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The Late Ordovician Tafilalt Biota, Anti-Atlas, Morocco: a high-latitude perspective on the GOBE

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Abstract

The extensive, predominantly siliciclastic deposits of the Upper Ordovician of the Tafilalt have long been the subject of scientific investigation. In the past 25 years, intensified collecting for commercial purposes has resulted in the discovery of several exceptionally-preserved faunas (*Konservat-Lagerstätten*) in the Tafilalt region, preserving a range of non-biomineralised and soft-bodied organisms. The preservation of these fossils in the coarse clastic sediments of the Tafilalt is surprising, and in the case of soft-bodied organisms, remarkably similar to the preservational mode of typical Ediacaran biotas. These relatively recent discoveries have increased the scientific significance of the Tafilalt Biota, providing an

unparalleled insight into the composition and temporal evolution of the shallow, open-marine ecosystems and their denizens during the later stages of the Great Ordovician Biodiversification Event. At least nine different phyla, in addition to several soft-bodied problematica are represented in the Tafilalt. While the highly diverse and remarkably well-preserved echinoderm and euarthropod faunas are most emblematic for the Tafilalt Biota, further studies have revealed a relatively high diversity of molluscs and brachiopods. Among soft-bodied fossils, the problematic paropsonemid eldonids are iconic for the Tafilalt and stand out both through their abundance, and their wide temporal and geographic range throughout the area.

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Situated at the eastern-most extremity of the Anti-Atlas, in south-eastern Morocco, the Tafilalt (or 'Tafilalelt') corresponds to a large plain covered by Quaternary sediments, separating markedly distinct Upper Ordovician successions on its western and eastern flanks (Fig. 1). The high hills of the western Tafilalt (e.g. Jbel Tijarfaiouine) are characterized by predominantly siliciclastic successions typical of the central and eastern Anti-Atlas (Destombes *et al.* 1985; Álvaro *et al.* 2022). However, in the western Tafilalt, the Upper Ordovician succession is characterized by particularly thick Sandbian–middle Katian deposits (Lower Ktaoua and Upper Tiouririne formations) along a narrow, 10 km wide, N-S orientated zone corresponding to a locally subsident area (Fig. 1; Destombes 2006). The Ktaoua Group in this region is unconformably overlain by the Upper Second Bani Formation (upper Hirnantian) (Fig. 2; Destombes 2006; Colmenar & Álvaro 2015; Álvaro *et al.* 2022). In this area, the absence of the upper part of the Upper Ktaoua Formation (upper Katian) and of the overlying Lower Second Bani Formation (lower Hirnantian) is most likely a result of erosion during the Hirnantian glaciation (Destombes *et al.* 1985; Colmenar & Álvaro 2015; Álvaro *et al.* 2022). In marked contrast, the low hills of the eastern Tafilalt (east of Erfoud) are characterized by the only known occurrence in the whole Anti-Atlas of upper Katian bryozoan- and echinoderm-dominated limestones of the Khabt-el-Hajar Formation (Fig. 2; Destombes *et al.* 1985; Álvaro *et al.* 2022). In the eastern Tafilalt, Palaeozoic rocks are unconformably overlain by the thick, almost tabular Plio-Pleistocene deposits forming the Hamada du Guir (Fig. 1).

After the pioneering field investigations of Neltner (1929) and Clariond (1933, 1934, 1935), who first provided evidence for the occurrence of Upper Ordovician fossils (trilobites) in the Tafilalt, all main geological features were already identified on the first 1:200.000 geological map of this area produced by Clariond (1944). In the second half of the 20th century, the stratigraphic framework of the Upper Ordovician succession in the Tafilalt area

was further developed by Choubert *et al.* (1952) and primarily by Destombes (1962, 1970, 2006; see also Destombes *et al.* 1985), who defined all main lithological units (Fig. 2; see Álvaro *et al.* 2022). Destombes' mapping efforts in the Tafilalt area provided abundant and diverse Late Ordovician faunas, comprising brachiopods (Havlíček 1971), echinoderms (Chauvel 1966, 1969, 1977, 1978; Termier and Termier 1970; Le Menn and Spjeldnaes 1986), hyoliths (Marek, 1983), gastropods and tergomyans (Horný 1997), machaeridians (Chauvel 1967), and trilobites (Destombes 1966, 1967, 1972). At the close of the 20th century, the Tafilalt was known for its diverse Late Ordovician shelly faunas, typical of the high-latitude Mediterranean Province (Destombes *et al.* 1985).

In the early 2000s, a marked increase in the activity of fossil traders in the eastern Anti-Atlas prompted the discovery and commercial exploitation of a large number of new fossiliferous sites in the Upper Ordovician of the Tafilalt, veritably inundating all main international fossil and mineral shows with all kinds of remarkable specimens (Lebrun 2018; Gutiérrez-Marco and García-Bellido 2018). A major outcome of this intensive commercial quarrying activity was the discovery of exceptionally preserved 'soft bodied' to lightly sclerotized taxa of the Tafilalt Biota (e.g. aglaspidid and cheloniellid arthropods, palaeoscolecoid worms, phyllodocid annelids, paropsonemid eldonioids; Samuelsson *et al.* 2001; Van Roy 2006a, b; Vinther *et al.* 2008; Gutiérrez-Marco & García-Bellido 2015; Parry 2017; MacGabhann *et al.* 2019) and several "starfish beds" (Konzentrat-Lagerstätten corresponding to the accumulation of thousands of fully articulated to slightly disarticulated echinoderms; Lefebvre *et al.* 2007, 2008, 2010; Hunter *et al.* 2010; Sumrall & Zamora 2011; Nardin & Régnault 2015). In some cases, trilobites retain traces of their internal anatomy, such as parts of their digestive system and muscle insertion surfaces (Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al.* 2019a; Budil & Fatka 2020).

Although not comparable to the Fezouata Biota from the Lower Ordovician of the Zagora area in terms of faunal diversity or the extent of labile part preservation (Van Roy *et al.* 2010, 2015; Lefebvre *et al.* 2016a; Martin *et al.* 2016a; Saleh *et al.* 2020a, b, 2021), the Tafilalt Biota represents another major Konservat-Lagerstätte from Morocco, embracing a series of assemblages stratigraphically distributed from the lower Sandbian (Izegguirene Formation) to the middle Katian (Upper Tiouririne Formation). Both shelly fossils (e.g. brachiopods, bryozoans, echinoderms, trilobites; Table 1) and non-biomineralised metazoans of the Tafilalt Biota are preserved in medium- to coarse-grained sandstones, the latter in a style reminiscent of the Ediacaran fossils of the Flinders Ranges in Australia (Samuelsson *et al.* 2001; Van Roy 2006a, 2011). Contrary to most other Late Ordovician Konservat-Lagerstätten (e.g. Beecher's Trilobite Bed, Llanfawr, William Lake), situated at relatively low palaeolatitudes and yielding low diversity assemblages (Young *et al.* 2007; Farrell *et al.* 2009; Botting *et al.* 2011), the Tafilalt Biota provides a valuable record of the composition and structuring of diverse high-latitude marine ecosystems during a critical phase of the Great Ordovician Biodiversification Event, which saw an exponential increase in diversity for most metazoan phyla, at the fastest rate of the entire Phanerozoic (see e.g. Webby *et al.* 2004 for an overview).

The Tafilalt Biota

A brief overview of all main invertebrate groups occurring in the Upper Ordovician of the Tafilalt is provided below. More detailed accounts are provided for most of them in this volume (Table 1; for a detailed list of all invertebrate genera see Álvaro *et al.* 2022, annex 1).

Cnidarians

Within the Tafilalt sites, cnidarians are represented by both common fossils, the conulariids, and much rarer forms, the hydroids. The Conulariida form a group of extinct Scyphozoa,

which possessed a very elongated pyramidal shell. In Morocco, the unusual dimensions (>50 cm) of some "giant" conulariids, such as *Archaeoconularia* cf. *imperialis*, may be explained by their slow growth in cool water conditions (Van Iten *et al.* 2018). In the Upper Ordovician of the Tafilalt, they are often found upright, in living position, in quartz rich sandstone horizons (Fig. 3). The exposed portions of their shells were then often colonized by epibionts such as brachiopods and echinoderms, more specifically edrioasteroids (see also Sumrall & Zamora 2011, 2018; Bruthansová & Van Iten 2020). In contrast, Hydrozoa are very rare organisms, seldom preserved in the fossil record. The only specimen discovered in the Tafilalt, although it is preserved in relief, unfortunately does not show sufficient anatomical characters to allow a detailed appraisal; it can only be identified as the probable hydroid *Webbyites?* sp. (see Gutiérrez-Marco *et al.* 2020a).

Annelids (machaeridians)

Machaeridians were first described based on isolated biomineralized shell plates (De Koninck 1857), but even after the discovery of complete articulated dorsal armours, their affinities long remained problematic. This conundrum was finally resolved with the discovery of a specimen preserving the soft parts in the Lower Ordovician Fezouata Biota, which conclusively demonstrated that machaeridians are a clade of biomineralizing annelids (Vinther *et al.* 2008). A further specimen from this fauna, which preserves the jaws, confirmed a position for Machaeridia as derived members of the annelid crown, resolving as in-group phyllodocids in phylogenetic analyses (Parry *et al.* 2019). With the exception of some derived biseriata lepidocoleids, the machaeridian dorsal armour is composed of four rows of metamericly arranged calcitic shell plates, which are homologous to the elytra of aphroditiform phyllodocids, both structures being likely derived from modified cirri (Vinther *et al.* 2008; Parry 2017; Parry *et al.* 2019); in an example of convergence with molluscs, these shell plates grow through marginal accretion. Machaeridians display a trend towards

reduction of the outer shell plates, with the most basal, and potentially paraphyletic, dorso-ventrally flattened epifaunal family Plumulitidae expressing all plates in full, whereas in the box-shaped Turrilepadidae and the worm-like infaunal Lepidocoleidae the outer plates are reduced in size, to the point of being completely lost in the most derived lepidocoleids (Dzik 1986; Adrain 1992; Högström & Taylor 2001; Högström *et al.* 2009; Parry 2017; Parry *et al.* 2014). While isolated machaeridian shell plates are fairly common as fossils, articulated armours tend to be exceedingly rare.

In the Tafilalt Biota, fully articulated armours of the plumulitid *Plumulites tafennaensis* Chauvel, 1967 are locally abundant at two adjacent sites in the Isthlou area and at Tizi Egidou, in the Katian Upper Tiouririne Formation (Fig. 4). A few additional complete armours are also known from the Mecissi area. At other Upper Ordovician sites in the Tafilalt, isolated shell plates of *P. tafennaensis* occur sporadically. The localities at Isthlou have proven particularly prolific, yielding several hundreds of complete armours, with slabs often preserving associations of multiple individuals; in fact, the number of articulated armours from Isthlou alone eclipses by a wide margin the total number of complete plumulitids from the rest of the world combined. The plumulitid assemblages at Isthlou are marked by the presence of a wide range of sizes, providing unparalleled insight into the ontogenetic development of the dorsal armour; in addition, the largest specimens reach lengths approaching 15 cm, making them among the largest machaeridians on record. Several of the fossils exhibit healed injuries on the shell plates, providing new information on machaeridian plate growth and repair, and ecological interactions (Parry 2017).

Molluscs

Although they can be locally abundant and diverse, molluscs (bivalves, cephalopods, gastropods, rostroconchs, tergomyans) are poorly investigated components of Ordovician

faunas from the Anti-Atlas (Termier & Termier 1950; Babin & Destombes 1990; Horný 1997; Kröger & Lefebvre 2012; Ebbestad & Lefebvre 2015; Ebbestad 2016; Polechová 2016; Ebbestad *et al.* 2019). This situation is particularly true in the Upper Ordovician of the Tafilalt, where only gastropods and tergomyans were previously described (Horný 1997), which are here reevaluated based on new material (Ebbestad *et al.* 2019). Late Ordovician bivalves have been formally described from various areas in the Anti-Atlas, but hitherto not from the Tafilalt (Babin & Destombes 1990; Ebbestad *et al.* 2019). Finally, cephalopods are here formally described for the first time in the Upper Ordovician of the Anti-Atlas (Ebbestad *et al.* 2019). In the Tafilalt, cephalopods, gastropods and tergomyans occur both in shales and silty sandstones of the Lower Ktaoua Formation and in coarser lithologies of the Upper Tiouririne Formation (Horný 1997; Destombes 2006; Ebbestad *et al.* 2019). In contrast, the distribution of bivalves in the Tafilalt is apparently restricted to the Upper Tiouririne Formation (Destombes 2006).

Ordovician molluscs from the Anti-Atlas display strong palaeobiogeographic affinities with other high-latitude assemblages of the Mediterranean Province: mostly with France (Armorican Massif, Montagne Noire) and the Iberian Peninsula in the Early and Middle Ordovician (Babin & Destombes 1990; Horný 1997; Kröger & Lefebvre 2012; Ebbestad 2016; Polechová 2016; Ebbestad *et al.* 2020), but rather with the Prague Basin (Czech Republic) in the Late Ordovician (Horný 1997; Ebbestad *et al.* 2019).

Bivalves. In the Upper Ordovician of the central and eastern Anti-Atlas, bivalves are diverse (13 taxa), though mostly occurring in coarse lithologies of the Lower Second Bani Formation (Hirnantian) (Ebbestad *et al.* 2019). Although rare remains of bivalves were reported in the Upper Tiouririne Formation (mid Katian) both in the western (e.g. Jbel Taklimt, N of Taguerroumt; Destombes 2006) and eastern Tafilalt (e.g. Oued Er Rosfa el Hamra;

Destombes 2006), few of them were so far formally identified in the Upper Ordovician of the Tafilalt (Ebbestad *et al.* 2019).

In the Early–Mid Ordovician, bivalves underwent a major diversification on soft, siliciclastic substrates of the peri-Gondwanan regions (Babin 1993; Babin & Destombes 1990; Cope & Babin 1999). During the Late Ordovician, bivalves expanded not only towards new substrates and modes of life, but also to other palaeocontinents (Cope & Babin 1999; Cope 2004; Cope & Kříž 2013). Late Ordovician (mostly Hirnantian) bivalves from the Anti-Atlas display affinities with both Bohemia (e.g. *Modiolopsis*, *Myoplusia*, *Praenucula* and *Sluha*) and Baltica (e.g. *Ambonychia*, *Cleionychia*, *Cyrtodonta* and *Nuculites*) (Ebbestad *et al.* 2019).

Cephalopods. In the western Tafilalt, unidentified remains of late Sandbian to early Katian cephalopods were reported from several localities in the Lower Ktaoua Formation (e.g. Bou el Koualb, Jbel Taklimt; Destombes 2006). In the eastern Tafilalt, the overlying Upper Tiouririne Formation yielded more abundant and better preserved specimens of the orthocerid *Tafadnatoceras tiouririnense* (Ebbestad *et al.* 2019).

Probably originating in tropical regions during the late Cambrian, cephalopods underwent a more or less continuous diversification during most of the Ordovician (Frey *et al.* 2004; Kröger *et al.* 2009). Most available data on Late Ordovician cephalopods are from low latitude regions, and mostly from Laurentia (Frey *et al.* 2004; Kröger 2013). Very little is known about Ordovician cephalopods from high-latitude areas of the Mediterranean Province (e.g. Marek 1999; Kröger & Evans 2011; Kröger & Lefebvre 2012; Aubrechtová 2015). Although the only Katian cephalopod described so far in the Tafilalt (*T. tiouririnense*) is endemic to this region, some Late Ordovician actinocerids occurring elsewhere in the Anti-Atlas (e.g. *Wadema*) suggest possible affinities with remote, low latitude peri-Gondwanan areas (e.g. Australia, Thailand; Ebbestad *et al.* 2019).

Gastropods and tergomyans. With 14 described taxa, gastropods and the closely related tergomyans are the most diverse molluscs occurring in the Upper Ordovician of the Anti-Atlas (Horný 1997; Ebbestad *et al.* 2019). Four of them are part of the Tafilalt Biota: the tergomyan *Sinuitopsis neglecta*, and the three gastropods *Daechospira amouguerana*, *Nonorios pater* and *Radvanospira antiquata* (Ebbestad *et al.* 2019). At Bou el Koualb (western Tafilalt), all four taxa co-occur in the Lower Ktaoua Formation (Horný 1997; Destombes 2006; Ebbestad *et al.* 2019). In the overlying Upper Tiouririne Formation, *R. antiquata* is widespread both in western (e.g. N of Taguerroumt) and eastern Tafilalt (e.g. Oued Er Rosfa el Hamra, Rkint ech Chih), whereas *D. amouguerana* is only known from one locality in the western Tafilalt (Jbel Taklimt) (Horný 1997; Destombes 2006; Ebbestad *et al.* 2019).

Late Ordovician gastropods and tergomyans from the Anti-Atlas display strong affinities with both earlier Moroccan faunas (e.g. *Sinuites* is present in the Fezouata and Tachilla formations; Horný 1997; Ebbestad 2016) and coeval assemblages from other high-latitude peri-Gondwanan regions. For example, all four genera occurring in the Tafilalt are also found in Bohemia (Czech Republic). One of them (*Daechospira*) also occurs in Baltica (Ebbestad *et al.* 2019).

Rostroconchs. Ongoing research on Late Ordovician rostroconch molluscs from the Anti-Atlas (Gutiérrez-Marco & Sá 2019) determined the presence of the Bohemian species *Ribeiria apusoides* Schubert and Waagen from a number of localities in the Upper Tiouririne Formation in the eastern Anti-Atlas. A single occurrence of *Technophorus* sp. is also known from the top of the Upper Ktaoua Formation of the central Anti-Atlas.

Brachiopods

With over 80 taxa described, brachiopods are one of the most diverse and most investigated groups of marine invertebrates in the Upper Ordovician of the Anti-Atlas (Havlíček 1971, 1990; Mergl 1983; Villas *et al.* 2006; Álvaro *et al.* 2007; Colmenar & Álvaro 2015; Colmenar *et al.* 2018; Villas & Colmenar 2018). In the eastern Anti-Atlas, brachiopods are usually rare in Sandbian–middle Katian starfish beds, but they are locally extremely abundant in low-diversity coquinas associated with shallow, high-energy, shoreface deposits typical of benthic associations BA3 *sensu* Boucot (1975) (Colmenar & Álvaro 2015). In the Tafilalt, the fossil record of brachiopods is particularly well known, with about 50 taxa belonging to successive assemblages documenting a regular and major increase in diversity from the early Sandbian (Izegguirene Formation) to the mid Katian (Upper Tiouririne Formation) (Havlíček 1971; Colmenar *et al.* 2018).

In the Anti-Atlas, the Izegguirene Formation (lower Sandbian) yielded low diversity brachiopod assemblages comprising only representatives of the two rhynchonelliformean genera *Mimella* and *Tafilaltia* (Colmenar *et al.* 2018). In the First Bani Group, these two taxa also occur in the Darriwilian Guezzart Formation (Havlíček 1971).

In the lowermost part of the overlying Lower Ktaoua Formation (Ouaglout Member, lower Sandbian), brachiopod assemblages are more diverse (about 10 taxa) and dominated by dalmanelloids (*Heterorthis retrorsistria*, *Onniella* sp., *Tafilaltia destombesi*) and plectorthoids (*Mimella* sp., *Tazzarinia drotae*, *T. foraminosa*), associated with a triplesoid (*Triplesia simplex*) and strophomenoids (e.g. *Rafinesquina* cf. *vinicensis*) (Colmenar *et al.* 2018). In the western Tafilalt, coeval sandstones of the lower part of the Lower Ktaoua Formation yielded mostly monospecific accumulations of fragmented shells of *Tafilaltia destombesi*, associated with rare other taxa (orthids indet., *Tissintia* sp.). This low-diversity assemblage was interpreted as a typical BA3 association occurring in high energy, shoreface environments (Colmenar & Álvaro 2015).

A moderately diverse brachiopod assemblage is present in the median part of the Lower Ktaoua Formation (Assif n'Rhart Member, upper Sandbian–lower Katian), with aegiromenids (e.g. *Aegiromena aquila*), draboviids (*Drabovia pentagonomya*, *D. tenuiseptata* and *Drabovinella regia*), heterorthids (e.g. *Heterorthis* cf. *retrosistria*), plectorthoids (e.g. *Gelidorthis partita*), and rafinesquinines (e.g. *Rafinesquina pseudoloricata*) (Havlíček 1971; Colmenar *et al.* 2018).

Brachiopod diversity increases significantly (18 taxa) in the upper part of the Lower Ktaoua Formation (Agadir-Tissint Member, lower Katian), with distinct assemblages associated with diverse environmental conditions and facies (Colmenar *et al.* 2018). In these levels, brachiopod assemblages are generally dominated by heterorthids (*Heterorthis alternata*, *H. planelliptica*, *Tafilaltia brevimusculosa*, *Svobodaina armoricana*) and rafinesquinines (*Rafinesquina pomoides* and *R. pseudoloricata*), associated with less common taxa, such as aegiromenids (e.g. *Aegiromena descendens*), dalmanellids (*Dalmanella agadirensis* and *Howellites altera*), leptostrophiids (e.g. *Eostropheodonta filicosta*), rhipidomellids (e.g. *Protomendacella eos*), trigonirhynchiids (e.g. *Rostricellula ambigena*), and trematid linguliformean brachiopods (Havlíček 1971; Colmenar *et al.* 2018). In the western Tafilalt, high energy coeval sandstones yielded abundant, fragmented brachiopod remains dominated by *Heterorthis alternata*, associated with common draboviids (e.g. *Destombesium* sp.), rafinesquinines (e.g. *Rafinesquina pseudoloricata*) and trigonirhynchiids (e.g. *Rostricellula ambigena*) and rare representatives of other taxa (*Drabovinella* sp., *Hirnantia plateana*, *Linguloidea* indet. and *Rafinesquina pomoides*) (Colmenar and Álvaro 2015).

In the Anti-Atlas, brachiopod diversity remains particularly high in the uppermost levels of the Lower Ktaoua Formation and the lowermost part of the overlying Upper Tiouririne Formation (middle Katian) (Havlíček 1971; Colmenar *et al.* 2018). Assemblages are

dominated by draboviids (*Destombesium akkaensis*, *D. pectiniferum*, *Drabovia circula*, *Drabovinella* sp. and *Hirnantia plateana*), heterorthids (*Heterorthis sosia*, *Svobodaina feisti*, *Tafilaltia brevimusculosa* and *T. occidentalis*) and rafinesquinines (*Rafinesquina* sp.). Less common elements include aegiromenids (e.g. *Aegiromena aquila*), leptaenines (e.g. *Kiaeromena? chouberti*), leptostrophiids (e.g. *Eostropheodonta filicosta*), trigonirhynchiids (e.g. *Rostricellula* sp.), triplesiids (e.g. *Cliftonia tenuicostata*), and both discinid and trematid linguliformean brachiopods (Havlíček 1971; Colmenar *et al.* 2018). In the western Tafilalt, two distinct low diversity BA3 brachiopod associations were described in the uppermost part of the Lower Ktaoua Formation (Colmenar & Álvaro 2015). The first one comprises only two taxa (*Drabovinella* sp. with less common *Schizocrania* sp.), whereas the second association is dominated by *Svobodaina feisti*, associated with common *Schizocrania* sp., and rare *Tafilaltia* sp. and *Rafinesquina* sp. (Colmenar & Álvaro 2015). Both associations occur in high energy shoreface sandstones.

In the western Tafilalt, another, distinct, low-diversity brachiopod assemblage associated with comparable high-energy, proximal environmental conditions was described from the uppermost part of the Tiouririne Formation (Colmenar & Álvaro 2015). This assemblage consists of abundant, fragmented remains belonging to only two taxa: *Destombesium akkaensis* and *Eostropheodonta? tafilaltensis*. In the eastern Tafilalt, the uppermost part of the Upper Tiouririne Formation yielded abundant, fragmented remains of a more diverse middle Katian brachiopod assemblage (8 taxa) comprising draboviids (e.g. *Hirnantia* sp.), leptaenines (e.g. *Kiaeromena? chouberti*), and trigonirhynchiids (e.g. *Rostricellula termieri*) (Villas & Colmenar 2018).

In the same area (E of Erfoud), a low diversity brachiopod fauna (three taxa) was found in the overlying bryozoan limestones of the Khabt-el-Hajar Formation. This late Katian

assemblage comprises dalmanellids (e.g. *Paucicrura catalanica*), draboviids (*Drabovia* sp.) and triplesiids (*Streptis?* sp.) (Villas & Colmenar 2018).

The Upper Second Bani Formation (upper Hirnantian) yielded two successive, low diversity brachiopod assemblages (Villas *et al.* 2006; Colmenar & Álvaro 2015; Colmenar *et al.* 2018). The earliest one (Tamekhardt Member) comprises only draboviids (e.g. *Destombesium ellipsoides*), heterorthids (e.g. *Arenorthis arenaria*) and leptostrophiids (e.g. *Eostropheodonta* sp.). In the overlying Amoukir Member, the second assemblage consists of draboviids (*Hirnantia sagittifera* and *Kinnella kielanae*), leptostrophiids (*Eostropheodonta jebiletensis*, *E. squamosa*) and a rynchotrematoid (*Plectothyrella crassicosta*) (Colmenar & Álvaro 2015; Colmenar *et al.* 2018).

Sandbian and early Katian brachiopod assemblages from the Tafilalt are dominated by aegiromenids, draboviids and heterorthids, which are typical faunal elements occurring in all other peri-Gondwanan regions of the high-latitude Mediterranean Province (e.g. Czech Republic, France, Italy, Portugal, Spain; Havlíček 1971, 1989; Colmenar *et al.* 2017, 2018). During the late Katian, a dramatic turnover in brachiopod assemblages took place in the Mediterranean Province, with the replacement of endemic taxa adapted to cool environments by the more cosmopolitan *Nicolella* Fauna, typical of lower latitude, more temperate regions (Villas *et al.* 1987; Villas 1995; Colmenar *et al.* 2013, 2017). This faunal change coincided with a major ecological transition (Boda Event; Fortey and Cocks 2005) and the shift from siliciclastic to carbonate-dominated sedimentation (Villas *et al.* 2002, 2018; Colmenar *et al.* 2018). In marked contrast with the situation in all other Mediterranean regions, low-diversity brachiopod assemblages adapted to cool environments persisted during the late Katian almost everywhere in the Anti-Atlas. The only exception is the eastern Tafilalt, where the bryozoan limestones of the Khabt-el-Hajar Formation yielded some more cosmopolitan elements (e.g. *Paucicrura catalanica*) (Villas & Colmenar 2018).

The low diversity assemblages with *Hirnantia* Fauna occurring in Morocco are clear representatives of the so-called Bani Province (Rong & Harper 1988), which extended around polar latitudes of Gondwana. In Morocco, differently from elsewhere, the first pulse of the end-Ordovician extinction, linked with the onset of the Hirnantian glaciation, barely affected, in both diversity and taxonomic composition, the Katian brachiopod faunas (Colmenar *et al.* 2018). After the first pulse, elements of the *Hirnantia* Fauna thrived in Morocco until the melting of the ice caps in the late Hirnantian that triggered the second and more significant extinction pulse that caused severe extinctions among the opportunistic *Hirnantia* Fauna (Colmenar *et al.* 2018). Afterwards, brachiopod diversity never recovered in the Ordovician of the Anti-Atlas.

Bryozoans

During most of the Ordovician (late Tremadocian–Katian), bryozoans undertook a major, almost continuous diversification mainly in low latitude, tropical settings (e.g. Kazakhstan, Laurentia, North China, Siberia; Taylor & Ernst 2004; Buttler *et al.* 2013). In the late Katian, the expansion of bryozoans into high-latitude regions of the Mediterranean Province (e.g. Czech Republic, France, Italy, Lybia and Spain) coincided with the shift from siliciclastic to carbonate sedimentation and the onset of more temperate conditions (Boda event; Jiménez-Sánchez & Villas 2010). In the Anti-Atlas, rare, currently undescribed, putative remains of bryozoans were reported both in the upper part of the Fezouata Formation (Floian; Van Roy *et al.* 2015) and in the First Bani Group (Darriwilian; Horný 1997). In the eastern Anti-Atlas (Alnif area, Tafilalt), the Lower Ktaoua Formation (Sandbian–lower Katian) and the overlying Upper Tiouririne Formation (middle Katian) yielded abundant remains of bryozoans (Termier & Termier 1950; Destombes *et al.* 1971; Horný 1997; Destombes 2006; Álvaro *et al.* 2007). However, the most diverse bryozoan assemblages (44 taxa) are found in

the Khabt-el-Hajar Formation (upper Katian) in eastern Tafilalt (Termier & Termier 1950; Jiménez-Sánchez *et al.* 2015a, b, 2016; Ernst 2019). In this area, their wide morphological disparity (e.g. delicate and branched, encrusting, massive) reflects their widespread occurrence in a large range of environmental conditions (Ernst 2019). Late Katian bryozoan faunas from the eastern Tafilalt are largely dominated by trepostomes (37 taxa), associated with less common cryptostomes, esthonioporines and fenestrates (Jiménez-Sánchez *et al.* 2015a, b, 2016; Ernst 2019). In some trepostomes from the Erfoud area, the unusually large size of colonies (e.g. *Anaphragma mirabile*, *A. undulata*) and/or zooecia (e.g. *Atactoporella moroccoensis*) was interpreted as a possible example of gigantism associated with a slow growth in cold, quiet environmental conditions (Jiménez-Sánchez *et al.* 2015a, b; Ernst 2019). From a palaeobiogeographic point of view, late Katian faunas from the eastern Tafilalt are very similar to coeval ones from other high-latitude regions of the Mediterranean Province, and more particularly the Montagne Noire (France), the Carnic Alps and Sardinia (Italy) (Jiménez-Sánchez & Villas 2010, Jiménez-Sánchez *et al.* 2016; Ernst 2019).

Palaeoscolecoid worms

Palaeoscolecids are a potentially paraphyletic group of Lower Palaeozoic cycloneuralian worms, with likely affinities among the scalidophorans, most probably belonging to the priapulid stem (Harvey *et al.* 2010; Smith 2015). They have elongated, multi-annulated bodies and an eversible pharynx with hooks; small hooks are often also present at the termination of the body. A defining characteristic of palaeoscolecids on which much of their internal systematics is based, is the possession of an elaborate scleritome composed of rows of minute phosphatised plates which often exhibit very complex morphologies (Fig. 5b,c). In more derived forms, these plates may show dorso-ventral differentiation, and may be partially

fused together, forming rigid ring-sections around the body. Palaeoscolecids were probably vagrant generalist epifaunal or infaunal hunters and scavengers.

A single species of palaeoscolecid, *Gamascolex vanroyi* (Fig. 5) was described from the Sandbian Izegguirene Formation at Bou Nemrou (Gutiérrez-Marco & García-Bellido 2015). The Moroccan fossils are similar to *Gamascolex herodes* from the Middle/Upper Ordovician Dobrotivá Formation of Bohemia (Kraft & Mergl 1989), but the Moroccan species is differentiated from its Czech counterpart by its plate morphology, denser and more regular annulation, and larger size. The cuticle of the Moroccan fossils is either preserved as an external mould, or through phosphatisation. Although flattened, preservational quality is remarkable, retaining the detailed morphology of the differentiated dorsal, ventral and intercalated microplates of the scleritome, and of the reticulated non-sclerotised cuticle; one specimen also shows evidence of the preserved foregut. In at least one case, a specimen of *Gamascolex vanroyi* was observed to be preserved directly on top of an eldonid (PVR personal observation); whether this association represents actual fossilised scavenging behaviour or is merely due to a chance superposition is currently unclear.

Euarthropods

The diverse Upper Ordovician euarthropod faunas of the Tafilalt are dominated by arthropods, with trilobites and vicissicaudates being the major members. In common with many other groups, there are marked similarities in systematic composition to coeval faunas from Bohemia.

Trilobites. Trilobites are among the most familiar and extensively studied fossil euarthropods, beloved by both researchers and collectors alike. The Ordovician of Morocco has long been prized for its high trilobite diversity and excellent preservation. Not unsurprisingly, trilobites represent, along with echinoderms, one of the most common and diverse groups within the

Tafilalt Biota, and have an extensive history of commercial exploitation (Fig. 6c; Gutiérrez-Marco & García-Bellido, 2018).

One of the most extensively collected sites of the Tafilalt Biota are the outcrops of the Sandbian Izegguirene Formation at Bou Nemrou. A thorough revision of the trilobite fauna from this site (Gutiérrez-Marco *et al.* 2019) reveals the presence of at least 11 different species, representing illaenids (*Cekovia* cf. *goetzi*, *Ectillaenus* cf. *benignensis*), lichids (*Uralichas tardus*), odontopleurids (*Selenopeltis macrophthalma*, *Selenopeltis* cf. *buchi*; Fig. 6b), dalmanitids (*Mytocephala* cf. *mytoensis*, *Crozonaspis* cf. *primula*), pliomerids (*Placoparia africana*), asaphids (*Nobiliasaphus?* cf. *ingens*; Fig. 6a), cyclopygids (*Degamella* cf. *princeps*) and harpetids (*Eoharpes* sp.). This assemblage shows great similarity to approximately co-eval trilobite faunas from Bohemia, in most cases down to the species level, with only three species being endemic to Morocco (*Uralichas tardus*, *Crozonaspis* cf. *primula* and *Placoparia africana*). Interestingly, some taxa, like for example *Selenopeltis*, often tend to occur in clusters of several individuals on the same bedding plane (Fig. 6c), which may indicate that the animals congregated to moult or mate, as has been documented in many other arthropod clades, both fossil and recent (Sekiguchi 1988; Tarling & Cuzin-Rudy 2003; Gutiérrez-Marco *et al.* 2009; Mattei *et al.* 2010; Brett *et al.* 2012; Haug *et al.* 2013; Vannier *et al.* 2019). Trilobites from Bou Nemrou quite often preserve the digestive system, as illustrated in rather spectacular fashion by e.g. some specimens of *Uralichas tardus* and *Nobiliasaphus?* cf. *ingens* (Fig. 6a; Gutiérrez-Marco & García-Bellido 2015; Gutiérrez-Marco *et al.* 2019a; Budil & Fatka 2020). Apart from the preserved digestive tract, additional soft tissue preservation is exhibited by some material of *Selenopeltis* in the form of phosphatized metamericly arranged pairs of axial bands located in the anterior thoracic region (Fig. 6d). These structures likely represent traces of intersegmental musculature or digestive glands (Gutiérrez-Marco *et al.* 2019a).

Vicissicaudates. Vicissicaudata is a major clade of artiopod euarthropods ranging from the early Cambrian to the early Devonian, and includes Aglaspidida and Cheloniellida as its most diverse members. The position of vicissicaudates within Artiopoda is uncertain, with some phylogenetic analyses placing them as sister group to Trilobitomorpha (Ortega-Hernández *et al.* 2013; Edgecombe *et al.* 2017; Lerosey-Aubril *et al.* 2017b), whereas other studies recovered them as sister to Chelicerata (Cotton & Braddy 2004; Edgecombe *et al.* 2011; Legg *et al.* 2013; Legg 2014). Likewise, the intrarelationships between the various vicissicaudate clades currently remain largely unresolved. A defining apomorphy uniting the group is the possession of a terminal cylindrical somite lacking tergopleura and carrying a pair of modified appendages preceding the telson (Cotton & Braddy 2004; Van Roy 2006a, b; Lerosey-Aubril *et al.* 2017b).

Cheloniellids are characterized by the sharply procurved posterior margin of the cephalic shield and the pronounced radial arrangement of the tergopleura of the trunk. A pair of elongate modified appendages attaches dorso-laterally to the terminal cylindrical somite, which is followed by a small, rounded, cap-shaped telson. With several thousands of specimens collected from the Sandbian Izegguirene Formation at Bou Nemrou and at a second adjacent locality in the El Caid Rami area, the weakly sclerotized cheloniellid *Duslia* sp. (Fig. 7a,b) is one of the most common euarthropods at both sites. The Tafilalt species of *Duslia* is largely similar in morphology to the approximately coeval but much rarer *Duslia insignis* Jahn from the Letná Formation of Bohemia (Chlupáč 1988, 1999a, b); however, ongoing research indicates that the Moroccan fossils may likely be differentiated from the Czech material by a slightly different shape of the anterior margin of the cephalic shield, and reach a considerably larger maximum size. Although the quality of preservation of the Moroccan specimens is generally not as good as that of the Czech *Duslia*, the alimentary canal is quite commonly preserved. A few rare specimens also show some indications of the

limb bases. Another, rare cheloniellid, known from a handful of specimens from a locality to the east of Erfoud and from Bou Nemrou belongs to the genus *Triopus* Barrande (Fig. 7c; Van Roy 2006b). A recent restudy of the Czech *Triopus draboviensis* from the Sandbian Letná Formation in Bohemia has for the first time allowed a complete reconstruction of this fossil (Van Roy *et al.* in review), enabling a closer comparison with the Moroccan representative of the genus. This shows that the Moroccan fossils had a narrower axis, and a more protruding anterior margin of the cephalic shield compared to the type species from the Czech Republic. As in the case of *Duslia*, they also attain a much larger size than their Czech counterpart. As is almost invariably the case elsewhere (Chlupáč 1988), cheloniellid fossils in the Tafilalt are always fully articulated and occur parallel to the bedding plane. This suggests they were preserved *in situ*, their flattened morphology suggesting a benthic or nekto-benthic lifestyle.

Aglaspidids exhibit a long, styliiform telson, which in most species is fused with the posterior cylindrical somite to form a tailspine (Van Roy 2006a, b; Lerosey Aubril *et al.* 2017a). Except for the most basal taxa (Lerosey Aubril *et al.* 2017a), the modified appendages associated with the cylindrical somite are plate-like and located ventrally; these so-called ‘postventral plates’ are connected along their midline by arthrodial membrane, or may be fused together in some representatives of the group. Their cuticle was very weakly biomineralized, usually with calcium phosphate. In the Tafilalt Biota, Aglaspida is represented by a single disarticulated specimen of *Chlupacaris dubia* from the Katian Upper Tiouririne Formation east of Erfoud (Fig. 7d). Unusually, while most aglaspidids had thinly phosphatised exoskeletons, *C. dubia* may have calcified its cuticle (Van Roy 2006a, b). The morphology of the cephalic shield of *Chlupacaris dubia* indicates it may have stirred up sediment with its limbs, with the vaulted shield creating a filter-feeding chamber that allowed extraction of suspended food particles (Van Roy 2006a, b). The cephalic shield of

Chlupacaris dubia shows similarities to the Bohemian *Zonozoe drabowiensis* and *Zonoscutum solum* from the Sandbian Letná Formation; however, due to the incomplete preservation of the Czech fossils, the significance of this apparent similarity is unclear.

Other taxa. A single undescribed fossil from the Sandbian Izegguirene Formation at Bou Nemrou shows some similarity to the Cambrian-Ordovician genus *Tremaglaspis*, but its exact affinities are currently uncertain. Additional rare finds from Bou Nemrou include a possible nektaspidid, fragmentary material probably belonging to a carcinosomatid eurypterid, and a few ovoid cephalic shields bearing small dorsal eyes. Interestingly, the latter show similarities to the prosomal shields of juveniles of an undescribed horseshoe crab from the Early Ordovician Fezouata Biota (Van Roy *et al.* 2010, 2015).

Echinoderms

In the last 20 years, the Upper Ordovician succession of the Tafilalt yielded a remarkable series of successive dense accumulations of echinoderm-dominated assemblages, collectively designated as 'starfish beds', although most of them are devoid of starfish (asteroid) remains (Lefebvre *et al.* 2007, 2008, 2010; Hunter *et al.* 2010). In these levels, echinoderms are generally exceptionally well preserved, fully articulated, often with their most delicate skeletal structures still in anatomic connection (e.g. blastozoan brachioles, stylophoran distal aulacophore). Taphonomic experiments on modern taxa indicate that the calcite skeleton of echinoderms usually disintegrates into several thousand plates, relatively quickly (within a few days to a few weeks) after the death of the organism (Donovan 1991; Brett *et al.* 1997; Kerr & Twitchett 2004). Consequently, the preservation of fully articulated individuals, as well as their frequent linear, non-random orientation strongly suggest that most starfish beds result from the rapid burial of *in situ* or parautochthonous gregarious populations of live or freshly killed echinoderms by obrution (storm-generated and/or turbiditic) deposits (Lefebvre

et al. 2008, 2010; Hunter *et al.* 2010; Nardin & Régnault 2015). In some localities, this interpretation is further supported by stylophorans preserved in their presumed feeding posture (i.e. aulacophore in extended position, with slightly ajar cover plates; Lefebvre *et al.* 2022a, b) and also of ophiuroids literally 'frozen in the act' of capturing, and presumably feeding on, young individuals of eocrinoids (Lefebvre *et al.* 2008). Consequently, the Upper Ordovician starfish beds of the eastern Anti-Atlas represent a cluster of echinoderm Lagerstätten (*sensu* Smith 1988) providing a series of snapshots documenting over 10 million years of evolution of high latitude echinoderm communities within a restricted geographic area (Tafilalt). They can be readily compared to the few other Late Ordovician echinoderm Lagerstätten known from similar high-latitude peri-Gondwanan areas (e.g. Letná Formation, Czech Republic; Nohejlová *et al.* 2019), or from various lower latitude Laurentian regions, such as the Brechin Lagerstätte (Ontario; Cole *et al.* 2018), the Bromide Formation (Oklahoma; Sprinkle 1982) or the Lady Burn Starfish Beds (Scotland; Bather 1913).

Comprising representatives of ten distinct classes (Asteroidea, Coronoidea, Crinoidea, Diploporita, Edrioasteroidea, Eocrinoidea, Ophiuroidea, Rhombifera, Soluta, and Stylophora), the Tafilalt Biota yielded not only one of the best preserved, but also one of the most diverse Late Ordovician echinoderm faunas from the Mediterranean Province. Although their composition varies from locality to locality, possibly reflecting subtle differences in environmental conditions, such as hydrodynamics and bathymetry, starfish beds from the eastern and western Tafilalt yielded comparable Sandbian–early Katian assemblages generally dominated by ophiuroids, solutans and/or stylophorans, with sometimes locally abundant edrioasteroids, eocrinoids and/or rhombiferans, and more occasional occurrences of asteroids, coronoids, diploporites and/or crinoids (Lefebvre *et al.* 2007, 2008, 2010, 2022a, b; Nardin 2007; Régnault 2007; Hunter *et al.* 2010; Sumrall & Zamora 2011, 2018; Nardin & Régnault 2015; Botting 2018; Zamora & Sumrall 2018, 2019; Zamora *et al.* 2019; Nohejlová

& Lefebvre 2021). These assemblages display strong palaeobiogeographic affinities with coeval faunas from Bohemia (Czech Republic) and, to a lesser extent, with the Armorican Massif (France) and the Iberian Peninsula (Portugal and Spain). In other regions of the Anti-Atlas, Sandbian–early Katian echinoderm assemblages are less diverse, dominated by diploporites and exhibit stronger faunal affinities with both the Armorican Massif and the Iberian Peninsula than with the Prague Basin (Chauvel 1966, 1969, 1977, 1978; Álvaro *et al.* 2007). In the eastern Tafilalt, the late Katian time interval corresponds to a major turnover in echinoderm communities (Boda event). Assemblages adapted to cool-water environments, living on soft, siliclastic substrates, dominated by ophiuroids and stylophorans were replaced by more temperate faunas dominated by crinoids and encrusting diploporitans (e.g. *Herpetocystis*) associated with bryozoan bioherms (Termier & Termier 1970; Le Menn & Spjeldnæs 1986; Álvaro *et al.* 2022). In the late Katian, a comparable shift in echinoderm faunas was documented in most other regions of the Mediterranean Province (Lefebvre 2007; Lefebvre *et al.* 2013).

Asterozoans. Asterozoa is a diverse subphylum of free-living echinoderms represented by the extant classes Asterozoa (starfish) and Ophiurozoa (brittle stars), and the extinct basal class Somasteroidea, which shares characteristics with both extant groups (Blake 2013; Blake & Guensburg 2015). In contrast to the Lower Ordovician Fezouata Shale, where asterozoans are represented exclusively by somasteroids (Lefebvre *et al.* 2016b; Hunter & Ortega-Hernández 2021), the Tafilalt Biota is dominated by ophiuroids (Figs 8–9), with asteroids only making an appearance in the youngest deposits of the area; somasteroids are entirely absent from the Tafilalt. Although asterozoan fossils are not common elements of all echinoderm Lagerstätten of the Tafilalt, they tend to be particularly diverse and locally abundant in many of the Sandbian – middle Katian sediments in the region (Lefebvre *et al.* 2007, 2008, 2010; Hunter *et al.* 2010). Two main assemblages can be distinguished among the asterozoan faunas of the

Tafilalt: the first one is largely composed of protasterids, a typical Palaeozoic clade of stem ophiuroids ranging from the Ordovician to the Permian (Hunter *et al.* 2016; Hunter & MacNamara 2017), while the second one contains a range of endemic taxa, which have few affinities with fossils from neighbouring regions of peri-Gondwana, such as the Montagne Noire (France), the Armorican Massif (France) and Bohemia (Czech Republic).

Outcrops of the lower Sandbian Izegguirene Formation at Bou Nemrou (Jbel Tijarfaïouine, western Tafilalt) yielded an assemblage of protasterids (Fig. 8d) within an autochthonous echinoderm fauna containing the eocrinoid *Ascocystites*. The late Sandbian ophiuroids of the Tafilalt belong to distinct endemic groups with little or no affinity to neighbouring regions and include unusual small 'asteroid'-like ophiuroids (Figs 9a–c). At the Piste de Jorf locality, ophiuroids (Figs 8b–c,e, 9a,c–d) are well-preserved alongside mitrocystitid mitrates and appear current aligned (Lefebvre *et al.* 2007, 2010). The lower Katian starfish beds, which include the dense echinoderm Lagerstätten of Tizi n'Mourghi are a source of further endemic forms, with ophiuroids (Fig. 9b) occurring in association with the solutan *Dendrocystites* aff. *sedgwicki* (Nohejlová & Lefebvre 2021). At Isthlou, the youngest assemblages (mid-Katian, Upper Tiouririne Formation) mark the first appearance of asteroids in the Tafilalt, while also heralding the return of protasterid faunas with affinities to Bohemia (Czech Republic).

Together with the parautochthonous Lady Burn Starfish Beds from the Katian of the Girvan district, Scotland (Harper 1982; Shackleton 2005), the asterozoan faunas of the Tafilalt are of particular significance as they represent a succession of snapshots documenting ophiuroid and asterozoan diversification during the later stages of the Great Ordovician Biodiversification Event (GOBE).

Coronoids. This small class (six genera) of stemmed blastozoans with a blastoid-like, bud-shaped theca is reported here for the first time in Morocco and Africa (Zamora & Sumrall

2018). In the western Tafilalt, coronoids are known from a single specimen collected at Piste de Tinerhad, in the Upper Tiouririne Formation (middle Katian).

This new occurrence of *Mespilocystites* confirms that this Sandbian–Katian genus was particularly widespread in all high-latitude regions of the Mediterranean Province, with other known occurrences from the Czech Republic (Barrande 1887; Mikuláš & Prokop 2003), France (Chauvel & Le Menn 1972; Touzeau *et al.* 2012), Italy (Botquelen *et al.* 2006; Sumrall *et al.* 2015), Portugal (Jacinto *et al.* 2015), and Spain (Chauvel & Le Menn 1979; Gutiérrez-Marco *et al.* 1996; Zamora *et al.* 2015a).

Crinoids. During the Ordovician, this clade of stemmed, arm-bearing echinoderms underwent an almost exponential diversification in the shallow tropical seas of Laurentia (Sprinkle & Guensburg 2004; Lefebvre *et al.* 2013; Guensburg *et al.* 2021). In contrast, crinoids were generally a minor component of Ordovician echinoderm faunas in high-latitude regions of the Mediterranean Province (see e.g. Ubaghs 1969, 1983; Ausich *et al.* 2002, 2007; Lefebvre *et al.* 2015; Cole *et al.*, 2017). In this context, two localities of the western Tafilalt yielded rare but unexpectedly diverse Late Ordovician crinoid remains (Botting 2018). At Bou Nemrou, fully articulated, complete camerates (monobathrid indet., *Trichinocrinus?* sp.) and disparids (*Iocrinus ouzammoui*, cincinnaticrinid? indet.), along with more fragmented material (e.g. columnals and anal tube of *Iocrinus* sp.) were found in the starfish beds of the Izegguirene Formation (lower Sandbian) (Lefebvre *et al.* 2008, 2010; Botting 2018). At Isthlou, the Upper Tiouririne Formation (middle Katian) yielded well preserved camerates (*Euptychocrinus? atelis*, monobathrid indet., *Trichinocrinus?* sp.) and cladids (*Isthloucrinus praecursor*) (Botting 2018). In the eastern Tafilalt (at Oued er Rosfa el Hamra), the same lithostratigraphic unit (Upper Tiouririne Formation) provided a monospecific accumulation of complete, fully articulated specimens of the camerate *Rosfacrinus robustus* (Le Menn & Spjeldnæs 1996; Botting 2018). In the overlying Khabt-el-Hajar Formation (late Katian),

crinoids are probably one of the dominant groups of echinoderms associated with bryozoan bioherms in the eastern Tafilalt (Destombes 2006; Villas & Colmenar 2018). However, their preservation as dissociated, recrystallized skeletal elements precludes any precise identification. Finally, the cladid *Superlininicrinus advorsa* was described based on two well preserved individuals occurring on the same slab, which was probably collected in the Lower Ktaoua Formation (lower Sandbian–lower Katian) at an unknown locality in the Tafilalt (Botting 2018).

The occurrence of iocrinids in the Upper Ordovician of the Tafilalt echoes earlier records of this camerate family both in the upper part of the Fezouata Formation (Floian; Lefebvre *et al.* 2016b) and in the Taddrist Formation (Darriwilian; Zamora *et al.* 2015b). Affinities of most other Late Ordovician taxa from the Tafilalt with the few other documented earlier occurrences of crinoids in the Anti-Atlas (e.g. Donovan & Savill 1988; Lefebvre *et al.* 2016b) are more difficult to identify, because of a particularly poor fossil record. From a palaeobiogeographic point of view, most crinoid taxa from the Tafilalt are endemic (e.g. *Isthlocrinus*, *Rosfacrinus* and *Superlininicrinus*). Conversely, the genus *Iocrinus* is almost ubiquitous with occurrences in other Gondwanan regions (e.g. Oman), but also in Avalonia, Laurentia, and possibly Baltica (Donovan & Gale 1989; Botting 2003; Donovan *et al.* 2011; Zamora *et al.* 2015b). Finally, the two camerates *Euptychocrinus? atelis* and *Trichinocrinus? sp.* are only tentatively assigned to Laurentian genera (Botting 2018).

Diploporites. Diploporites are a polyphyletic assemblage of early blastozoans that only convergently share the presence of double pore-like respiratory structures (Sheffield & Sumrall 2019). The Upper Ordovician rocks of the Anti-Atlas have provided a relatively diverse assemblage of diploporites. In the western Tafilalt, the Lower Ktaoua Formation provided remains of *Aristocystites bohemicus* associated with ophiuroids and edrioasteroids at Isthlou, and *Arachnocystis infaustus*, *Aristocystites bohemicus*, aristocystitid indet.,

Codiacystis bohémica, *Destombesia diedra*, *Glaphocystis* sp. and *Maghrebocystis pachythea* at another locality, N of Taguerroumt (Destombes 2006). The Upper Tiouririne Formation is comparatively less diverse and yielded only *Maghrebocystis pachythea* (N of Taguerroumt; Destombes 2006). In the eastern Tafilalt (east of Erfoud), the Khabt-el-Hajar Formation provided the enigmatic encrusting form *Herpetocystis destombesi*. These early finds were mostly made by J. Destombes and described by Chauvel (1966, 1978) and Termier & Termier (1970). Recent excavations in the locality of Tizi n'Mouri provided articulated specimens of the rare diploporite *Asterocystis* associated with ophiuroids, the solutan *Dendrocystites* aff. *sedgwicki* (Nohejlová & Lefebvre 2021) and the glyptocystitid rhombiferan *Homocystites adidiensis* (Zamora *et al.*, 2019).

Most diploporite genera from the Upper Ordovician of the Tafilalt also occur in one or several other regions of the Mediterranean Province (e.g. Czech Republic, France, Spain), for example *Aristocystites*, *Codiacystis* and *Destombesia* (Chauvel 1966, 1978; Lefebvre *et al.* 2007). The Late Ordovician diploporite assemblages from the Tafilalt also include endemic taxa (e.g. *Herpetocystis*), as well as rare occurrences of asteroblastids, a low-diversity clade previously documented mostly from Baltica (Hunter *et al.* 2010).

Edrioasteroids. Edrioasteroids are rare components in the echinoderm assemblages from Gondwana, but the rocks of the Anti Atlas represent a notable exception. Chauvel (1966, 1978) was first to report and describe a few edrioasteroid taxa from the Upper Ordovician of Morocco based on the collections of J. Destombes. Because of their presence in siliciclastic rocks, edrioasteroids from Morocco have been critical for the recognition of internal and external characters that play an important role in edrioasteroid classification and phylogenies (Sumrall & Zamora 2011). The oldest Upper Ordovician edrioasteroids were reported from the Izegguirene Formation and consist of *Isorophus africanus* and *Belochthus? chauveli* (Sumrall & Zamora 2011). Levels of the Lower Ktaoua Formation provided a rich

monospecific assemblage of *Spinadiscus lefebvrei* (Sumrall & Zamora 2018). This is one of the best preserved pyrgocystid edrioasteroids known so far based on internal and external features. The upper levels of the Lower Ktaoua Formation and the Upper Tiouririne Formation yielded several rich assemblages of edrioasteroids that originally included *Streptaster nodosus* and *Isorophusella gutii* from the Lower Ktaoua Formation and *Streptaster nodosus*, *Euryeschatia reboulorum* (Fig. 10c) and *Moroccopyrgus matacarros* from the Upper Tiouririne Formation (Sumrall & Zamora 2011). The latter also provided specimens of *Panidiscus tamiformis* (Sumrall & Zamora 2018). Most edrioasteroids appear attached to larger organisms like conulariids (Fig. 10c), other echinoderms or trilobites; while in some cases the edrioasteroids likely only attached themselves post-mortem, in other instances they may have been epibionts on their living hosts (Sumrall & Zamora 2011, 2018). This provides important evidence of live interactions between edrioasteroids and other organisms. Some of the edrioasteroid assemblages also provided the enigmatic edrioasteroid-like mimic *Hexedriocystis* that consists of two species *H. inexpectatus* from the Izegguirene Formation and *H. mimus* from the Upper Tiouririne Formation (Sumrall & Zamora 2011). Additional material of the latter confirms its abundance in edrioasteroid colonies attached to living organisms like rhombiferans (Zamora & Sumrall 2019). As Sumrall and Zamora (2011) first pointed out there are important affinities between the edrioasteroids from Morocco and those from North America (Laurentia) and Bohemia (Gondwana).

Eocrinoids. The 'class' Eocrinoidea corresponds to a paraphyletic assemblage of basal blastozoans (i.e. stemmed, brachiole-bearing Cambrian-Ordovician echinoderms) lacking key morphological features diagnostic of more advanced taxa (Sprinkle 1973; Smith 1984; Sprinkle & Collins 2006; Zamora *et al.* 2009). In the Upper Ordovician of the eastern Anti-Atlas, eocrinoids are known from two distinct localities both situated in the western Tafilalt. The first one, Bou Nemrou (Izegguirene Formation, lower Sandbian), yielded thousands of

fully articulated, often current-orientated individuals of *Ascocystites* sp. (Fig. 10d), which is one of the most abundant and iconic elements of the Tafilalt Biota (Lefebvre *et al.* 2007, 2008, 2010; Régnault 2007; Hunter *et al.* 2010; Nardin & Régnault 2015; Lebrun 2018; Gutiérrez-Marco *et al.* 2020b). In the lower part of the Lower Ktaoua Formation (Sandbian), rare, remarkably preserved specimens of *Cardiocystites bohemicus* (Fig. 10b) were found at Piste de Jorf (Lefebvre *et al.* 2007, 2010; Nardin 2007; Hunter *et al.* 2010).

Although abundant and diverse remains of eocrinoids were described in Cambrian and Lower Ordovician deposits of the Anti-Atlas (Chauvel 1971, 1978; Chauvel & Régnault 1986; Smith *et al.* 2013; Lefebvre *et al.* 2016b; Allaire *et al.* 2017), putative affinities of the two Late Ordovician taxa from the Tafilalt with earlier regional occurrences are impossible to identify in the absence of a well-defined phylogenetic framework for basal blastozoans. In Darriwilian–Katian times, *Ascocystites* was a relatively widespread genus in shallow settings of the Mediterranean Province: it was also described in Algeria (Ougarta; Makhoul *et al.* 2018), the Czech Republic (Prague Basin; Barrande 1887), France (Normandy; Régnault 1990), and Portugal (Dornes; Young & Donovan 1993). The Late Ordovician genus *Cardiocystites* occurs not only in peri-Gondwanan areas (*C. bohemicus*: Bohemia and Tafilalt; Barrande 1887; Nardin 2007), but also in Avalonia (*C. pleuricostatus*: Shropshire; Dean & Smith 1998).

Rhombiferans. Rhombiferans are a polyphyletic assemblage of stemmed echinoderms that are locally abundant but exhibit low diversity in the Upper Ordovician rocks of the Anti-Atlas. First studies on rhombiferans were carried out by Termier & Termier (1950) and Chauvel (1966, 1969, 1977) and included *Macrocystella* spp. from the Lower Ordovician, *Echinosphaerites belgicus* Jaekel from the Middle Ordovician and different species of *Echinosphaerites* and *Heliocrinites* from the Upper Ordovician (see Zamora *et al.* 2019 for a complete review of old literature). Recent discovery of starfish beds with abundant and

articulated specimens of *Homocystites adidiensis* (Fig. 10a) provides important information about the palaeoecology of glyptocystitid rhombiferans. In the Lower Ktaoua Formation, *H. adidiensis* appears to be associated with rare occurrences of the palaeogeographically widespread genus *Rhombifera*. Another important occurrence of rhombiferans includes the caryocystitid *Echinosphaerites diana*e from the Upper Tiouririne Formation. This is one of the few caryocystitid rhombiferans that preserve stem and brachioles, thus providing interesting additional information on the morphology of this group of echinoderms. Some specimens were epibiontically colonized by edrioasteroids and the enigmatic *Hexedriocystis*. The presence of *Homocystites* in Morocco is remarkable because this genus is also present in the Avalonian part of Great Britain and other peri-Gondwanan areas like Spain and Bohemia (Barrande, 1887; Regnéll & Paul, 1981; Gil Cid *et al.* 1996b).

Solutans. This small clade includes free-living echinoderms characterized by a moderately flattened theca, a short feeding appendage (brachiole), and a much longer stem-like structure (homoiostele) used for locomotion on soft, siliciclastic substrates (Noailles *et al.* 2014; Nohejlová & Lefebvre 2021). In the western Tafilalt, all known occurrences of Late Ordovician solutans can be assigned to a single taxon, *Dendrocystites aff. sedgwicki*, which is a typical faunal element in most Sandbian–lower Katian starfish beds of the Lower Ktaoua Formation (e.g. Jbel Taklimt, piste de Jorf, Tarafin Signit; Nohejlová and Lefebvre 2021). One locality (Tizi n'Mourghi) yielded impressive accumulations of thousands of fully articulated, current-orientated dendrocystitid solutans (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010; Nohejlová & Lefebvre 2021).

In the Anti-Atlas, earlier, more diverse solutan occurrences are known in the Lower Ordovician Fezouata Formation, but all of them belong to a distinct order (Syringocrinida; Lefebvre *et al.* 2016b). Within the long-ranging family Dendrocystitidae (Sandbian–Emsian), *Dendrocystites* is a typical Late Ordovician genus from the high-latitude Mediterranean

Province, with other occurrences documented in the Prague Basin, Czech Republic (Bather 1913; Caster 1968; Noailles *et al.* 2014) and the Central Iberian Zone, Spain (Gil Cid *et al.* 2016a; Gutiérrez-Marco *et al.* 2018).

Stylophorans. Representatives of this class of free-living (unattached), flattened echinoderms characterized by a single feeding appendage (aulacophore) were particularly diverse and locally abundant in most Sandbian–lower Katian starfish beds of the Tafilalt (Lefebvre *et al.* 2007, 2008, 2022a, b; Hunter *et al.* 2010). At Bou Nemrou (Jbel Tijarfaïouine, western Tafilalt), the lower Sandbian Izegguirene Formation yielded the most diverse stylophoran assemblage comprising the three cornutes *Arauricystis clariondi*, *Milonicystis reboulorum*, *Thoralicarpus bounemrouensis* and the four mitrates *Anatifopsis* sp., *Aspidocarpus discoidalis*, *Diamphidiocystis regnaulti* and *Eumitrocystella savilli* (Lefebvre *et al.* 2008, 2022a, b). In the overlying Lower Ktaoua and Upper Tiouririne formations (Sandbian–middle Katian), cornutes were reported so far only in the eastern Tafilalt, where the amygdalothecid *Domfrontia milnerorum* occurs massively in a low diversity assemblage (Lefebvre *et al.* 2022b). In most localities of the western Tafilalt (e.g. Isthlou, piste de Jorf, Tafset, Tarafin Signit, Tifrit n'Ougnaou), both kirkocystid (*Anatifopsis*) and mitrocystitid mitrates (e.g. *Aspidocarpus*, *Barrandeocarpus*, *Eumitrocystella*) are relatively common elements of most Late Ordovician benthic assemblages (Lefebvre *et al.* 2007, 2008, 2010, 2022a).

All stylophoran clades occurring in the Upper Ordovician of the Tafilalt are known from earlier deposits in the Anti-Atlas, as for example in the Fezouata (Tremadocian–Floian: amygdalothecid, cothurnocystid and scotiaecystid cornutes, kirkocystid and mitrocystitid mitrates; Lefebvre *et al.* 2016b) and Ouine-Inirne formations (upper Darriwilian: scotiaecystid cornutes, kirkocystid and mitrocystitid mitrates; Cripps 1990; Beisswenger 1994; Gutiérrez-Marco *et al.* 2003). Similarly to most other Late Ordovician echinoderms

from the Tafilalt, stylophorans display strong affinities with coeval and/or slightly older (Darriwilian) peri-Gondwanan assemblages from the Armorican Massif (France), Bohemia (Czech Republic) and the Iberian Peninsula (Spain).

Graptolites

This important group of early Palaeozoic fossils is scarcely recorded in the Upper Ordovician of the Tafilalt region, mainly because of the predominance of sandy lithofacies, generally too coarse to preserve the fine and delicate organic skeleton of the graptolite colonies. Moreover, the extensive shallow-water, high-energy inshore environments are unsuitable for the more common planktonic forms. Nevertheless, benthic graptolites are sometimes recorded from sandstones in places showing exceptional preservation, such as the Bou Nemrou assemblage (top of the First Bani Group), becoming more abundant in certain silty beds intercalated in sandstones of the Lower Ktaoua Group (Fig. 11), where three different benthic genera coexist in the same horizon (Gutiérrez-Marco *et al.* 2020a). In these latter horizons, as well as in the nodules from the Upper Ktaoua Formation, the occurrence of a low-diversity assemblage of planktonic graptolites (the biserial genera *Climacograptus*, *Normalograptus* and *Neodiplograptus*) adds some biostratigraphical information to help assist the poorly known stratigraphic placement of some echinoderm or trilobite-dominated faunas of the Tafilalt Biota.

With regard to the palaeobiogeographic affinities, some of the Tafilalt graptolites are similar to Bohemian species, indicating faunal links between the Mediterranean regions during the Late Ordovician.

Soft-bodied organisms of uncertain affinity

The preservation of soft-bodied organisms in the coarse clastic sediments characteristic of the Upper Ordovician of the Tafilalt is particularly noteworthy, as it shows great similarity to the mould/cast preservation typically associated with Ediacaran fossils (Van Roy 2006a; MacGabhann 2012; MacGabhann *et al.* 2019). Detailed study of eldonids indicates that only structures composed of complex biopolymers can be preserved in this particular mode of preservation, limiting the types of soft-bodied organisms and tissues that may be fossilised through this taphonomic pathway (MacGabhann 2012; MacGabhann *et al.* 2019).

Eldonids. Eldonioidea is a clade of problematic Paleozoic metazoans ranging from the early Cambrian to the late Devonian. They are characterized by the possession of a discoidal body with one convex and one flat or slightly concave side. Most species are entirely soft bodied, with a leathery convex side, but in the genus *Rotadiscus*, the convex side is sclerotised (Dzik *et al.* 1997). The mouth and anus open close to each other on the concave side, the anal opening being located slightly closer to the margin of the discoidal body than the oral opening. Four pairs of branching feeding tentacles are positioned around the mouth. The alimentary canal is coiled into an almost complete circle and is surrounded by a distinct, thick-walled peri-alimentary coelom termed the 'coiled sac'. In all eldonids, the coiled sac curves outwards in a clockwise direction when viewed from the convex side of the body. Within the discoidal body, a high number of lobes radiate out from the center towards the edge. These lobes bifurcate distally. Among eldonids, the paropsonemids are noteworthy because of their complex structure, with up to three tiers of bifurcation exhibited by the internal lobes, and an elaborate concentric and radial ornament on their convex sides (MacGabhann 2012). The systematic affinities of eldonids are uncertain; together with the equally problematic *Herpetogaster* and *Phlogites*, they are placed in the Cambroernida, a deuterostome clade which is considered to likely belong to the ambulacrarian stem (Caron *et al.* 2010). Their mode of life is equally problematic; on account of their medusoid bodies,

they were long considered to be pelagic swimmers or floaters. This, however, appears unlikely considering their heavy, inflexible construction and the lack of any apparent flotation devices. They were therefore more likely benthic, either sessile with their convex side down buried in the substrate (Dzik 1997 *et al.*; Van Roy 2006b), or vagrant epibenthic, crawling over the substrate using their oral tentacles for locomotion (Friend 1995; MacGabhann 2012).

Paropsonemid eldonids (Fig. 12) are by far the most common soft-bodied organisms in the Tafilalt Biota, with several thousands of specimens collected since the turn of the century. While they occur in great abundance at the classical Bou Nemrou locality, they are present throughout the El Caid Rami area, and are also documented from multiple sites to the east of Erfoud (Van Roy 2006a; MacGabhann 2012; MacGabhann *et al.* 2019), ranging from the uppermost strata of the First Bani Group to the top of the Upper Tiouririne Formation. Unverified but reliable reports also suggest the presence of eldonids in Upper Ordovician strata near Alnif, and the area around Tafetchna, north of Zagora. At least two different paropsonemid taxa are represented: while a large portion of the collected specimens can be placed in *Discophyllum peltatum* Hall, 1847 (Fig. 12), a second new taxon currently awaits formal description (MacGabhann 2012; MacGabhann *et al.* 2019). They often occur in high densities, with sometimes over a dozen of specimens covering a slab. In many cases, specimens partially overlap, and rolled and torn individuals are also known, suggesting at least some measure of transport before burial (MacGabhann 2012; MacGabhann *et al.* 2019). *Discoidal holdfasts and fronds.* Other, considerably less common soft-bodied discoidal problematica are also known from the Tafilalt. The affinities of these fossils are unclear; they may represent some kind of holdfast (Van Roy 2006a). A few, extremely rare specimens of a possible frondose organism are known from Bou Nemrou (Van Roy 2006a; personal

observation PVR); it is possible that the supposed holdfasts may have belonged to organisms like these.

Trace fossils

Concluding this overview, the shallow, well-oxygenated sediments that document the high energy environmental conditions prevailing in the Tafilalt Biota preserve an assemblage of trace fossils and sedimentary structures. Examples include *Neoeione moniliformis*, a common epirelief in the Upper Tiouririne Formation of the Eastern Anti-Atlas (Fig. 13), recorded among other 23 different trace fossils cited, and partly illustrated, by Gutiérrez-Marco *et al.* (2019b).

A less diverse ichnoassemblage was reported from the upper part of the First Bani Group (Bou Nemrou locality) by MacGabhan (2012), Muir *et al.* (2018) – indicating the succession of the *Cruziana* and *Arenicolites* ichnofacies – and Gutiérrez-Marco *et al.* (2019b). From the same locality, Gutiérrez-Marco *et al.* (2019b) cited the widespread occurrence of textured organic surfaces recorded in the bedding planes of laminated sandstones, assimilated to wrinkles or microbially induced sedimentary structures (MISS). Some of the more abundant types of the so-called "elephant skin" or "Kinneyia", generated by the widespread development of microbial mats, were recently ascribed to the ichnofossil *Rugalichnus matthewii* (Stimson *et al.* 2017).

Muir *et al.* (2018) described from a number of Late Ordovician Tafilalt localities the occurrence of agglutinated tubes, composed of mica flakes, which are commonly recorded on bedding surfaces of sandstones. Although they describe these tubes as a new body fossil (*Onuphionella corusca*, an incertae sedis), agglutinated tubes are still regarded as trace fossils by other palaeontologists (see discussion in Muir *et al.*, 2018).

Conclusions

While the highly diverse faunas from the Upper Ordovician of the Tafilalt have been well-known for almost a century, and extensive mapping of the area has taken place over the past decades, the majority of the most remarkable and significant discoveries in this area were only made in the past 25 years as a result of greatly increased commercial collecting. This fact highlights the double-edged sword presented by the international fossil trade: while on the one hand, commercialisation of fossils unfortunately opens the door wide to pillaging, exploitation and a host of other poor practices by unscrupulous individuals (Gutiérrez-Marco & García-Bellido 2018), concerted efforts by dedicated local collectors (Fig. 14) have resulted in some of the most significant and iconic palaeontological discoveries and contributions to science of the past two centuries (e.g. Brett *et al.* 1999; Norman 1999; Lefebvre *et al.* 2016a).

Among the most significant discoveries of the past 25 years in the Tafilalt are the discovery of multiple echinoderm Lagerstätten, preserving articulated skeletons of a wide variety of delicate echinoderms in impressive detail; the most prolific locality anywhere for articulated machaeridian armours, disclosing significant new information about the ontogeny and mode of life of these extinct annelids; and the excavation of several sites preserving non-biomineralised and soft parts throughout the greater El Caid Rami area, but foremost centered on Bou Nemrou hill. The latter discovery is of particular significance, as it shows that the typically Ediacaran taphonomic window allowing mould/cast preservation of soft parts in coarse clastic sediments occasionally still remained ajar during the Early Palaeozoic. Study of the Bou Nemrou soft-bodied fossils has further revealed that only organisms, and parts of organisms composed of complex biopolymers can be fossilized in this fashion (MacGabhann 2012; MacGabhann *et al.* 2019), which has consequences for the interpretation of problematic Ediacaran organisms and assemblages.

Taphonomic processes involved in the Late Ordovician Tafilalt Biota are markedly distinct from those occurring in the Early Ordovician Fezouata Biota, thus preventing any straightforward comparison of their faunas. Consequently, evaluating the significance of compositional differences between the Fezouata Shale and the Tafilalt Biota is compounded by the fact that it could result from either a taphonomic bias and/or from originally different environmental conditions (nearshore settings in the Tafilalt, offshore environments in the Zagora area). In spite of these limitations, the two Ordovician Moroccan Konservat-Lagerstätten share the occurrence of some exceptionally preserved, lightly sclerotized taxa, such as aglaspidids, cheloniellids and palaeoscolecids (Van Roy 2006*a, b*; Van Roy *et al.* 2010, 2015; Gutiérrez-Marco & García-Bellido 2015; Martin *et al.* 2016*b*). In contrast, the comparison of invertebrate faunal elements with mineralized hard parts occurring in these two stratigraphically distinct Lagerstätten highlights a transition from assemblages still dominated by Cambrian-like taxa in the Fezouata Shale (e.g. eocrinoids, inarticulate brachiopods, cornute stylophorans and hyolithids) to more standard Ordovician faunas in the Tafilalt Biota (e.g. articulate brachiopods, asteroids, bryozoans and crinoids).

This long-term faunal turnover provides new insights into the GOBE in high-latitude, siliclastic-dominated settings (Hunter *et al.* 2022), with some marked differences with regional patterns documented at lower latitude areas (e.g. Baltica and Laurentia). For example, the Tafilalt Biota does not show any evidence of the major diversification observed for several groups of invertebrates (e.g. crinoids and nautiloid cephalopods) during the Sandbian–Katian time interval in tropical regions. Contrary to other regions of the Mediterranean Province, the Anti-Atlas is also characterized by the persistence of relatively low-diversity assemblages associated with soft, siliclastic substrates during the late Katian (i.e. no impact of the Boda Event; Lefebvre 2007; Colmenar *et al.* 2018).

The Upper Ordovician assemblages of the Tafilalt contain representatives of at least nine different phyla, and several soft-bodied problematica. In most cases, faunal comparisons reaffirm and strengthen the long-documented extensive similarities, often down to the species level, with co-eval deposits from Bohemia. However, some endemics are present in the fauna, and a few clades do seem to buck the trend of faunal similarity with Bohemia, showing episodes of more marked endemism instead. The new taxa described in this volume include:

- nine new genera: one cephalopod (*Tafadnatoceras*), two crinoids (*Isthloucrinus*, *Superlininicrinus*), two edrioasteroids (*Panidiscus*, *Spinadiscus*), two gastropods (*Allossospira*, *Radvanospira*), and two stylophorans (*Destombesicarpus*, *Thoralicarpus*)
- 26 new species: one agglutinated tube (*Onuphionella corusca*), one bivalve (*Praenucula pojetai*), two cephalopods (*Tafadnatoceras tiouririnense*, *Wadema tattai*), four crinoids (*Euptychocrinus? atelis*, *Iocrinus ouzzamoui*, *Isthloucrinus praecursor*, *Superlininicrinus advorsa*), two edrioasteroids (*Panidiscus tamiformis*, *Spinadiscus lefebvrei*), three gastropods (*Lophospira latilabra*, *Radvanospira baniensis*, *Tritonophon grandis*), two graptolites (*'Dictyonema' khadijae*, *'Dictyonema' villasi*), two rhombiferans (*Echinosphaerites diana*, *Homocystites adidiensis*), eight stylophorans (*Arauricystis clariondi*, *Bohemiaecystis chouberti*, *Destombesicarpus izegguirensis*, *D. budili*, *Diamphidiocystis regnaulti*, *Milonicystis reboulorum*, *Thoralicarpus bounemrouensis*, *T. prokopi*), and one trilobite (*Placoparia africana*).

Work on many of the clades present in the Tafilalt Biota is currently still ongoing, and this list could be extended significantly over the coming years. As such, like Fezouata, the Tafilalt Biota represents another prime example of how international scientists and local collectors can develop a highly successful and mutually beneficial synergy. We can only hope this trend

will continue to expand in the future, and look forward to the coming decades of Tafilalt Biota research.

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Figure Captions

Fig. 1. (a) Schematic geological map of north-western Africa, with distribution of Ordovician rocks and location of (b). (b) Simplified geological map of the Anti-Atlas, showing the distribution of Ordovician rocks and location of (c). (c) Geological sketch of the eastern Anti-Atlas, illustrating the extension of Ordovician rocks in the Maïder and the Tafilalt; lines correspond to the isopachs of the (cumulated) Lower Ktaoua and Upper Tiouririne formations (redrawn and modified after Destombes 2006); stars indicate the location of main Late Ordovician starfish beds, with: (1) Tarhia area; (2) Piste de Jorf; (3) Tizi n'Mourghi; (4) Bou Nemrou; (5) Isthlou; (6) Tarafin. Red squares indicate the location of main occurrences of soft-bodied organisms of uncertain affinity belonging to the Tafilalt Biota.

Fig. 2. Chrono- and lithostratigraphic charts for the Upper Ordovician of the western and eastern Tafilalt, based on Colmenar & Álvaro (2015), Goldman *et al.* (2020), and Álvaro *et al.* (2022).

Fig. 3. *Archaeoconularia* aff. *consobrina*, a conulariid from the Upper Tiouririne Formation (middle Katian) east of Erfoud, which preserves the finely ornamented periderm. (a) Inflated, terminal-schott-bearing specimen MGM-6882X. (b) Detail of MGM-6880X with transverse dark-brown colour bands. (c) Large specimen MGM-6879X; (d) Detail of MGM-6879X with ornament. Scale bars equal 10 mm (a–b) and 5 mm (c–d).

Fig. 4. Specimens of the plumulitid machaeridian *Plumulites tafennaensis*. All specimens from the middle Katian Upper Tiouririne Formation, Isthlou (coll. JCG-M, Madrid). Scale bars equal 5 mm.

Fig. 5. The palaeoscolecid *Gamascolex vanroyi*, from the lower Sandbian Izegguirene Formation, Bou Nemrou (Museo Geominero, Madrid). (a) Large specimen, paratype MGM-6503X. (b–c) Holotype MGM-6502X showing contracted annuli and details of elongated dorsal plates, respectively. Scale bar equals 5 mm (a, b) and 100 µm (c).

Fig. 6. Trilobites from the lower Sandbian Izegguirene Formation, Bou Nemrou (a-b) and middle Katian Upper Tiouririne Formation, east of Erfoud (c). **(a)** *Nobiliasaphus* cf. *ingens*. Note impression of hypostome and preserved alimentary canal (Senckenberg Research Institute, Frankfurt am Main, SMF 96342). **(b)** *Selenopeltis macrophthalma*. A poorly prepared specimen showing traces of alimentary canal in posterior part of the body (collection B. Tahiri). **(c)** Giant slab with mass occurrence of *Selenopeltis buchi*, possibly indicating gregarious moulting and/or mating behaviour (photographed at *Macro Fossiles Kasbah*, Erfoud, presently in a private collection, USA). **(d)** Specimen of *Selenopeltis* cf. *buchi* with preserved intersegmental muscle bands or digestive glands (Museo Geominero, Madrid, MGM-7164X). Scale bars equal 10 mm (a–b, d).

Fig. 7. Vicissicaudates. **(a)** and **(b)** the cheloniellid *Duslia* sp. from the lower Sandbian Izegguirene Formation, Bou Nemrou. Note traces of the alimentary canal in **(a)** and the typical spine fringe in **(b)** (collection PVR). **(c)** the cheloniellid *Triopus* sp. from the middle Katian Upper Tiouririne Formation, E of Erfoud (collection PVR). **(d)** disarticulated holotype of the aglaspidid *Chlupacaris dubia* (National Museums of Scotland, Edinburgh, NMS G.2005.103.1). Scale bars equal 10 mm.

Fig. 8. Late Ordovician asterozoans from the Tafilalt Biota, eastern Anti-Atlas, Morocco. **(a)** Large, fully articulated ophiuroid associated with abundant, well-preserved crinoids and kirkocystid mitrates; Tarafin area, Lower Ktaoua Formation (uppermost part), UCBL-FSL 712481. **(b–c, e)** Well-preserved ophiuroids from Piste de Jorf, Lower Ktaoua Formation. **(b)** MHNM.15406.1. **(c)** MHNM.15406.14. **(e)** MHNM.15406.29. **(d)** Protasterid ophiuroid from Bou Nemrou; Izegguirene Formation; MHNM.15406.32. Scale bars represent 10 mm. Abbreviations (repositories): MHNM: Muséum d'Histoire Naturelle, Marseille, France; UCBL-FSL: Collections de Paléontologie, Université Lyon 1, Villeurbanne, France.

Fig. 9. Late Ordovician asterozoans from the Lower Ktaoua Formation, western Tafilalt, Morocco. (a–c) Unusual, small, fully articulated ‘asteroid-like’ ophiuroids. (a) MHNM.15406.25, Piste de Jorf. (b) MHNT.PAL.2005.0.142, Tizi n'Mourghi. (c) MHNM.15406.9, Piste de Jorf. (d) Well-preserved ophiuroid from Piste de Jorf, MHNN.P.035381. Scale bars represent 10 mm. Abbreviations (repositories): MHNM: Muséum d'Histoire Naturelle, Marseille, France; MHNN: Muséum d'Histoire Naturelle, Nantes, France; MHNT: Muséum d'Histoire Naturelle, Toulouse, France.

Fig. 10. Late Ordovician echinoderms from the Tafilalt Biota, eastern Anti-Atlas, Morocco. (a) Cluster of fully articulated individuals of the rhombiferan *Homocystites adidiensis*, with long portions of stems and well-preserved brachioles; Lower Ktaoua Formation, MGM-6931X. (b) Complete, fully articulated specimen of the eocrinoid *Cardiocystites bohemicus*, with particularly elongate, delicate stem and full set of brachioles; MHNM.15406.13, Lower Ktaoua Formation. (c) Cluster of densely packed, remarkably preserved individuals of the edrioasteroid *Euryeschatia reboulorum* attached to a large conulariid; BMNHUK.EE.14803, Upper Tiouririne Formation. (d) Current-orientated, well-preserved specimens of the eocrinoid *Ascocystites* sp., with fully articulated brachioles and partial stems (distal parts missing) associated with several individuals of protasterid MHNM.15406.39, Izegguirene Formation. Scale bars represent 50 mm (a, d) and 10 mm (b, c). Abbreviations (repositories): BMNHUK: Natural History Museum, London, UK; MGM: Museo Geominero, Madrid, Spain; MHNM: Muséum d'Histoire Naturelle, Marseille, France.

Fig. 11. Late Ordovician benthic graptolites (c. Sandbian 2–Katian 1) from the upper part of the Lower Ktaoua Formation, El Caid Rami. (a) *Ptilograptus* aff. *glomeratus*, AA.KST.OS.1. (b) ‘*Dictyonema*’ *villasi*, holotype AA.KST.05.7. Marrakech collection. Scale bars: 10 mm.

Fig. 12. The paropsonemid eldonid *Discophyllum peltatum*. (a) Lower Sandbian Izegguirene Formation, Bou Nemrou (field photograph, unknown repository). (b) Middle Katian Upper

Tiouririne Formation, E of Erfoud (collection PVR). Note the prominent coiled sac. Scale bars equal 10 mm.

Fig. 13. *Neoeione moniliformis*, a common trace fossil in the Upper Tiouririne Formation (middle Katian), east of Erfoud. **(a)** Field photographs of a large surface with some long traces preserved as convex epichnia in full relief. **(b)** Closer view of their consecutive knobs. Scale bars represent 50 cm (a) and 10 cm (b).

Fig. 14. Photograph of Lahcen Ouzemmou, one of the most prominent collectors of the Tafilalt Biota, and, together with his family, responsible for some of the most significant discoveries in the Tafilalt region of the past 25 years. He is active throughout the greater El Caid Rami area, but until 2010 his efforts were foremost centered on Bou Nemrou hill, where this photograph was taken. To the left of Lahcen is a freshly split slab revealing multiple specimens of the eocrinoid *Ascocystites*.

Table Caption

Table 1. Generic diversity of major groups of invertebrates in the Upper Ordovician of the Tafilalt (number of taxa partly estimated from faunal lists compiled in Álvaro *et al.* 2022). In this area, although bryozoans are present in all lithostratigraphic units, taxonomic studies have so far focused exclusively on assemblages from the Khabt-el-Hajar Formation (Termier & Termier 1950; Jiménez-Sánchez *et al.* 2015a, b, 2016).

	Izegguirene Formation	Lower Ktaoua Formation	Upper Tiouririne Formation	Khabt-el-Hajar Formation
brachiopods	2	22	18	4
bryozoans	?	?	?	22
echinoderms	16	25	20	2
graptolites	2	6	2	0
molluscs	0	5	5	0
trilobites	11	22	10	4

Table 1

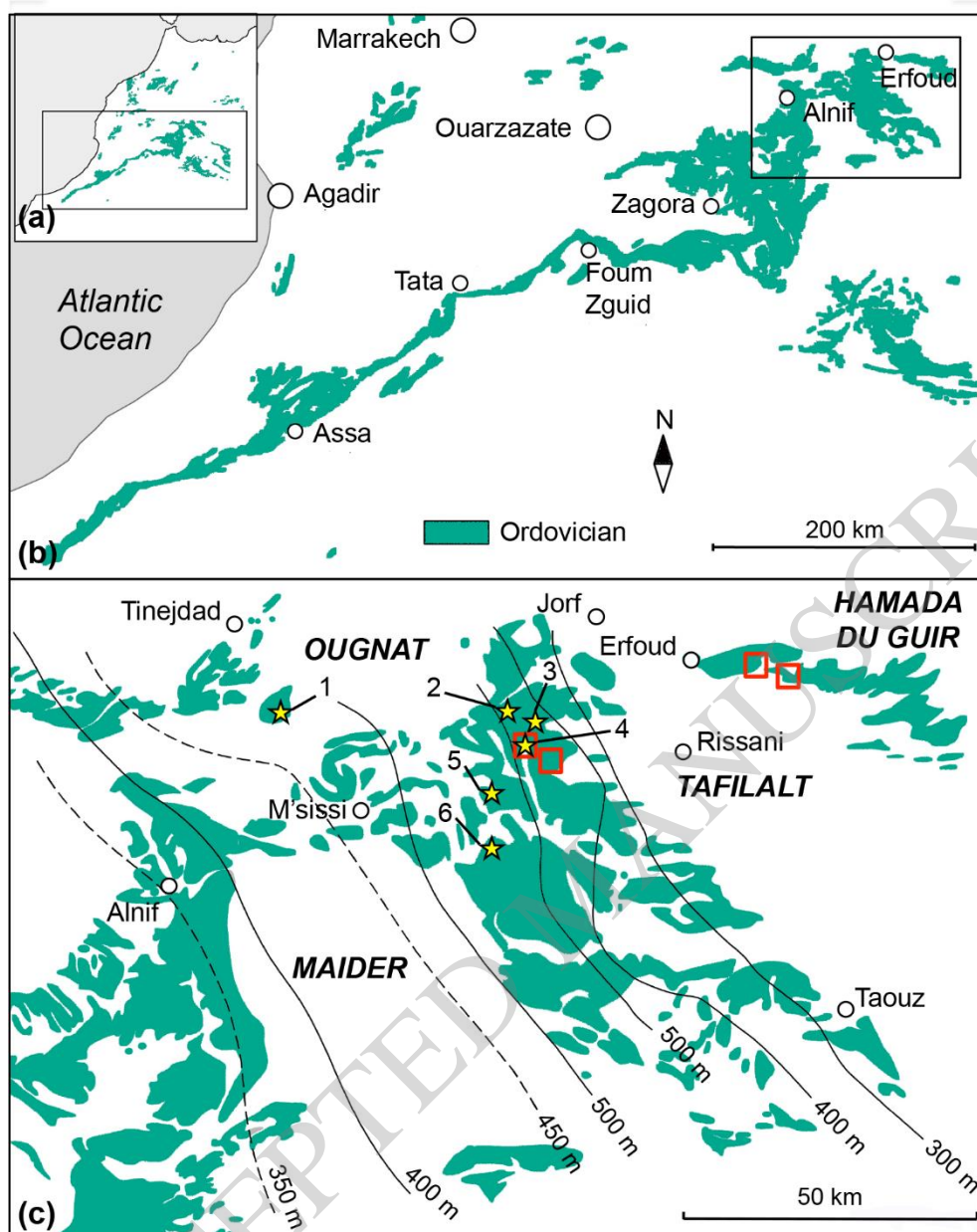


Figure 1

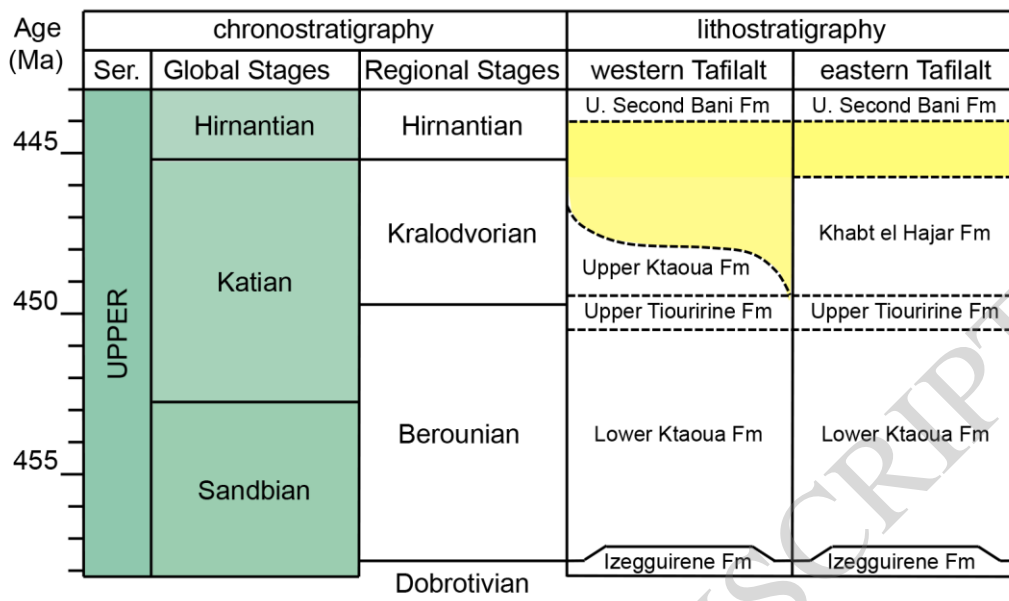


Figure 2

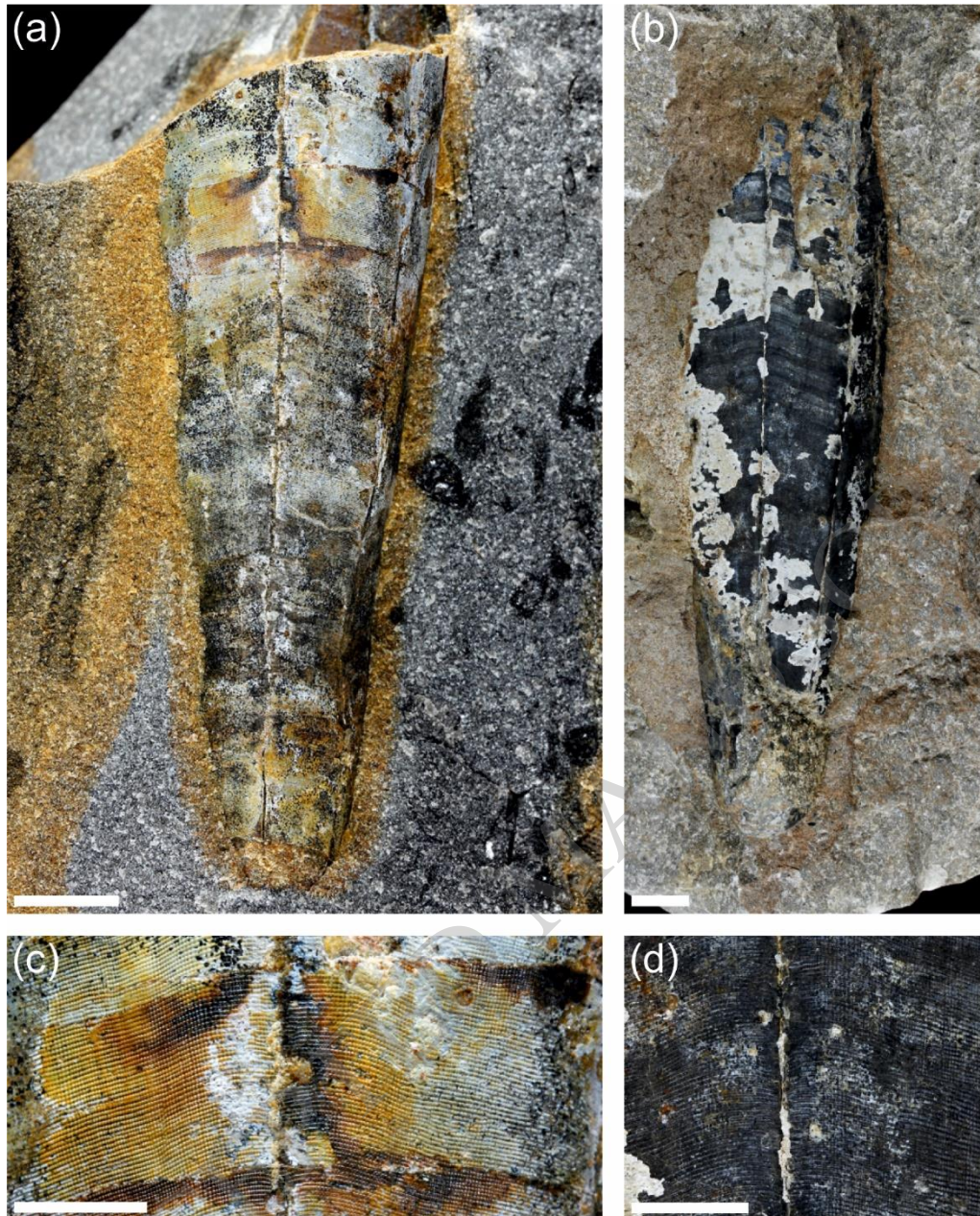


Figure 3

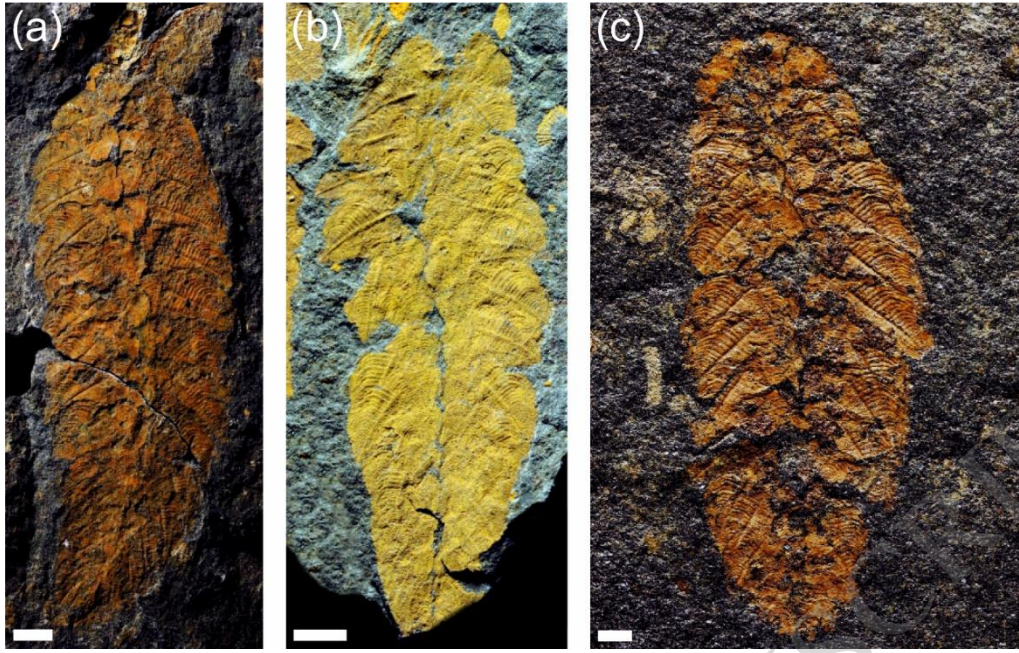


Figure 4



Figure 5

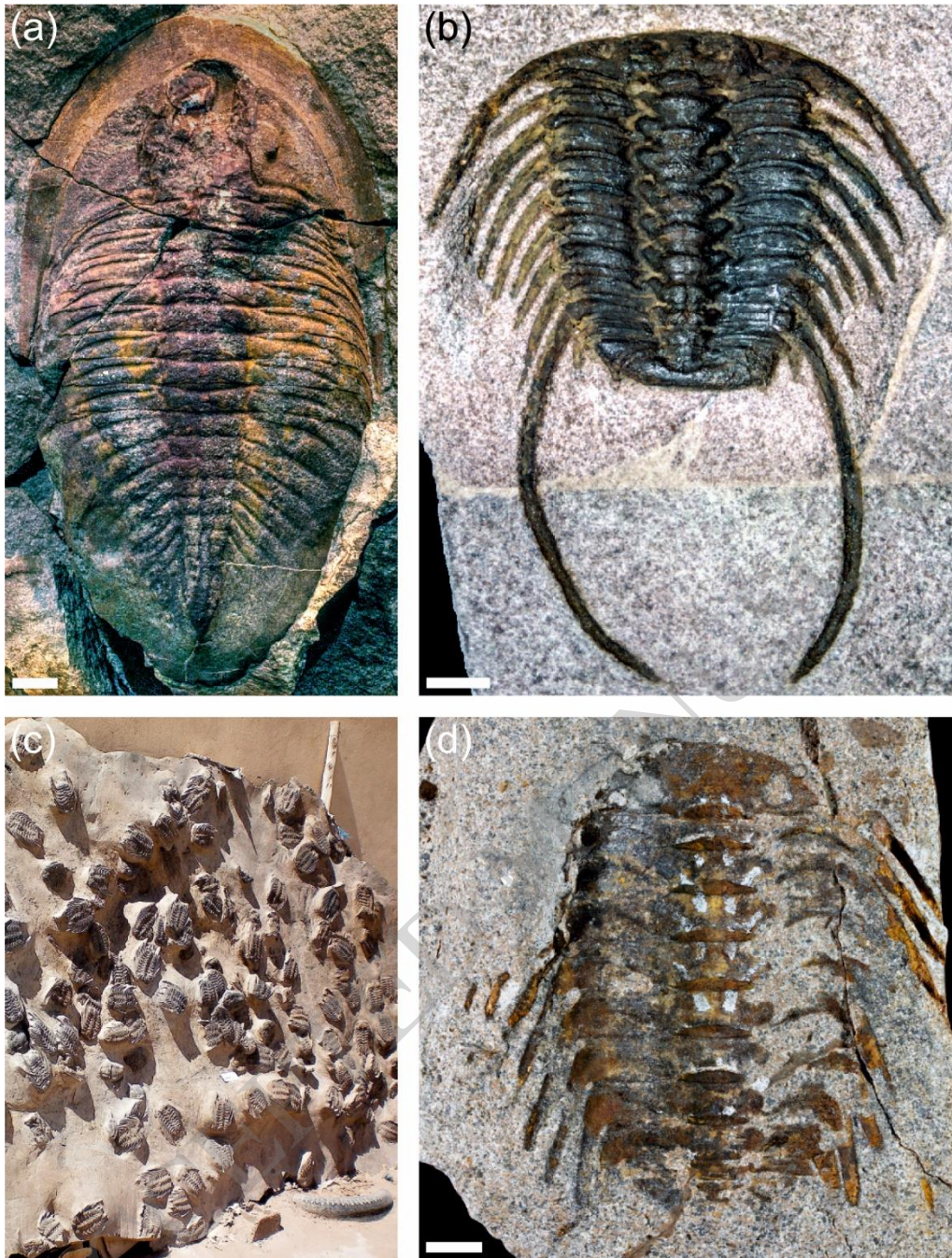


Figure 6

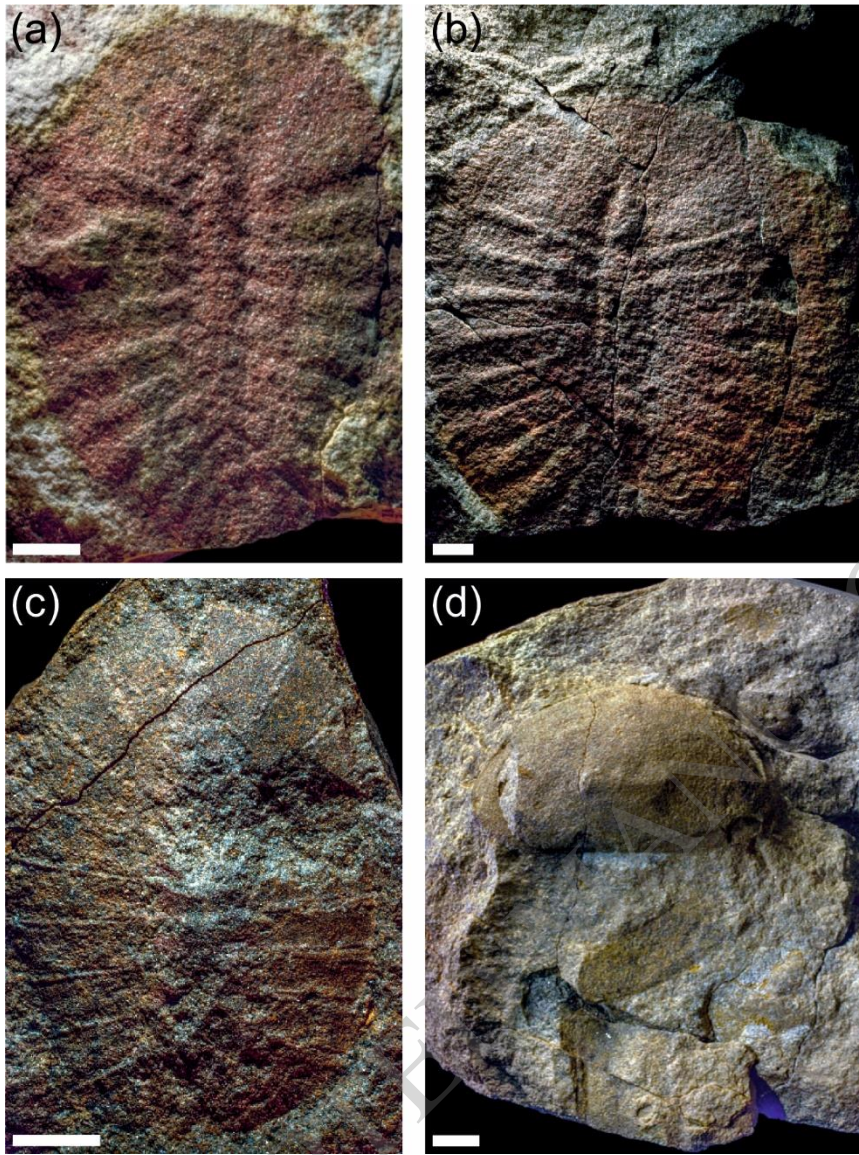


Figure 7

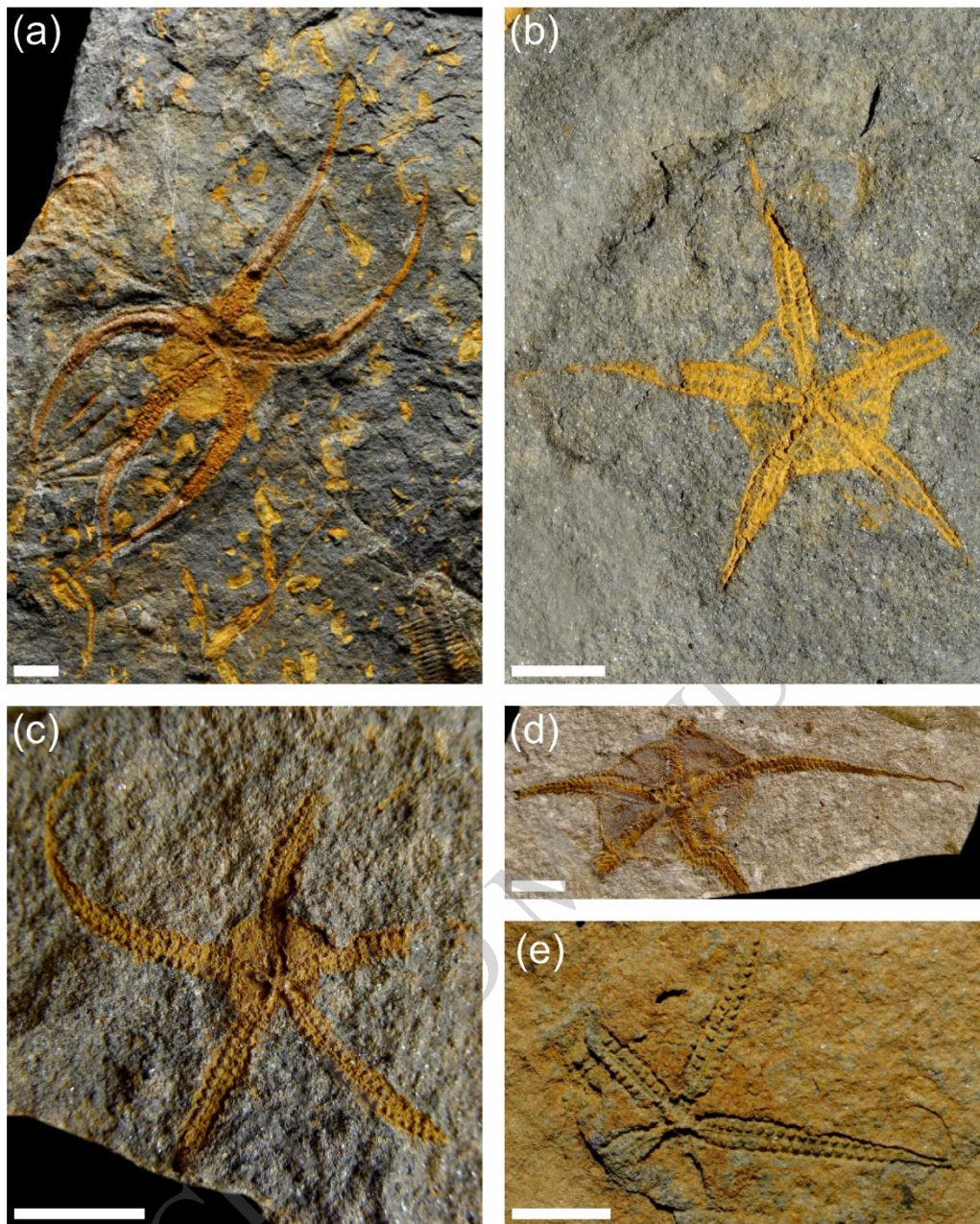


Figure 8



Figure 9

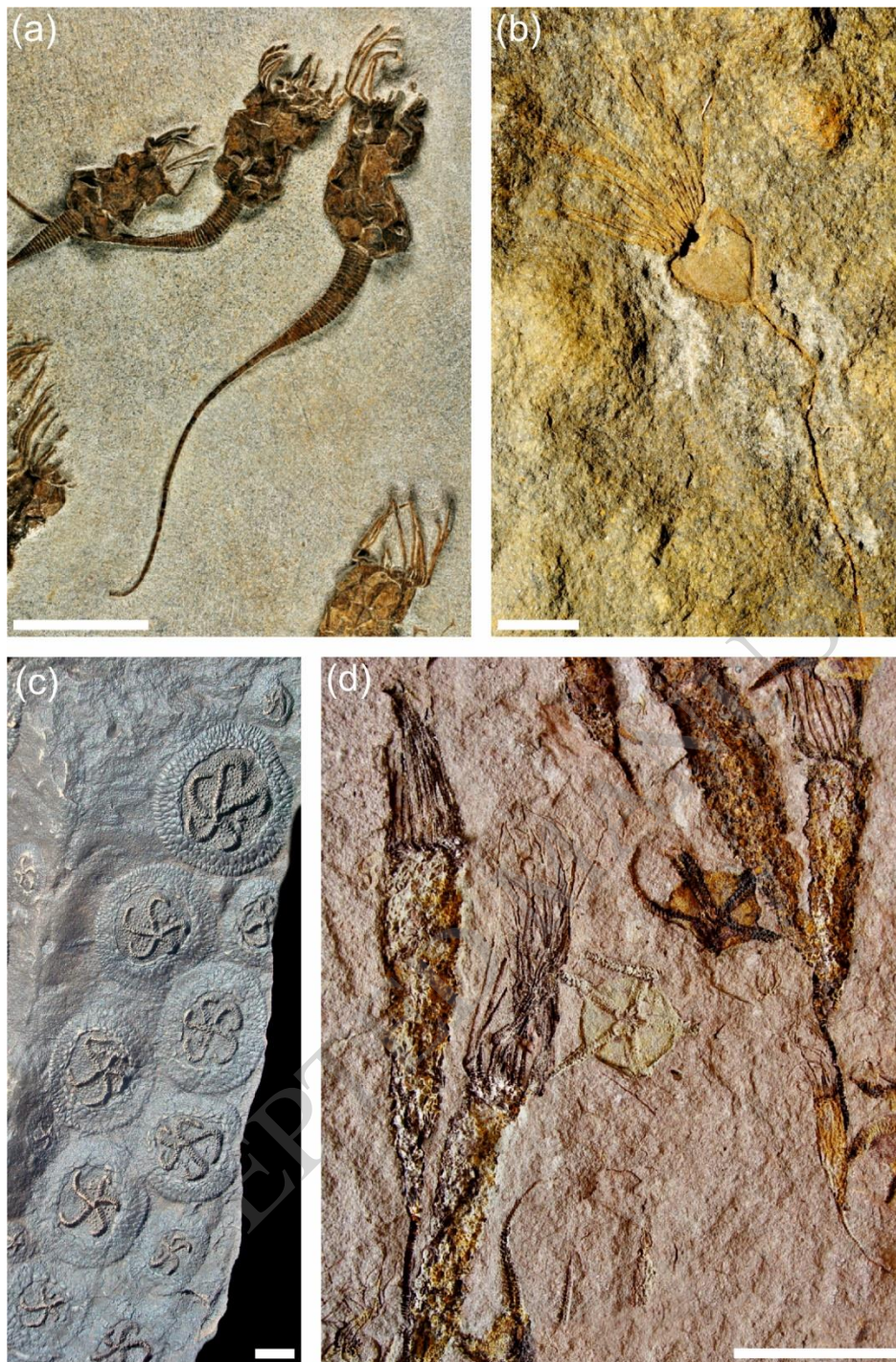


Figure 10

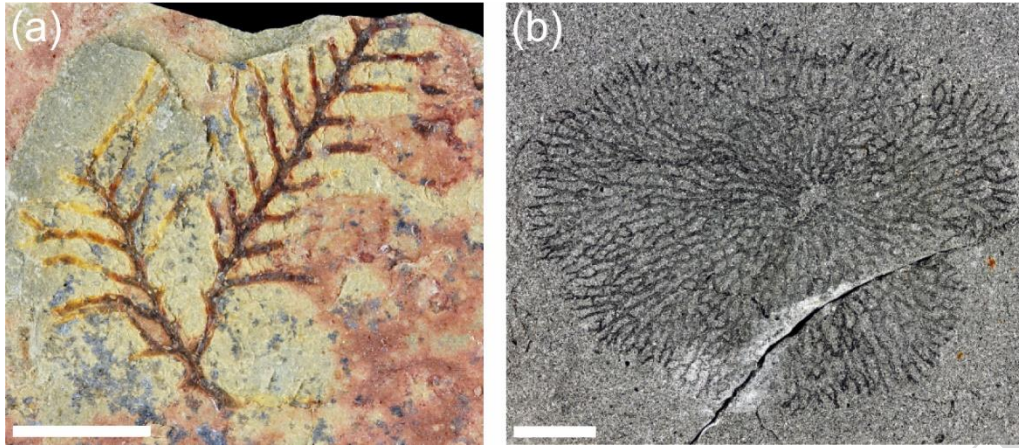


Figure 11

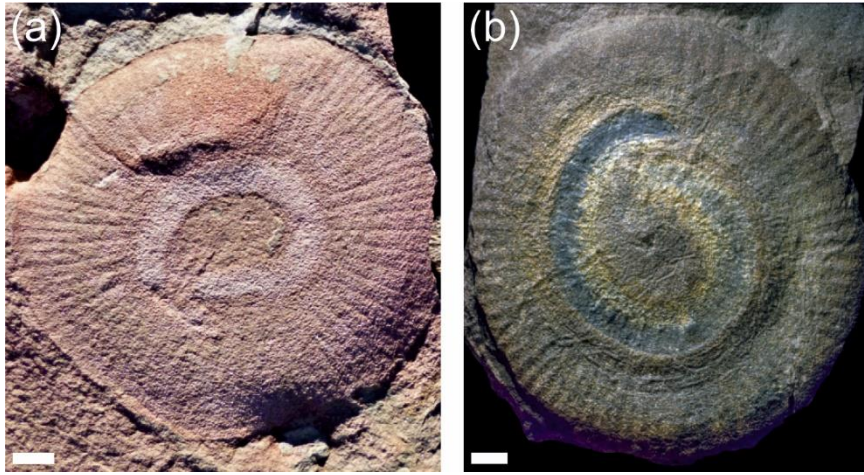


Figure 12

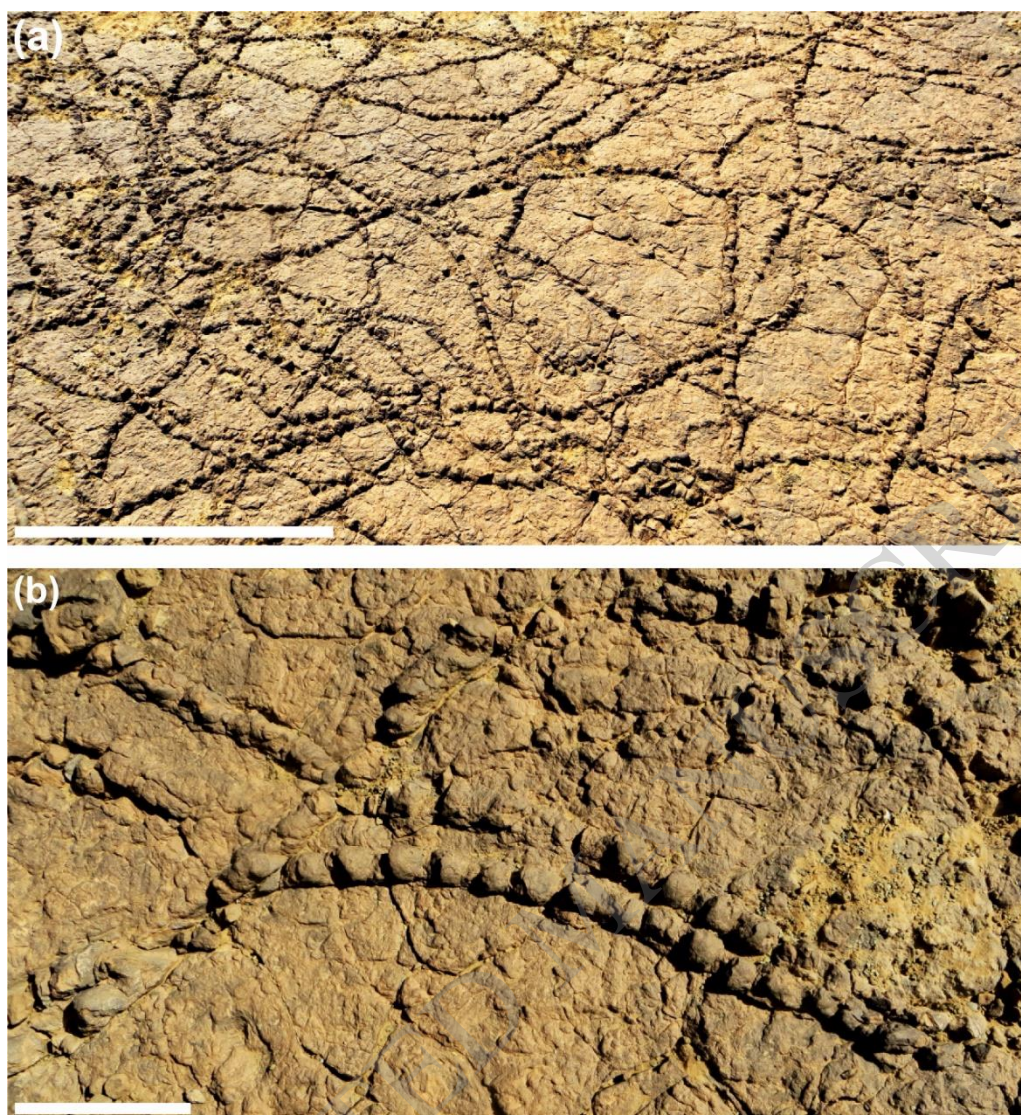


Figure 13



Figure 14