a result of limited transport and show evidence of current aligned fossil echinoderms. Nevertheless, these assemblages provide a record of localised and exceptionally preserved echinoderm meadows at a critical juncture in the history of life.

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