The Fezouata Shale (Lower Ordovician, Anti-Atlas, Morocco):
a historical review

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Abstract

Exceptionnally preserved fossils yield crucial information about the evolution of Life on Earth. The Fezouata Biota from the Lower Ordovician of Morocco is a *Konservat-Lagerstätte* of major importance, and it is today considered as an ‘Ordovician Burgess Shale.’ This biota was discovered only some 15 years ago, but geological studies of the area date back to the beginning of the 20th century. Pioneering geological investigations lead to the discovery of Ordovician strata in the Anti-Atlas (1929) and ultimately resulted in their formal

subdivision into four main stratigraphic units (1942). In the Agdz area, the presence of fossiliferous Tremadocian (Lower Ordovician) strata was suspected as early as 1939, but only definitively confirmed in 1955. In the 1960s-1990s, Jacques Destombes provided the first detailed biostratigraphic framework for the Lower Ordovician of the Anti-Atlas, and collected thousands of fossils that were subsequently described in a series of monographs. In the early 2000s, exceptionally preserved fossils were discovered in the Fezouata Shale (Tremadocian-late Floian) in the central Anti-Atlas by Mohamed 'Ou Saïd' Ben Moula. This biota, now known as the Fezouata Biota, is of the utmost importance, for it demonstrates the extent in the fossil record of non-biomineralizing animals typical of the 'Cambrian Explosion' into the Ordovician, during the 'Great Ordovician Biodiversification.' Although most components are still in need of formal descriptions, a fairly good picture of the composition and organisation of this biota, and how it contributes to our understanding of the early evolution of metazoan communities, can now be depicted. Moreover, recent studies have substantially clarified the biostratigraphical and palaeoenvironmental context of the Fezouata Shale, and are now being followed up by detailed investigations of the taphonomy, geochemistry and micropalaeontology of this unique *Konservat-Lagerstätte*. These efforts will soon greatly benefit from the recovery of fresh, unweathered samples from drill cores.

Keywords: Anti-Atlas, Fezouata Biota, Konservat-Lagerstätten, Morocco, Ordovician

1. Introduction

Seilacher (1970) created the term *Fossil-Lagerstätte* (feminine; plural: *Fossil-Lagerstätten*) using the German word *Lagerstätte* (that can be translated into English as

'natural mineral deposit', 'ore deposit', or just 'deposit') in combination with the word *Fossil*. Thus, a correct translation of the term *Fossil-Lagerstätte* would be 'natural fossil deposit'. This term was proposed to refer to strata that are remarkable for the richness (*Konzentrat-Fossil-Lagerstätte*) or the quality of preservation (*Konservat-Fossil-Lagerstätte*) of their fossil contents. Seilacher's concepts have been rapidly and widely accepted, but it was at the expense of the terms he had initially proposed; these were simplified to *Konzentrat-Lagerstätte* and *Konservat-Lagerstätte*, thus becoming virtually meaningless in German. Even more linguistically incorrect is the term *Lagerstätte* alone, now commonly used for sake of simplicity in reference to sites of exceptional preservation. Truth be told, it does not matter if the term *Lagerstätte* is linguistically vague, and despite its Germanic origin, its melody sounds to the ear of a palaeontologist as sweet as 'gold' to that of a miner.

The reason for that is simple: *Fossil-Lagerstätten*, especially those preserving soft tissues, provide unparalleled details on the anatomy of extinct organisms and the composition of the communities they formed. Because of that, one *Lagerstätte* can potentially contribute more significantly than a hundred classical localities (i.e. yielding exclusively shelly fossils) to the understanding of a major evolutionary event. For instance, our understanding of the Cambrian explosion – the first major animal radiation – and its aftermaths have greatly benefited from the study of *Lagerstätten*. Indeed, the early and middle Cambrian epochs have proven particularly rich in such sites of exceptional preservation (Allison and Briggs, 1993), although the reasons for that remain unclear (e.g. Butterfield, 2012; Gaines et al., 2012a). Sirius Passet (Greenland; Peel and Ineson, 2011), Emu Bay (Australia; Paterson et al., in press) and Guanshan (China; Hu et al., 2013) in the Cambrian Series 2, and Kaili (China; Zhao et al., 2011) and the Wheeler and Marjum formations (USA; Robison et al., 2015) in the Cambrian Series 3 have become famous localities for those interested in the early diversification of eumetazoans. However, none of them as-yet rivals with Chengjiang (Cambrian Series 2,

China; Hou et al., 2004) and even less with the worldwide celebrated Burgess Shale (Cambrian Series 3, Canada; Briggs et al., 1994; Caron and Rudkin 2009) in terms of quality of preservation, abundance, and diversity of their non-biomineralised faunas.

Unfortunately, not all major evolutionary events have their ‘Burgess Shale’ and the history of Life is still scattered with grey areas. For instance, the Great Ordovician Biodiversification Event (GOBE) – the massive increase in diversity of marine invertebrates throughout most of the Ordovician – was until recently almost solely documented by the fossil record of biomineralised organisms (Allison and Briggs 1993). Indeed, the main oldest post-Cambrian *Lagerstätten* representing normal open marine environments were the Silurian Herefordshire in England (Briggs et al., 1996, 2008) and the Lower Devonian Hunsrück Slate in Germany (Bartels et al., 1998); both had yielded diverse marine faunas, but those are radically different in composition compared to those of the Burgess Shale and other Cambrian *Lagerstätten*. The question of how marine ecosystems had evolved in-between could only be addressed using shelly faunas, with the strong biases that it implies.

The discovery of an Early Ordovician *Lagerstätte* in the Anti-Atlas of Morocco preserving for the first time a rich and diverse normal, open marine fauna was of critical significance. For the first time, the transition between the Cambrian world, and its ‘weird wonders’ (Gould, 1989), and the post-Cambrian world, with its more modern marine ecosystems, would be enlightened using exceptionally-preserved fossils. A c. 70 Myr-long gap in the fossil record of non-biomineralised animals would finally be filled. Although only discovered some fifteen years ago, the Fezouata Biota has already radically modified our understanding of the evolution of Early Palaeozoic marine life. Its shelly fauna is typical of the Early Ordovician; its soft-bodied fauna, however, is strongly reminiscent to those of Cambrian *Lagerstätten*, except for the presence of representatives of several derived groups as-yet known from considerably younger strata (e.g. various chelicerates, cheloniellid arthropods; Van Roy et al.

2010, 2015a). The composition of this non-biomineralised fauna, especially the persistence of so many Burgess Shale-type taxa, questions the widely accepted view of an early diversification of animals involving two distinct events: the Cambrian explosion and the GOBE. An alternative view can now be proposed, that of a more continuous diversification dynamic spanning the entire Early Palaeozoic (Droser & Finnegan, 2003; Klug et al., 2010; Van Roy et al., 2010, 2015a). This hypothesis finds supports in recent palaeodiversity studies (e.g. Alroy et al., 2008, Nardin et al., 2009) and discoveries of exceptionally-preserved fossils in the upper Cambrian (Zamora et al., 2013; Lerosey-Aubril, 2015; Ortega-Hernández et al. 2015). The study of the Fezouata Biota will evidently continue to play a central role in this debate.

The Fezouata Shale has already been the subject of a dozen articles, dealing with its exceptionally-preserved fauna (e.g. Vinther et al., 2008; Van Roy and Briggs, 2011; Van Roy et al., 2010, 2015a, b) and its preservation (Gaines et al. 2012b), or its environmental and stratigraphical contexts (Martin et al. in press). Yet, very little is known about the discovery of this Lagerstätte and the early years of its study. In addition to filling this gap, this contribution aims at placing the research on the Fezouata Shale within the historical framework of geological investigations in the Moroccan Anti-Atlas. From the realisation that Ordovician strata outcropped widely in this region to the first discovery of soft-bodied fossils, it summarizes the works of generations of geologists and palaeontologists, which now form the basis of our understanding of the geological context of these exceptional deposits.

2. Initial steps in the knowledge of the Anti-Atlas

Although it has been populated continuously from at least the late Palaeolithic (as suggested by the numerous chipped stones, cave paintings and tumuli occurring in this area)

and in spite of its strategic location at the crossroads between trade routes from Mediterranean regions and Sub-Saharan Africa, the Anti-Atlas long remained a *terra incognita* for geographers and geologists until the late 19th to early 20th century (de Foucault, 1888; Gentil, 1929; Despujols, 1933; Choubert, 1952a; Willefert, 2004; Destombes, 2006a).

2.1. Beyond the High Atlas

The Atlas system is a 2,500 km long mountain range extending from Morocco (High Atlas and Middle Atlas) to Tunisia (Tunisian Atlas), and resulting from the convergence between Africa and Europe during the Cenozoic (Frizon de Lamotte et al., 2000; Bracène and Frizon de Lamotte, 2002). This major geomorphologic structure appears distinctly in the first descriptions and maps of the world produced by the Greek geographers Herodotus (c. 484 BC - 425 BC), Eratosthenes of Cyrene (c. 276 BC - c. 194 BC) and Strabo (c. 64 BC - c. 24 AD), who coined the name Atlas after the Titan who held up the sky. The Atlas mountains gave their name to the nearby Atlantic ocean ("sea of Atlas"), and also to the mythical city of Atlantis ("island of Atlas"), which was located nearby (after Herodotus), possibly in the Sous plain in between the High Atlas and the Anti-Atlas (Hübner, 2011). The first detailed map of North Africa was produced by Ptolemy (c. 90 AD - 168 AD), who separated clearly the Rif (minor Atlas) from the Atlas mountains (major Atlas).

In his *Naturalis Historiae*, the Roman geographer and naturalist Pliny the Elder (23 - 75 AD) provided the first data on the regions located beyond the Atlas. Pliny's knowledge relied on the accounts of three former exploratory expeditions. Those of the Carthaginian explorer Hanno the Navigator (5th c. BC) and of the Greek historian Polybius (c. 208 BC - 126 BC) along the western coast of Africa both probably reached the mouth of the Draa river (then called *Darat*). Pliny the Elder also reported the military expedition lead by the Roman general

Suetonius Paulinus, who crossed the High Atlas, lead his troops through the Tafilalt (eastern Anti-Atlas) and finally reached the Sahara in 41 AD. Finally, Pliny the Elder indicated that "Dyris" was the name given to the Atlas mountains by the local populations.

In the following centuries, major advances in the knowledge and the description of the regions located south of the Atlas were achieved by a series of Andalusian/Moroccan geographers and explorers. In his book *Kitâb Nuzhat al Mushtâq*, Al Idrissi (c. 1100 - c. 1165) provided a remarkably detailed and accurate account of the geography of North Africa. His map of the world (*Tabula Rogeriana*, c. 1154) clearly shows the Atlas mountains as a single continuous range extending from the Atlantic coast through North Africa, and subdivided into *gebel Daran* (High Atlas, Morocco) and *gebel Auras* (Aurès, Algeria). South of the Atlas, Al Idrisi reports *Tarudant* (Taroudant) in the *bilad al Sus* (Sous region), the *Dar'a* (Draa), and the city of *Sigilmasa* (eastern Tafilalt, near Rissani). The *Catalan Atlas* (c. 1375), produced by the Jewish geographer Abraham Cresques, is another remarkable example of a medieval map providing some information on the regions beyond the Atlas range (e.g. *Sigilmasa* in the eastern Tafilalt). Detailed descriptions of the Anti-Atlas, and in particular of the Tafilalt area, were also provided by the two explorers Ibn Battuta (1304-1369) and Hassan al-Wazzan (c. 1494-1548). In 1341-1342, the first one spent several months in the city of Sijilmasa, before heading to Timbuktu and Gao, in the Mali Empire. The second one, also known as Leo Africanus, described his travels, and in particular his journey through the Tafilalt to Timbuktu (in the early 1510s) in his book (*Africanus*, 1526).

In the next three centuries (mid 16th to mid 19th c.), the development of regular maritime commercial trade routes by most European countries (Britain, France, the Netherlands, Portugal and Spain) along the western coasts of Africa provided an unprecedented amount of data, observations and measurements, which made it possible to draw more and more detailed and accurate maps of the Moroccan coasts and coastal areas (see e.g. Ortelius, 1570; Sanson,

1655; Bellin, 1764; Chénier, 1787; Jackson, 1809; Badia y Leblich, 1814; Renou, 1844; Beaudouin, 1848). Several detailed descriptions of the northern part of Morocco were published by diplomats, adventurers and travellers (e.g. Chénier, 1787; Potocki, 1792; Jackson, 1809; Badia y Leblich, 1814; Washington, 1831). In contrast, no major advance was achieved in the knowledge of the unexplored areas located on the southern side of the High Atlas. On most maps, the southern slopes of the High Atlas were fringed by the Sahara desert and only few names of rivers (Draa, Ziz), localities (Sijilmassa) and regions (Tafilalt) were reported. With the remarkable exception of Jackson's map (1809), the existence of the Anti-Atlas range remained unknown until the second half of the 19th century (Willefert, 2004). Jackson (1809) was the first to mention and illustrate the occurrence of a long mountain range (*South Atlas mountains*) extending along the southern side of the High Atlas (*North Atlas mountains*) from the Atlantic ocean, south of the Sous plain (*Suse*, in the SW) to the Tafilalt (*Bled Fillely*, in the NE). Beaudouin's map (1848) was the first one to mention the names of the city of Zagora (*Zagoura*) and of the two large plains, Ternata and Fezouata (*Fezzouâta*) N and S of it, respectively.

2.2. First scientific explorations of the Anti-Atlas

In 1871, during his scientific exploration of the western High Atlas, the British geologist George Maw (1832-1912), accompanied by the botanist Joseph Hooker (1817-1911) and the geographer John Ball (1818-1889) could observe from the summit of Jbel Tezah, a long mountain range, which was running south of, and more or less parallel to, the High Atlas. By analogy with the Anti-Lebanon mountains, which are parallel to the Mount Lebanon range and separated from it by the Beqaa valley, the name *Anti-Atlas* was then coined for this

mountain range opposite (Greek prefix *anti-*) and parallel to the High Atlas (Hooker and Ball, 1878).

In 1872, the German scientific expedition lead by the geologist Karl Wilhelm von Fritsch (1838-1906) and the botanist Johan Rein (1835-1918) focused mostly on the northern side of the High-Atlas (Asni area, about 40 km S of Marrakech; von Fritsch, 1879). The first extensive exploration of the High Atlas was achieved in 1888 by the Scottish geologist Joseph Thomson (1858-1895). Although he never went farther to the South, he provided a relatively accurate map of the Anti-Atlas (1888), as well as the first geological interpretation of this mountain range (as an extensive Cretaceous plateau), extrapolated from what he could see from the summits of the High Atlas (Fig. 1A; Thomson, 1899).

The German geographer and adventurer Friedrich Rohlf (1831-1896; Fig. 2B) gave relatively detailed descriptions of the Anti-Atlas area he visited during his 1862 transect from Agadir to Rissani, through Taroudant, Tazenakht, Zagora and Tazzarine (Rohlf, 1868, 1874). However, the first scientific transect through the Anti-Atlas range was achieved in 1880 by the German geologist Oskar Lenz (1848-1925; Fig. 2C), who collected Devonian brachiopods (e.g. *Productus*) in the Jbel Ouarkziz, about 50 km S of Foug el Hassan (Lenz, 1884).

In 1883-1884, the scientific expedition of the French explorer and geographer Charles de Foucauld (1858-1916; Fig. 2A) provided an unprecedented wealth of precise observations and measurements (e.g. altitudes, latitudes and longitudes) along his transect through the whole Anti-Atlas, from the Jbels Ougnat and Sarhro (in the East) through the Draa valley (Tamnougalt), Tazenakht, Tissint and Agadir (in the West). De Foucauld was the first to describe the elongate geomorphologic structure formed by the quartzitic cliffs of the Jbel Bani on the southern side of the Anti-Atlas (de Foucauld, 1888).

All geographic data accumulated through the late 19th century expeditions were summarised on the maps produced by Schnell (1892) and de Flotte de Roquevaire (1897),

which both provided, for the first time, extremely detailed and accurate representations of the main geomorphologic structures located south of the High Atlas (Anti-Atlas and Jbel Bani).

2.3. First geological investigations

Geological investigations began with the study of the Rif mountains by the French geologist Henri Coquand (1813-1881), who collected and described the first fossils from Morocco (Coquand, 1847). In the following 80 years, geological and palaeontological studies focused almost exclusively on the High Atlas and the regions located North of it (Mourlon, 1870; Hodgkin, 1866; Balansa, 1868; Brives, 1902, 1905, 1909; Gentil, 1905a, 1905b, 1906, 1912, 1920; Lemoine, 1905). The presence of Palaeozoic rocks in Morocco was first pointed out by Coquand (1847) in the Rif area, based on the presence of Siluro-Devonian fossils (e.g. brachiopods, corals, crinoids, nautiloids, trilobites). In the High Atlas, Carboniferous plant remains were first reported by Balansa (1868) and an abundant and diverse assemblage of Silurian graptolites was mentioned by Gentil (1905b). The first Cambrian Moroccan fossils (e.g. *Paradoxides*) were described from the Casablanca area by Lecointre (1918). The first evidence of Ordovician strata in Morocco was reported by Barthoux (1924), who mentioned the occurrence of the typical trilobite genus *Calymene* in sandstones of the Djebilet hills. The first diverse Ordovician faunas were described by Termier (1927) in the Oulmès area (e.g. *Trinucleus*), and by Roch (1930a) in the High Atlas (e.g. *Bellerophon*, *Orthoceras*, *Placoparia*, *Stropheodonta*).

In the beginning of the 20th century, extensive field work was performed by the two French geologists Abel Brives (1868-1928) from 1901 to 1907, and Louis Gentil (1868-1925) from 1904 to 1911. In 1904, Brives travelled through the Sous plain as far south as the Tiznit area, where he explored the northern flank of the western Anti-Atlas at Jbel Tachilla.

However, Brives could not collect any fossils and, relying exclusively on the lithologies, he interpreted the thick sedimentary series of Jbel Tachilla (shales and massive quartzites) as Cenomanian (Brives, 1909). During his 1905-1906 field campaign, Gentil (Fig. 3B) crossed the High Atlas, reached the Sous plain and explored the geology of Jbel Siroua (large Neogene volcano located in between the High Atlas and the Anti-Atlas; Chorowicz et al., 2001). Although by then, no fossils had been collected in the whole Anti-Atlas, Brives (1905, 1909) and Gentil (1906, 1912, 1920) both largely followed Thomson's interpretation (1899). Consequently, on the *Provisional map of Morocco* (Gentil, 1920), the western part of the Anti-Atlas was represented as a narrow and elongate Hercynian structure (consisting of magmatic rocks and Devonian sediments), with both its northern and southern flanks capped by a thick Cenomanian succession (Fig. 3A). The Jbel Bani, as well as the central and eastern parts of the Anti-Atlas (Jbels Sarhro and Ougnat) were all interpreted as extensive tabular plateaux consisting of a thick Cenomanian series (Figs. 1A). More cautiously, Roch (1930b) figured the western part of the Anti-Atlas as a wide, blank area on his provisional geological map of the western Atlas.

3. Initial steps in the knowledge of the Ordovician of the Anti-Atlas

3.1. First investigations

In 1923, during his last field campaign in southern Morocco (in the Sous plain and western Anti-Atlas), Gentil collected the first Ordovician fossils (*Orthis*) in the quartzites of Jbel Bani in the Tissint area (Neltner, 1938). However, these brachiopods were erroneously considered as Devonian by Lecointre (1929). Consequently, in his posthumous book, published four years after his death, Gentil (1929) acknowledged the absence of Cretaceous deposits in the

western Anti-Atlas, and he reinterpreted this massif as mostly composed of Lower to Middle Devonian sedimentary rocks (Fig. 1B). In the late 1920s-early 1930s, the geological exploration and mapping of the Anti-Atlas were boosted by the foundation of the Geological Survey of Morocco (1921) by Pierre Despujols (1888-1981), and (from 1934) the access to the detailed topographic maps produced by the Geographic Survey of the French Army (Despujols, 1933; Choubert, 1952a; Medioni, 2011).

The discovery of abundant and diverse Cambrian faunas (e.g. archaeocyathids, trilobites) in the Tiznit area (Bourcart, 1927) prompted a critical re-evaluation of previous geological schemes: the bulk of the western Anti-Atlas was not made of Cretaceous (Fig. 1A; Thomson, 1899; Brives, 1909; Gentil, 1912, 1920) or Devonian strata (Fig. 1B; Gentil, 1929), but of Precambrian and Cambrian rocks (Bourcart and Le Villain, 1929, 1931; Neltner, 1929a, 1929b; Bondon et al., 1934).

In the eastern Anti-Atlas (Tafilalt), the occurrence of fossiliferous Ordovician strata (yielding *Trinucleus*) was first mentioned by Neltner (1929a, p. 556). In the western Anti-Atlas, a putative Ordovician age was also suggested by Neltner (1929b, p. 872), though without any palaeontological evidence, for the quartzites overlying the green Cambrian shales. In the Tiznit area, the Middle Ordovician age ('Llandeilo', i.e. late Darriwilian) of the Jbel Tachilla quartzites, previously interpreted as Cretaceous (Brives, 1909) or Devonian (Gentil, 1929), was definitively established by Bigot and Dubois (1931), based on the presence of a rich and diverse fossiliferous assemblage (Bourcart, 1933, 1935; Ségaud, 1933; Ségaud and Termier, 1933; Termier, 1936; Roch, 1950; Choubert, 1952b). Similarly, in 1932, the discovery of an isolated pygidium of *Homalonotus* in the quartzites of Jbel Bani at Fom Zguid prompted their re-evaluation as Ordovician (Bondon in Termier, 1936; Bourcart, 1938; Neltner, 1938; Choubert, 1952a). As a consequence, the extent of Ordovician rocks in the

Anti-Atlas on Yovanovitch's 1936 geological map of Morocco was already relatively accurate and matched closely that of the Jbel Bani (and Jbel Tachilla) quartzites.

The first detailed descriptions of a relatively complete Ordovician succession ('Arenig', 'Llandeilo' and 'Caradoc') were produced by Clariond (1933, 1934) in the Maïder and Tafilalt (eastern Anti-Atlas), and by Bondon et al. (1934) in the Tazzarine area (central Anti-Atlas). However, in these regions, the identification of putative Lower Ordovician strata (about 200 m of green shales) was not based on the presence of any index fossil, but relied only on their stratigraphic position between the stratigraphically better constrained middle Cambrian ('Acadian') and Middle Ordovician ('Llandeilo') quartzites. The Lower Ordovician age of the green shales was questioned (Clariond, 1935) and rejected (Termier, 1936; Roch, 1950; but see Choubert et al., 1952; Destombes, 2006e), because of the occurrence of a typical early Darriwilian ('Llanvirn') assemblage in their upper part. As a consequence, no Lower Ordovician rocks were indicated on the first provisional geological map (1:200.000) of the eastern Anti-Atlas (Clariond, 1944).

In the Anti-Atlas, the first definitive Early Ordovician fossils (*Ogygia desiderata*, *Onchometopus? volborthi*; Figs. 4A-B) were collected in the Agdz area (Jbel Kissane) by Bondon (Bondon in Roch, 1939: p. 62; Choubert, 1952a). Although a probable Tremadocian age was suggested by Pruvost (in Roch, 1939) for these trilobites, most authors considered them as more likely Floian ('Arenig', 'Skiddavian'), for purely conceptual reasons (Choubert, 1946, 1951, 1952a; Choubert and Termier, 1947; Termier and Termier, 1947, 1950; Roch, 1950; Choubert et al., 1952). Most other regions of the "Mediterranean Province" (e.g. Armorican Massif, Iberian Chains, Pyrenees, Sardinia) are characterised by a late Cambrian to Tremadocian stratigraphic gap resulting from the sardic phase of the Caledonian orogeny (Choubert, 1952a; Michard, 1976). The description of late Cambrian to early Ordovician volcanism in the western Tafilalt (Clariond and Gubler, 1937; Choubert et al., 1952)

supported the idea of sardic tectonic events in the Anti-Atlas, and thus seemed to make the presence of Tremadocian strata (and fossils) highly improbable.

3.2. Choubert's stratigraphic framework

The first comprehensive, overarching stratigraphic framework for the Ordovician series of all regions of the Anti-Atlas was proposed by the French geologist Georges Choubert (1908-1986; Fig. 5B), based on large scale correlations and the identification of lateral variations in facies and thicknesses (Choubert, 1942, 1943a, 1951, 1952a, 1952b, 1956; Choubert and Termier, 1947; Choubert and Jacquemont, 1952; Choubert et al., 1952; Choubert and Marçais, 1956). Choubert (1942) defined four main lithostratigraphic subdivisions in the Ordovician series of the Anti-Atlas: (1) the External Feijas Shales; (2) the Bani Quartzites (or First Bani); (3) the Ktaoua Shales; and (4) the Bani Selmane Quartzites (or Second Bani). The total maximum thickness of the whole Ordovician succession in the Anti-Atlas was successively estimated at around 2,000 m (Choubert, 1942) and 2,850 m (Choubert and Termier, 1947; Choubert, 1951, 1952a; Choubert and Jacquemont, 1952).

The four lithostratigraphic units defined by Choubert (1942) were assigned to the 'Skiddavian-Llanvirn' (Floian to early Darriwilian; External Feijas Shales), the 'early to middle Llandeilo' (late Darriwilian; First Bani), the 'late Llandeilo' (latest Darriwilian; Ktaoua Shales), and the 'Caradoc' (Sandbian to early Katian; Second Bani) by Choubert and Termier (1947), based on their faunal contents (bivalves, brachiopods, echinoderms, hyolithids and trilobites; Fig. 1C). The ages of these four units were slightly re-evaluated by Choubert (1951, 1952a) as 'late Arenig to early Llandeilo' (late Floian/Dapingian to late Darriwilian; External Feijas Shales), 'Llandeilo' (late Darriwilian; First Bani), 'late Llandeilo to early Caradoc'

(latest Darriwilian to Sandbian; Upper Ktaoua Shales), and 'Caradoc' (late Sandbian-early Katian; Second Bani).

All major classical Ordovician localities of the Anti-Atlas (e.g. Foum Zguid, Jbel Kissane, Jbel Tachilla) were visited during the two field excursions of the 19th international geological congress in Algiers (Choubert, 1952b; Choubert et al., 1952). Extensive field work during the months preceding these field excursions lead to the discovery of a new Lower Ordovician fossiliferous site, in between Agdz and Zagora (Tansikht bridge; Choubert et al., 1952b, 1953, 1955; Ubaghs, 1963; Destombes, 2006a; Allaire et al., 2015). During the excursion of the 19th international congress, this new locality yielded abundant echinoderm remains, which were later described by Choubert et al. (1953). The description of the Lower Ordovician glyptocystitid rhombiferan *Macrocystella bohémica* (Fig. 4C) by Choubert et al. (1953) was the first systematic paper devoted to an Ordovician fossil from the Anti-Atlas. In contrast, several monographs already had been published on Cambrian faunas (e.g. archaeocyathids, trilobites) from the same area (e.g. Bourcart and Le Villain, 1931; Hupé, 1952).

3.3. A geological definition of the Anti-Atlas

As originally described by Hooker and Ball (1878), the Anti-Atlas corresponds exclusively to the mountain range separated from the western High Atlas by the Sous plain (in the West), and connected to it by the Jbel Siroua (in the East). This first definition of the Anti-Atlas was later extended by most geographers and explorers, to include the Jbels Sarhro and Ougnat as well (e.g. de Foucauld, 1888; Schnell, 1892; de Flotte de Roquevaire, 1897). However, the Jbel Bani was interpreted as a narrow, separate range, running more or less parallel to the southern edge of the Anti-Atlas (de Foucauld, 1888; Schnell, 1892; de Flotte de Roquevaire, 1897).

The wider extension of the Anti-Atlas proposed by the geographers was refuted by both Brives (1905, 1909) and Gentil (1906, 1912, 1920). The two French geologists argued that, for geological reasons, the name Anti-Atlas should be restricted to its original definition. Strongly influenced by Thomson (1899), they considered that the Anti-Atlas *sensu* Hooker and Ball (1878) was a narrow, folded, Hercynian massif capped by Cenomanian rocks, geologically and structurally distinct from the *Draa and Tafilalt Plateaux* (Jbels Saghro and Ougnat), which were interpreted as thick, tabular, Cenomanian high plains. Although this geological interpretation was refuted by later studies (e.g. Neltner, 1929a, 1929b; Bourcart and Le Villain, 1931), the distinction between the Anti-Atlas *sensu stricto* (in the SW) and the Draa and Tafilalt Plateaux (or *Jbel Saghro-Maïder-Tafilalt*, in the NE) long persisted in the literature (e.g. Neltner, 1929a, 1938; Clariond, 1933, 1934, 1935, 1944; Bondon et al., 1934; Termier, 1936; Yovanovitch, 1936; Roch, 1950).

Choubert (1942, 1943b, 1951, 1952a) was the first to understand that the Anti-Atlas *sensu* Hooker and Ball (1878), the Jbels Bani, Ougnat and Saghro, the Maïder and the Tafilalt were all part of a same and single geological structure: the Anti-Atlas. He also produced the first synthetic, global scenario reconstructing the complex geological history of the Anti-Atlas and interpreted its thick Palaeozoic series as deposited in a subsididing, intra-cratonic basin (Choubert, 1943b, 1951, 1952b; Michard, 1976; Burkhard et al., 2006). The subdivision of the Anti-Atlas into western, central and eastern regions was also proposed by Choubert (1951), based on geological arguments (Fig. 6). Finally, in the early 1950s, Choubert initiated the project of geological mapping of the whole Anti-Atlas (at the scale 1:200,000) with the publication of the western Anti-Atlas sheet (Service géologique du Maroc, 1956).

4. Initial steps in the knowledge of the Lower Ordovician of the central Anti-Atlas

4.1. First investigations

Early Ordovician fossils from the Anti-Atlas were figured for the first time in the fourth volume of the comprehensive treatise on Moroccan palaeontology (*Paléontologie marocaine*) by Termier and Termier (1950). This material consisted of the two specimens of large trilobites collected by Bondon in the Agdz area (Jbel Kissane) in the early 1930s and assigned to *Ogygia desiderata* and *Onchometopus? volborthi* by Pruvost (in Roch, 1939; see above, Figs. 4A-B). A third Early Ordovician species, the rhombiferan echinoderm *Macrocystella bohémica* (Fig. 4C) was described from Tansikht bridge (in between Agdz and Zagora) by Choubert et al. (1953). All three taxa were generally considered as Floian (Choubert, 1946, 1951, 1952a; Choubert and Termier, 1947; Termier and Termier, 1947, 1950; Roch, 1950; Choubert et al., 1952, 1953; but see Pruvost in Roch, 1939). However, successive field campaigns at Tansikht bridge (from 1952 to 1954) yielded a diverse assemblage of large, well-preserved trilobites typical of the late Tremadocian time interval: *Asaphellus* cf. *homphtayi*, *Asaphopsis* sp., *Parapilekia olesnaensis* and *Platypeltoides crofti* (Choubert et al., 1955). This material was the first definitive, unambiguous evidence of Tremadocian faunas in both the Anti-Atlas and Morocco (Fig. 1D; Choubert, 1956; Choubert and Marçais, 1956). Consequently, a late Tremadocian age was deduced for the three other taxa previously reported from Lower Ordovician deposits in the same area (*Ogygia desiderata*, *Onchometopus? volborthi*) and the same locality (*Macrocystella bohémica*).

Further evidence of Tremadocian faunas in the central Anti-Atlas was provided by Destombes and Willefert (1959) and Destombes (1960a). In the Nekob area (about 40 km NE of Tansikht bridge), Destombes and Willefert (1959) reported the occurrence of a diverse graptolite fauna, typical of the latest early Tremadocian time interval. This age assignment was in good agreement with the stratigraphic position of the graptolite beds, about 25 to 35

meters below the estimated position of the Tansikht bridge level (late Tremadocian) yielding *Macrocyrtella bohémica* and large trilobites. Five additional late Tremadocian fossiliferous levels yielding echinoderms, graptolites and trilobites were described by Destombes (1960a) both in the Agdz (Jbel Kissane) and Zagora areas (E. of Jbel Bou Dehir). Moreover, another late Tremadocian graptolite assemblage was also reported from the Taouz area (Tafilalt), thus extending the occurrence of Tremadocian deposits to the eastern Anti-Atlas (Destombes, 1960a, 1963). Finally, the first definitive Floian assemblages (bivalves, inarticulate brachiopods, graptolites, trilobites) were briefly described by Destombes (1960b) in the western Anti-Atlas.

4.2. Destombes' stratigraphic framework

In the western Anti-Atlas, Destombes (1960b) proposed the first subdivision of the External Feijas Shales into three main lithostratigraphic units: (1) c. 300 m of green shales and argillites; (2) c. 300 m of sandstones and quartzites; and (3) c. 40 to 60 m of shales and siltstones. A Floian ('early to middle Arenig') age was tentatively assigned by Destombes (1960b) to the lower shales, based on the presence of typical Floian graptolites in their upper part (no evidence of Tremadocian index fossils in this region). The intermediate unit was named 'Zini Sandstone and Quartzite' and interpreted as equivalent to the late Floian ('middle Arenig') Armorican Quartzites of western France and Spain (Destombes, 1960b). Finally, a late Floian to early Darriwilian age ('middle Arenig to Llanvirn') was deduced for the upper shale member, based on its graptolite assemblages (Destombes, 1960b).

This first subdivision of the External Feijas Shales was later formalised and extended to the whole Anti-Atlas by Destombes (1962a), who defined: (1) the Fezouata Shale; (2) the Zini Sandstone and Quartzite; and (3) the Tachilla Shale. In this new lithostratigraphic scheme

(Fig. 1E), the Fezouata Shale was subdivided into the Lower Fezouata Shale (Tremadocian) and the Upper Fezouata Shale (Floian), based on the presence of a glauconitic and ferruginous oolitic level separating them in the eastern Anti-Atlas (Destombes, 1962a). The Zini Sandstone and Quartzite (late Floian) was reinterpreted as a regional facies mostly expressed in the western part of the Anti-Atlas, and laterally equivalent of the uppermost part of the Fezouata Shale. The Tachilla Shale (early Darriwilian) was considered as a transgressive unit lying unconformably above either the middle Cambrian Tabanite Sandstone (Tiznit area, western Anti-Atlas; Destombes, 1962b) or the Zini Sandstone and Quartzite (Destombes, 1962a).

Four formal lithostratigraphic units (formations) were later defined by Destombes (1970) within the External Feijas Shales (Fig. 1F): (1) the Lower Fezouata Shale Formation; (2) the Upper Fezouata Shale Formation; (3) the Zini Sandstone and Quartzite Formation; and (4) the Tachilla Shale Formation. The presence of late Cambrian billingsellid brachiopods (e.g. *Saccogonum saccatum*) in the lowermost levels of the Lower Fezouata Shale Formation was mentioned by Destombes (1970, 1971) in the Tazenakht area (central Anti-Atlas; see also Havlíček, 1971). Consequently, the lower boundary of this formation was -at least locally- located within the Furongian. This observation prompted Destombes (1971) to reject Spjeldnaes's proposal to erect a Lower Ordovician 'Zagorian' regional stage for the Mediterranean Province (Spjeldnaes, 1967). Finally, all four main subdivisions of the Ordovician originally identified by Choubert (1942) in the Anti-Atlas were redefined as formal lithostratigraphic units (groups) by Destombes (1971): (1) the External Feijas Group; (2) the First Bani Group; (3) the Ktaoua Group; and (4) the Second Bani Group (Fig. 1; see also Michard, 1976; Destombes et al., 1985; Destombes, 2006a).

Finally, the stratigraphy of the Lower Ordovician series in the central Anti-Atlas (Zagora area) was further elaborated by two successive studies focusing on palynomorphs (acritarchs

and chitinozoans) extracted from material collected by Destombes (Elaouad-Debbaj, 1984, 1988; Destombes et al., 1985; Destombes, 2006b). The first one focused on a 200 m-thick section including the uppermost part of the Upper Fezouata Shale Formation, the Zini Sandstone and Quartzite Formation, and the lower part of the Tachilla Shale Formation (Elaouad-Debbaj, 1984). A late Floian age was obtained for the uppermost part of the Upper Fezouata Shale Formation based on chitinozoans (*Eremochitina brevis* Biozone), whereas an early Darriwilian age was supported by both acritarchs and chitinozoans (*Desmochitina bulla* Biozone) for the lower part of the Tachilla Shale Formation, thus suggesting a stratigraphic gap including the whole Dapingian time interval (Elaouad-Debbaj, 1984; Destombes et al., 1985; Gutiérrez-Marco et al., 2014). The second study investigated the stratigraphic distribution of palynomorphs along a 250 m-thick section exposing the lowermost part of the Lower Fezouata Shale Formation (Elaouad-Debbaj, 1988). The abundant and diverse, well-preserved acritarch material made it possible to identify six successive assemblages, corresponding to the early Tremadocian (i.e., the lower four assemblages) and the early late Tremadocian (i.e., the upper two assemblages), thus confirming that no Furongian deposits were present in this area in the lower part of the Lower Fezouata Shale Formation (Destombes et al., 1985; Elaouad-Debbaj, 1988).

4.3. Destombes' legacy

In the second half of the 20th century, major advances in the stratigraphy and the systematic palaeontology of the Lower Ordovician of the Anti-Atlas were achieved thanks to the intense field activity of the French geologist Jacques Destombes (1926-; Fig. 5A), who was in charge of the mapping of Cambro-Ordovician deposits on the nine 1:200,000 geological maps of the Anti-Atlas published by the Service géologique du Maroc (1969,

499 1970a, 1970b, 1971, 1977, 1982, 1986, 1988, 1989). His detailed descriptions of the Cambro-
500 Ordovician series of the whole Anti-Atlas (written between 1983 and 2003) were finally
501 published as a series of explanatory notes (Destombes, 2006a, 2006b, 2006c, 2006d, 2006e,
502 2006f, 2006g, 2006h, 2006i, 2006j).

503 From the late 1950s to the late 1990s, Destombes discovered over 2,000 Cambro-
504 Ordovician localities throughout the whole Anti-Atlas (Destombes, 2006a). In the Lower
505 Ordovician of the Zagora area, he identified and described 26 distinct fossiliferous horizons in
506 the Lower Fezouata Shale Formation, and 22 levels in the Upper Fezouata Shale Formation
507 (Destombes, 2006b). In this area, his reference section was located on the eastern side of Jbel
508 Bou Dehir, about 20 km NE of Zagora. These localities yielded thousands of specimens,
509 which were sent to various specialists for systematic description. Over 180 taxa of marine
510 invertebrates and palynomorphs were described from the material collected by Destombes in
511 both the Lower and the Upper Fezouata Shale formations (Destombes et al., 1985;
512 Destombes, 2006a), including acritarchs (Deunff, 1968a, 1968b; Elaouad-Debbaj, 1988;
513 Snape, 1993), bivalves (Babin and Destombes, 1990), brachiopods (Destombes, 1970;
514 Havlíček, 1971; Mergl, 1981), chitinozoans (Elaouad-Debbaj, 1984, 1988), conodonts (El
515 Bourkhissi and Sarmiento, 1997), conulariids (Destombes et al., 1985), echinoderms (Ubaghs,
516 1963; Chauvel, 1966a, 1966b, 1969, 1971a, 1971b, 1978; Chauvel and Régnault, 1986;
517 Donovan and Savill, 1988), gastropods (Horny, 1997), graptolites (Destombes and Willefert,
518 1959; Destombes, 1960a, 1960b, 1962a, 1963, 1970; Destombes et al., 1985), hyolithids
519 (Marek, 1983), rostroconchs (Babin and Destombes, 1990), and trilobites (Destombes, 1967,
520 1970, 1972; Destombes et al., 1985; Rabano, 1990; Vidal, 1996, 1998). The complete list of
521 all fossils collected from 1950 to 2000 is available in Appendix 1.

522 Apparently only a single borehole crossed the Fezouata Shale Formation. This borehole,
523 AZ-1, was drilled in 1963-1964 at Adrar Zouggar Mountain, some 300 km southwest of

Zagora and the fossil sites with exceptional preservation. The drilling was executed by the Belgian petroleum company Petrofina for oil exploration. The core material is now housed at the ONHYM (Office National des Hydrocarbures et des Mines) at Rabat. The interval between 624 m and 1134.8 m depth was assigned to the Fezouata Formation on lithological arguments. Cutting samples do not allow to recognise macrofossils, but palynomorphs allow a correlation with the Fezouata Formation in the outcrop areas (Nowak et al., 2015).

5. An Ordovician Burgess Shale: the Fezouata Biota

5.1. Discovery and history of research

The Fezouata Biota was discovered by Mohamed ‘Ou Said’ Ben Moula, a local collector from Taichoute, near Alnif (Fig. 7). During prospection in the Lower Ordovician of the Zagora area in late 1999 or early 2000, he discovered a complete specimen of the aglaspidid arthropod *Tremaglaspis* (Fig. 8a). This specimen was acquired by a local fossil dealer and collector, Brahim Tahiri, who showed it to Peter Van Roy, then a graduate student starting a Ph.D. on exceptionally preserved fossils from the Upper Ordovician of the Tafilalt area. For two years, this *Tremaglaspis* specimen remained the sole exceptionally preserved fossil known from the Zagora area. However, in June 2002, Tahiri provided Van Roy with three specimens of a cheloniellid arthropod recently collected by Ben Moula, by far the oldest representative of the group (Fig. 8b). This fact, together with the exquisite preservation of the material, convinced Van Roy of the potential of the newly discovered sites. Accordingly, in November 2002, he set out with Ben Moula’s son Lahcen to visit Bou Chrebeb, the locality NE of Zagora that had yielded the cheloniellids. The limited funds at his disposal prevented Van Roy from renting a car – as a result, the ca 250 kilometers-long drive from Alnif to Bou

Chrebeb, including the final ca 35 km through the desert, was made using a regular taxi. Such a trip would no longer be possible, as the track leading to the site has deteriorated considerably and requires now the use of dedicated off-road vehicles. Half a day of collecting at Bou Chrebeb yielded a rich shelly assemblage, carapaces of non-biomineralised bivalved arthropods and a few soft-bodied vermiform fossils (likely annelids; Van Roy, 2006: p. 40-43, fig. 3.6). A year later, a 10-day field campaign conducted by an extended party (M. Ben Moula, Joseph Botting, Dirk Van Damme, Thijs Vandenbroucke, and P. Van Roy) recovered more exceptionally preserved fossils, including Burgess Shale-type demosponges, from Bou Chrebeb and a couple of new sites on Jbel Tigzagzaouine, near Oued Ezegzaou (Van Roy, 2006; Botting, 2007).

Independently, on the 28th November 2001, several specimens of exquisitely preserved cornute stylophorans from the Lower Fezouata Formation were fortuitously discovered by Bertrand Lefebvre... in Brittany, France (Lefebvre and Fatka, 2003). This material, originally collected by Ben Moula in the Zagora area, was then acquired by two French amateur palaeontologists, Christophe Guillou and Patrick Catto, during a field trip to Morocco. This finding was significant, as only two specimens of Early Ordovician cornutes were known from the whole Anti-Atlas at that time (the holotypes of *Chauvelicystis ubaghsi* and *Thoralicystis zagoraensis*; Chauvel, 1966b, 1971b). In early 2002, Roland and Véronique Reboul, a couple of French amateur palaeontologists, visited most excavations produced by Ben Moula in the Fezouata Shale, and confirmed the occurrence of several *echinoderm Lagerstätten* (*sensu* Smith, 1988) in the Zagora area. The same year, a collaboration between the universities of Burgundy (Dijon) and Cadi-Ayyad (Marrakesh) was initiated by B. Lefebvre and Khadija El Hariri. The primary aims of this project were both to collect exceptionally preserved echinoderm assemblages from the Fezouata Shale *in situ*, and to permit the establishing of palaeontological collections at Marrakesh University.

574 In this context, two successive field trips were organized to the Lower Ordovician of the
575 Zagora area in January 2003 and January 2004 (Roland and Véronique Reboul, Daniel and
576 Framboise Vizcaïno, Bertrand and Myriam Lefebvre). During these two campaigns, several
577 hundreds of exquisitely preserved, fully articulated echinoderms (edrioasteroids, eocrinoids,
578 rhombiferans, solutans, somasteroids, stylophorans) were collected *in situ* from several of Ben
579 Moula's localities (Lefebvre, 2007; Lefebvre and Botting, 2007; Lefebvre and Ware, 2007;
580 Van Roy et al., 2010; Sumrall and Zamora, 2011; Allaire et al., 2015; Martin et al., 2015).
581 The occurrence of such abundant and diverse echinoderm faunas in the Fezouata Shale was
582 totally unexpected, as previous investigations of these strata had only yielded rare, low-
583 diversity, late Cambrian-like assemblages dominated by eocrinoids (*Rhopalocystis*) and
584 glyptocystitid rhombiferans (*Macrocystella*; Choubert et al., 1955; Ubaghs, 1963; Chauvel,
585 1966b, 1969, 1971a, 1978; Destombes et al., 1985; Chauvel and Régnault, 1986). The newly
586 collected material prompted the re-evaluation of the Fezouata Shale as one of the rare Early
587 Ordovician *echinoderm Lagerstätten* documenting the initial stage of the GOBE (Noailles et
588 al., 2010; Lefebvre et al., 2013). Other examples include the Saint-Chinian and Landeyran
589 formations in Montagne Noire, France (Thoral, 1935; Ubaghs, 1970, 1983; Vizcaïno and
590 Lefebvre, 1999; Vizcaïno et al., 2001), the Ninemile Shale in Nevada, USA, and the Fillmore
591 Formation in Utah, USA (Guensburg and Sprinkle, 1992, 2003; Sprinkle and Guensburg,
592 1995).

593 During the 2003-2004 French-Moroccan field campaigns, however, not only abundant
594 echinoderm remains were collected, but also extensive samples of the associated fauna,
595 including both shelly and exceptionally preserved fossils (e.g. demosponges, and the first
596 marrellomorph specimen). Inevitably, it did not take long for Lefebvre and Van Roy to
597 become aware of each other's activities. In December 2003, they met in Leicester at the
598 annual meeting of the Palaeontological Association, and along with Joseph Botting and Lucy

599 Muir, started an informal collaboration, exchanging information and specimens (Van Roy,
600 2006; Van Roy and Tetlie, 2006; Botting, 2007; Lefebvre and Botting, 2007; Van Roy et al.,
601 2010).

602 Over the next couple of years, several additional soft-bodied taxa, including
603 marrellomorphs and problematica, were discovered (Van Roy, 2006; Van Roy and Tetlie,
604 2006), but overall, exceptional preservation remained scarce. During these years, the support
605 of private collectors, namely Patrick Bommel, Didier Broussy, P. Catto, François Escuillié,
606 Laurent Lacombe, R. and V. Reboul and B. Tahiri, who allowed access to specimens in their
607 collections, proved indispensable. The study of components of the shelly faunas also started
608 to reveal a much greater diversity than initially assessed (e.g. Lefebvre and Fatka, 2003;
609 Lefebvre and Botting, 2007; Fortey, 2009, 2011, 2012; Van Roy et al., 2010, 2015a; Sumrall
610 and Zamora, 2011; Kröger and Lefebvre, 2012; Ebbestad and Lefebvre, in press).

611 By late 2006, Ben Moula had come to grips with the stratigraphic and spatial occurrences
612 of exceptional preservation in the area N of Zagora (Fig. 9), and as a result, discoveries of
613 exceptionally preserved fossils became more common. Two major finds were made in
614 December 2006 (field party: M. Ben Moula, Wim De Winter, Breandán MacGabhann, Roland
615 and Véronique Reboul, Bert Van Bocxlaer and P. Van Roy), with the discovery of the oldest
616 horseshoe crabs (Fig. 10E; Van Roy et al., 2010, 2015a) and the first machaeridian specimen
617 preserving soft tissues (Fig. 10F). The latter resolved the 150-year old enigma of
618 machaeridian affinities, unequivocally placing them among annelids (Vinther et al., 2008).
619 The work on the machaeridian also marked the entry of the Yale Peabody Museum of Natural
620 History, and Derek Briggs, the museum's director at the time, into Fezouata research. Under
621 Briggs' aegis, the Peabody Museum was soon to become the prime repository for Fezouata
622 fossils.

Further field work in February 2008 (M. Ben Moula, B. MacGabhann, B. Van Bocxlaer, and P. Van Roy) resulted in the recovery of an increasingly-diverse exceptionally preserved fauna, including a halkieriid-like mollusc (Fig. 10C). By this time, the collaboration between Ben Moula and Van Roy had become close enough that Ben Moula now retained all exceptionally preserved material he collected for the palaeobiologists working on the Fezouata Biota. An ever increasing number of soft-bodied taxa left no doubt about the importance of the biota, and in September 2008, a successful application was made to the National Geographic Society for a Research and Exploration grant to allow extensive field work in the area. The National Geographic-funded field season of April 2009 (field party: M. Ben Moula, Joseph and Lucy Botting-Muir, Derek Briggs, Patrick Orr, Chris Upton, P. Van Roy and Jakob Vinther) proved to be a watershed moment in the history of research on the Fezouata Biota: that year, an unexpectedly large diversity of non-biomineralised organisms was discovered from a host of sites. Importantly, the recovered faunas include essentially all classical Burgess Shale-type taxa, including giant anomalocaridids (Fig. 10A), together with significantly more advanced, typically post-Cambrian forms (Van Roy et al., 2010, 2015a, 2015b; Van Roy and Briggs, 2011; Fig. 10). This trend has continued to the present, and currently, over 160 different taxa, represented by several thousand specimens, are known from the Fezouata Biota (Van Roy et al. 2015b).

During the same period, after several field campaigns devoted to Late Ordovician *echinoderm Lagerstätten* in the western Tafilalt (Lefebvre et al., 2007, 2008, 2010; Hunter et al., 2010), Lefebvre (Lyon 1 University) and K. El Hariri (Cadi-Ayyad University) applied successfully for a CNRS (France)/CNRST (Morocco) cooperation project focusing on the Fezouata Biota. This project (funded 2009-2012) allowed extensive field work and logging in the Zagora area, promoted scientific exchanges between Moroccan and (mostly) European researchers and students, and also largely contributed to the development of the

palaeontological collections of Cadi-Ayyad University in Marrakesh (incl. over 3,000 referenced specimens from the Fezouata Shale).

In 2010 and 2011, large-scale funding for Fezouata research was obtained from NSF (EAR-1053247) in the U.S.A. (primary team members Derek Briggs, Robert Gaines and Peter Van Roy) and ANR (RALI) in France (primary team members Bertrand Lefebvre, Thomas Servais and Jean Vannier). Additional financial support was obtained from Lyon 1 University (Bernard Pittet), and through a second CNRS/CNRST project (VALORIZ) (primary team members Khadija El Hariri, Bertrand Lefebvre, Moussa Masrour and Muriel Vidal). All three projects were conceived to be complementary, with the NSF team focussing primarily on systematics, taphonomy and geochemistry (Van Roy and Briggs, 2011; Gaines et al., 2012b; Van Roy et al., 2015a, 2015b; Legg, in press; Ortega-Hernández et al., in press), and the ANR-CNRS/CNRST group zooming in on stratigraphy, depositional environment and palaeoecology (Kröger and Lefebvre, 2012; Martin et al., 2014, 2015, in press; Allaire et al., 2015; Nowak et al., 2015; Ebbestad and Lefebvre, in press). All projects are ongoing at the time of writing. One of the chief achievements of this international collaboration was the opening of three large-scale excavations (over 30 sq. m each) at Bou Izargane, in January 2014, to investigate both the lateral and vertical extent of several horizons yielding exceptionally preserved organisms (field party: 28 participants).

5.2. Age, depositional environment and preservation

Originally, exceptional fossil preservation was believed to occur from the top of the Lower Fezouata Formation (latest Tremadocian) throughout the entire Upper Fezouata Formation (early-late Floian), thus ranging in age from the latest Tremadocian to the late Floian, spanning some 8 Myr (Van Roy, 2006; Van Roy and Tetlie, 2006; Van Roy et al., 2010; Van

Roy and Briggs, 2011). However, recent work led by Bernard Pittet, Romain Vaucher, Emmanuel Martin and Bertrand Lefebvre claimed that in the area N of Zagora, exceptional preservation is restricted to only two stratigraphic intervals, of ca 25 m and 15 m respectively. Both intervals have a latest Tremadocian age, the lower falling in the *Araneograptus murrayi* graptolite biozone, and the upper extending into the *Hunnegraptus copiosus* graptolite zone (Martin et al., in press). However, unpublished data indicate the presence of at least one more level with exceptional preservation considerably higher up, well into the Floian (Gutierrez-Marco, pers. comm. 2015), which suggests that environmental conditions conducive to exceptional preservation were maintained for several Myr. The description of this limited distribution of exceptional preservation within the 1200 m-thick Fezouata Shale should considerably facilitate future investigations on the Fezouata Biota, especially on its spatial extent and variation.

The composition of the shelly assemblages is typical of an Early Ordovician fauna inhabiting an open marine environment (Van Roy et al., 2010, 2015b). At first regarded as a relatively deep water fossil association (Van Roy et al., 2010), the Fezouata Biota may actually have lived in a somewhat shallower-marine environment slightly above (lower shoreface) or below (upper offshore) storm wave base (Martin et al., in press).

While generally preserving some three-dimensionality, the great majority of Fezouata fossils is preserved flattened, with labile tissues replicated in pyrite, which in most cases has weathered into iron oxides, lending the fossils their striking colours. Preservation of original organic carbon might have been relatively common, but intense weathering of the rocks led to its removal in most cases. Biomineralised structures are replicated in clay minerals (Vinther et al., 2008; Van Roy et al., 2010, 2015b). This preservational mode appears very similar to that of the early Cambrian Chengjiang exceptionally preserved fauna from China (Gabbott et al.,

2004). More rarely, large organisms are preserved three-dimensionally in massive concretions, which show a unique silica-chlorite-calcite composition (Gaines et al., 2012b).

5.3. Scientific importance

Exceptionally preserved fossils yield crucial information about the evolution of the groups to which they belong. The exquisite preservation of soft part anatomy in various taxa in the Fezouata Biota allows more complete, accurate reconstructions of their biology, phylogenetic affinities and ecology than has hitherto been possible (e.g. Van Roy, 2006; Van Roy and Tetlie, 2006; Van Roy and Briggs, 2011; Botting, 2007; Vinther et al., 2008; Fatka et al., 2013; Van Roy et al., 2015b; Legg, in press; Ortega-Hernández et al., in press).

Unlike the Cambrian explosion, the Great Ordovician Biodiversification Event (GOBE) has been documented almost exclusively from classic shelly faunas, which provide an incomplete view of the ecosystems they represent. Under normal taphonomic conditions, up to 80% of taxa in a living marine community are not preserved (e.g. Dorjes 1972; Driscoll & Swanson 1973). If *Konservat-Lagerstätten* have proved critical to our understanding of the Cambrian explosion, their scarcity in the Ordovician had as-yet considerably limited the use of the high-resolution data they provide for the study of the GOBE. Moreover, the previously known exceptionally preserved Ordovician faunas represented low-diversity communities inhabiting atypical environments. Until recently, only two exceptional sites, both of Late Ordovician age, were known: the Beecher's Trilobite Bed (Briggs et al., 1991) and adjacent localities from the Sandbian of New York (Farrell et al., 2009), and the Soom Shale, from the Hirnantian to Rhuddanian (Vandenbroucke et al., 2009) of South Africa (Aldridge et al., 2001). The former represents a low oxygen environment, characterized by a low diversity

fauna dominated by the trilobite *Triarthrus eatoni*, while the latter includes mainly nektonic organisms, and probably accumulated under euxinic conditions.

Major recent additions include the Middle Ordovician (Darriwilian) Winneshiek *Konservat-Lagerstätte* of Iowa (Liu et al. 2006), and the Upper Ordovician (Sandbian) William Lake and Airport Cove biotas of Manitoba (Young et al., 2007). These three faunas preserve low-diversity assemblages from near-shore marginal environments. Other sites yielding some limited preservation of non-biomineralised tissues have been reported recently from Wales: the late Tremadocian Afon Gam fauna (Botting et al., 2015), the Darriwilian Llanfallteg Formation (Whittington, 1993; Legg and Hearing, 2015), and the Sandbian Llanfawr mudstones (Botting et al., 2011). Afon Gam and Llanfawr represent unstable open marine settings, yielding fairly low-diversity and probably short-lived communities; soft-part preservation at these sites is generally poor. Llanfallteg represents a deeper water setting, and exceptionally preserved fossils at this site are extremely rare. Lastly, the recent discovery of non-biomineralised fossils in the open marine Floresta Formation (Tremadocian) of Argentina (Aris and Palomo, 2014) is promising, as it could lead to the description of another diverse marine exceptionally preserved biota in the Ordovician, approximately coeval with the Fezouata Biota. However, only two exceptional fossils have as-yet been recovered from these deposits. Prior to the discovery of the Fezouata Biota, the oldest diverse post-Cambrian exceptionally preserved fauna, representative of a normal, open marine setting, was that of the Silurian (Wenlock) Herefordshire *Konservat-Lagerstätte* in U.K. (Briggs et al., 1996, 2008). Thus, the Fezouata Biota is virtually the only source of detailed data concerning marine ecosystems and their evolution during the c. 70 Myr-interval between the early late Cambrian and the Silurian (Van Roy et al., 2010, 2015a).

Significantly, the Fezouata Biota contains most of the emblematic components of Cambrian Burgess Shale-type faunas (Van Roy et al., 2010, 2015a, b; Van Roy and Briggs,

2011) side-by-side with considerably more advanced forms, typical of post-Cambrian strata; until its discovery, it was believed that Burgess Shale-type taxa had essentially disappeared after the middle Cambrian. The persistence of typical Burgess Shale-type taxa into the Ordovician indicates that the sudden replacement of the Cambrian Evolutionary Fauna by the Palaeozoic Evolutionary Fauna depicted by the shelly fossil record has no equivalent in the fossil record of soft-bodied and lightly-sclerotised organisms. The latter reveals that the decline of typical Cambrian organisms, including those once regarded as ‘weird wonders’, was slow, gradual, and all along accompanied with the evolution of components of the Palaeozoic Evolutionary Fauna. Actually, the stratigraphical range of several Burgess Shale-type “hold-overs” is known to extend well after the Ordovician: up to the Silurian for naraoiids (Caron et al., 2004), the Early Devonian for marrellomorphs (Kühl et al., 2008; Kühl and Rust, 2010), radiodont arthropods (Kühl et al., 2009) and eldonioids (Friend et al., 2002), and the Carboniferous for some Cambrian-type lobopodians (Haug et al., 2012). At the same time, the presence of a significant number of advanced, typically post-Cambrian soft-bodied taxa alongside Burgess Shale-type elements in the Fezouata Biota indicates that significant evolutionary developments must have occurred well before the Tremadocian. This implies that the GOBE was considerably more advanced at this time than has been appreciated, hinting at Cambrian origins and diversification for several typically post-Cambrian non-biomineralised groups (e.g. chelicerates). This ultimately leads to question whether the Cambrian and Ordovician radiations were discrete events, or rather the initial and latest stages of the same large-scale diversity dynamic (Droser and Finnegan, 2003; Van Roy et al., 2010, 2015a).

To sum up, some fifteen years after its discovery, the Fezouata Biota already rivals the most celebrated exceptionally preserved biotas of the Cambrian (i.e. Burgess Shale, Chengjiang), both in terms of diversity and abundance of soft-bodied taxa. It also represents

by far the most significant *Konservat-Lagerstätte* for the Ordovician period (Van Roy et al., 2010, 2015a). The scientific importance of the Fezouata Biota for our understanding of the evolution of Early Palaeozoic marine life in general, and the Great Ordovician Biodiversification Event (GOBE) in particular, are now acknowledged worldwide, as evidenced by the fact that over 50 scientists of 13 different nationalities have been or are currently involved in its study. Obviously, the research on this ‘Ordovician Burgess Shale’ has a bright future and should continue to shed light on the early history of animal evolution for decades.

5.4. Scientific perspectives and impact on society

Of the thousands of exceptionally preserved specimens collected to date, only a minute fraction has been studied in detail, yet these fossils already have provided major new insights into the early evolution and phylogeny of major clades and the GOBE (Vinther et al., 2008; Van Roy and Briggs, 2011; Van Roy et al., 2010, 2015b; Legg, in press; Ortega-Hernández et al., in press). The study of the available collections, together with future discoveries, will continue to yield new and improved insights into early metazoan evolution and the functioning and dynamics of Early Palaeozoic ecosystems.

The majority of sites yielding exceptionally preserved fossils are located in an area ca 20-25 km N of Zagora. Exploration, however, has revealed that exceptional preservation is also present in the Fezouata Shale at least 50 km to the W, and some 150 km to the N. Given the expansive area over which the Fezouata Shale crops out, future prospecting in other areas is likely to reveal further exceptionally preserved faunas. This will provide an expanded opportunity to compare changes in faunal composition, both laterally, as a result of environmental factors, and vertically, due to evolution over time.

Improved insights into the stratigraphy, depositional environment, and the factors responsible for exceptional preservation in the Fezouata Biota will help guide prospecting to target the most promising areas. A better understanding of the Fezouata taphonomy will also allow us to assess more accurately the significance of observed differences between faunas from different localities, and may also aid morphological interpretations; this knowledge will be widely applicable to exceptional fossil sites beyond the Fezouata Biota. Unweathered sediments to be obtained from a drill core planned for the near future will greatly advance these efforts.

Finally, the extensive material (including numerous types and figured specimens) collected in the Fezouata Shale through the successive collaboration projects between Marrakesh and Dijon (2003-2006), and then Marrakesh and Lyon (2007-) now constitutes the core of the palaeontological collections of the future Natural History Museum of Marrakesh. Promoting and protecting the main fossiliferous localities yielding the Fezouata Biota represents a real challenge for the coming years.

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References

- Africanus, L., [Hassan Al Wazzan], 1556. Historiale description de l'Afrique, tierce partie du monde. Plantin, Antwerp, 413 pp.
- Aldridge, R.J., Gabbott, S.E., Theron, J.N., 2001. The Soom Shale. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology II. Blackwell Science, Oxford, pp. 340-342.
- Allaire, N., Lefebvre, B., Martin, E., Nardin, E., Vaucher, R., 2015. Taphonomy of new *Rhopalocystis* assemblages in the Lower Ordovician of the Zagora area (central Anti-Atlas, Morocco). In: Zamora, S., Rabano, I. (Eds.), Progress in Echinoderm Palaeobiology. Cuadernos del Museo Geominero 19, 21-26.

845 Allison, P.A., Briggs, D.E.G., 1993. Exceptional fossil record: distribution of soft-tissue
 846 preservation through the Phanerozoic. *Geology* 21, 527-530.

847 Alroy, J., Aberhan, M., Bottjer, D.J., Foote, M., Fürsich, F.T., Harries, P.J., Hendy, A.J.W.,
 848 Holland, S.M., Ivany, L.C., Kiessling, W., Kosnik, M.A., Marshall, C.R., McGowan, A.J.,
 849 Miller, A.I., Olszewski, T.D., Patzkowsky, M.E., Peters, S.E., Villier, L., Wagner, P.J.,
 850 Bonuso, N., Borkow, P.S., Brenneis, B., Clapham, M.E., Fall, L.M., Ferguson, C.A.,
 851 Hanson, V.L., Krug, A.Z., Layou, K.M., Leckey, E.H., Nürnberg, S., Powers, C.M., Sessa,
 852 J.A., Simpson, C., Tomašových, A. & Visaggi, C.C. 2008. Phanerozoic trends in the global
 853 diversity of marine invertebrates. *Science* 321, 97-100.

854 Aris, M.J., Palomo, M., 2014. Primer registro de una fauna Ordovícica 'tipo Burgess Shale' en
 855 Argentina y Sudamérica. Abstracts 19 Congreso Geológico Argentino, Córdoba, S2-S4.

856 Babin, C., Destombes, J., 1990. Les mollusques bivalves et rostroconches ordoviciens de
 857 l'Anti-Atlas marocain : intérêt paléogéographique de leur inventaire. *Géol. Méditerran.* 17,
 858 243-261.

859 Badia y Leblich, D. [Ali Bey El Abbasi], 1814. Voyages en Afrique et en Asie pendant les
 860 années 1803, 1804, 1805, 1806 et 1807. Didot, Paris, 1269 pp.

861 Balansa, B., 1868. Voyage de Mogador à Maroc au point de vue botanique. *Bull. Soc. géogr.*
 862 Paris 27, 312-332.

863 Bartels, C., Briggs, D.E.G., Brassel, G., 1998. The Fossils of the Hunsrück Slate: Marine Life
 864 in the Devonian. Cambridge University Press, Cambridge, 324 pp.

865 Barthoux, J.C., 1924. Les massifs de Djebilet et des Rehamna (Maroc). *C. R. Acad. Sci. Paris*
 866 179, 504-506.

867 Beaudouin, L.J., 1848. Carte de l'Empire de Maroc indiquant les communications principales,
 868 la division en gouvernemens et la répartition de la population des diverses races sur le sol

869 ainsi que l'état d'obéissance des tribus qui sont comptées comme faisant partie de l'Empire
870 de Maroc. Kaepelin, Paris.

871 Bellin, J.N., 1764. Petit atlas maritime. Recueil de cartes et de plans des quatre parties du
872 monde. Tome 3 contenant 1° l'Asie, 2° l'Afrique avec les détails intéressans de ces deux
873 parties. Bellin, Paris, 124 pp.

874 Bigot, A., Dubois, J., 1931. Sur la présence de l'Ordovicien dans l'Anti-Atlas marocain. C. R.
875 Acad. Sci. Paris 193, 282-283.

876 Bondon, J., Clariond, L., Neltner, L., 1934. Une nouvelle coupe du Djebel Sarro (Maroc
877 saharien). C. R. Acad. Sci. Paris 198, 590-591.

878 Botting, J.P., 2007. 'Cambrian' demosponges in the Ordovician of Morocco: insights into the
879 early evolutionary history of sponges. *Geobios* 40, 737-748.

880 Botting, J.P., Muir, L.A., Sutton, M.D., Barnie, T., 2011. Welsh gold: a new exceptionally
881 preserved pyritized Ordovician biota. *Geology* 39, 879-882.

882 Botting, J.P., Muir, L.A., Jordan, N., Upton, C., 2015. An Ordovician variation on Burgess
883 Shale-type biotas. *Sci. Reports* 5, 9947.

884 Bourcart, J., 1927. Découverte du Cambrien à *Archaeocyathus* dans l'Anti-Atlas marocain. C.
885 R. somm. Soc. Géol. France 1-2, 10-11.

886 Bourcart, J., 1933. Sur l'Ordovicien du Djebel Tachilla dans le Sous (Sud marocain). C. R.
887 somm. Soc. Géol. France 4, 46.

888 Bourcart, J., 1935. Reconnaissance géologique dans les confins autonomes du Dra. *Rev.*
889 *géogr. phys. géol. dyn.* 8, 115-132.

890 Bourcart, J., 1938. Une coupe géologique de l'Oued Noun à l'Ouarkziz par Torkoz (Sahara
891 marocain). C. R. somm. Soc. Géol. France 8, 12-14.

892 Bourcart, J., Le Villain, G., 1929. L'Acadien de l'Anti-Atlas marocain. C. R. Acad. Sci. Paris
893 188, 1423-1425.

894 Bourcart, J., Le Villain, G., 1931. La faune des calcaires cambriens de Sidi Mouça d'Aglou
895 (Anti-Atlas marocain). Notes et Mém. Serv. géol. Maroc 15, 1-44.

896 Bracène, R., Frizon de Lamotte, D., 2002. The origin of intraplate deformation in the Atlas
897 system of western and central Algeria: from Jurassic rifting to Cenozoic-Quaternary
898 inversion. Tectonophysics. 357, 207-226.

899 Briggs, D.E.G., Bottrell, S.H., Raiswell, R., 1991. Pyritization of soft-bodied fossils:
900 Beecher's Trilobite Bed, Upper Ordovician, New York State. Geology 19, 1221-1224.

901 Briggs, D.E., Erwin, D.H., Collier, F.J., 1994. The Fossils of the Burgess Shale. Smithsonian
902 Institution Press, Washington DC, 238 pp.

903 Briggs, D.E.G., Siveter, D.J., Siveter, D.J., 1996. Soft-bodied fossils from a Silurian
904 volcanoclastic deposit. Nature 382, 248-250.

905 Briggs, D.E.G., Siveter, D.J., Siveter, D.J., Sutton, M.D., 2008. Virtual fossils from 425
906 million-year-old volcanic ash. Amer. Scientist 96, 474-481.

907 Brives, A., 1902. Sur la constitution géologique du Maroc occidental. C. R. Acad. Sci. Paris
908 134, 922-925.

909 Brives, A., 1905. Contribution à l'étude géologique de l'Atlas marocain. Bull. Soc. géol.
910 France 5, 379-398.

911 Brives, A., 1909. Voyages au Maroc. Jourdan, Alger, 612 pp.

912 Burkhard, M., Caritg, S., Helg, U., Robert-Charrue, C., Soulaïmani, A., 2006. Tectonics of
913 the Anti-Atlas of Morocco. C. R. Geoscience 338, 11-24.

914 Butterfield, N.J. 2012. Does
915 cement-induced sulfate limitation account for Burgess Shale-type preservation? PNAS 109
(28). E1901.

916 Caron, J.-B., Rudkin, D. 2009. A Burgess Shale Primer: History, Geology, and Research
917 Highlights. The Burgess Shale Consortium, Toronto. 108 pp.

- 918 Caron, J.B., Rudkin, D.M., Milliken, S., 2004. A new Late Silurian (Pridolian) naraoiid
919 (Euarthropoda: Nektaspida) from the Bertie Formation of southern Ontario, Canada -
920 delayed fallout from the Cambrian explosion. J. Paleont. 78, 1138-1145.
- 921 Chauvel, J., 1966a. Présence du genre *Anatifopsis* Barrande (Crustacés) dans l'Ordovicien du
922 Maroc. C. R. somm. Soc. Géol. France 8, 301-302.
- 923 Chauvel, J., 1966b. Echinodermes de l'Ordovicien du Maroc. Ed. CNRS, Paris, 120 pp.
- 924 Chauvel, J., 1969. Les échinodermes macrocystellides de l'Anti-Atlas marocain. Bull. soc.
925 géol. minéral. Bretagne 1, 21-32.
- 926 Chauvel, J., 1971a. *Rhopalocystis* Ubaghs : un échinoderme éocrinoïde du Trémadocien de
927 l'Anti-Atlas marocain. Mém. Bur. Rech. Géol. Min. 73, 43-49.
- 928 Chauvel, J., 1971b. Les échinodermes carpoïdes du Paléozoïque inférieur marocain. Notes et
929 Mém. Serv. géol. Maroc 237, 49-60.
- 930 Chauvel, J., 1978. Compléments sur les échinodermes du Paléozoïque marocain (diploporites,
931 éocrinoïdes, édrioastéroïdes). Notes et Mém. Serv. géol. Maroc 272, 27-78.
- 932 Chauvel, J., Régnault, S., 1986. Variabilité du genre *Rhopalocystis* Ubaghs, éocrinoïde du
933 Trémadocien de l'Anti-Atlas marocain. Geobios 19, 863-870.
- 934 Chénier, L., 1787. Recherches historiques sur les Maures et Histoire de l'Empire du Maroc.
935 Tome troisième. Imprimerie Polytype, Paris, 564 pp.
- 936 Chorowicz, J., Emran, A., Alem, E.M., 2001. Tectonique et venues volcaniques en contexte
937 de collision, exemple du massif néogène du Siroua (Atlas marocain) : effets combinés
938 d'une transformante et de la suture panafricaine. Can. J. Earth Sci. 38, 411-425.
- 939 Choubert, G., 1942. Constitution et puissance de la série primaire de l'Anti-Atlas. C. R. Acad.
940 Sci. Paris 215, 445-447.
- 941 Choubert, G., 1943a. L'Acadien et l'Ordovicien de l'Anti-Atlas. C. R. Acad. Sci. Paris 216,
942 158-160.

- 943 Choubert, G., 1943b. Note au sujet du terme 'Anti-Atlas'. Rev. géogr. marocaine 20, 3-20.
- 944 Choubert, G., 1946. Aperçu de la géologie marocaine. Rev. géogr. marocaine 23, 1-19.
- 945 Choubert, G., 1951. Note sur la géologie de l'Anti-Atlas. Intern. Geol. Congr. London (1948)
- 946 14, 29-44.
- 947 Choubert, G., 1952a. Histoire géologique du domaine de l'Anti-Atlas. Notes et Mém. Serv.
- 948 géol. Maroc 100, 77-194.
- 949 Choubert, G., 1952b. Livret-guide de l'excursion A 36. Anti-Atlas occidental. 19ème Congr.
- 950 géol. intern. Alger (1952) Maroc 10, 1-69.
- 951 Choubert, G., 1956. Lexique stratigraphique du Maroc. Notes et Mém. Serv. géol. Maroc 134,
- 952 39-165.
- 953 Choubert, G., Jacquemont, P., 1952. Nouvelles mesures des épaisseurs des séries
- 954 paléozoïques de l'Anti-Atlas. Notes et Mém. Serv. géol. Maroc 95, 19-25.
- 955 Choubert, G., Marçais, J., 1956. Les grands traits de la géologie du Maroc. Notes et Mém.
- 956 Serv. géol. Maroc 134, 1-38.
- 957 Choubert, G., Termier, H., 1947. Sur la stratigraphie de l'Ordovicien. C. R. somm. Soc. Géol.
- 958 France 16, 335-337.
- 959 Choubert, G., Clariond, L., Hindermeyer, J., 1952. Livret-guide de l'excursion C 36. Anti-
- 960 Atlas central et oriental. 19ème Congr. géol. intern. Alger (1952) Maroc 11, 1-89.
- 961 Choubert, G., Termier, H., Termier, G., 1953. Présence du genre *Mimocystites* Barrande dans
- 962 l'Ordovicien du Maroc. Notes et Mém. Serv. géol. Maroc 117, 137-143.
- 963 Choubert, G., Hindermeyer, J., Hupé, P., 1955. Découverte du Trémadoc dans l'Anti-Atlas
- 964 (Maroc). C. R. Acad. Sci. Paris 241, 1592-1594.
- 965 Clariond, L., 1933. Les terrains primaires et la hammada de Taouz (confins algéro-marocains
- 966 du Sud). C. R. somm. Soc. Géol. France 4, 47-48.

- 967 Clariond, L., 1934. La série paléozoïque des territoires du Tafilalet (Maroc). C. R. Acad. Sci.
968 Paris 198, 2270-2272.
- 969 Clariond, L., 1935. Etude stratigraphique sur les terrains du Sud marocain : la série primaire
970 du Sarro, du Maïder et du Tafilalet. Ass. Et. géol. Méditerranée occidentale, Barcelone, 3-
971 10.
- 972 Clariond, L., 1944. Carte géologique provisoire des Plateaux et Chaînes du Sarhro-Tafilalt et
973 Maïder. Notes et Mém. Serv. géol. Maroc 62.
- 974 Clariond, L., Gubler, Y., 1937. Sur la présence de roches éruptives acadiennes et post-
975 acadiennes au sud du Djebel Ougnat (sud marocain). C. R. Acad. Sci. Paris 204, 706-709.
- 976 Coquand, H., 1847. Description géologique de la partie septentrionale de l'Empire du Maroc.
977 Bull. Soc. géol. France 4, 1188-1249.
- 978 Despujols, P., 1933. Historique des recherches géologiques au Maroc (zone française) des
979 origines à 1930. Notes et Mém. Serv. géol. Maroc 25, 1-79.
- 980 Destombes, J., 1960a. Sur l'extension du Trémadoc dans le Sud marocain. C. R. Soc. Sc. nat.
981 phys. Maroc 3, 45-47.
- 982 Destombes, J., 1960b. Stratigraphie de l'Ordovicien de la partie occidentale du jbel Bani et du
983 jbel Zini, Anti-Atlas occidental (Maroc). Bull. Soc. géol. France 2, 747-751.
- 984 Destombes, J., 1962a. Stratigraphie et paléogéographie de l'Ordovicien de l'Anti-Atlas
985 (Maroc) : un essai de synthèse. Bull. Soc. géol. France 4, 453-460.
- 986 Destombes, J., 1962b. Sur le caractère transgressif de l'Arenig supérieur dans l'Anti-Atlas
987 nord-occidental. C. R. somm. Soc. Géol. France 1, 14-15.
- 988 Destombes, J., 1963. Le Cambrien et la base de l'Ordovicien dans la partie orientale et
989 méridionale du Tafilalet (Maroc). Bull. Soc. géol. France 5, 938-945.
- 990 Destombes, J., 1967. Distribution et affinités des genres de trilobites de l'Ordovicien de l'Anti-
991 Atlas (Maroc). C. R. somm. Soc. Géol. France 4, 133-134.

- 992 Destombes, J., 1970. Cambrien et Ordovicien. Notes et Mém. Serv. géol. Maroc 229, 161-
993 170.
- 994 Destombes, J., 1971. L'Ordovicien au Maroc. Essai de synthèse stratigraphique. Mém. Bur.
995 Rech. Géol. Min. 73, 237-263.
- 996 Destombes, J., 1972. Les trilobites du sous-ordre des Phacopina de l'Ordovicien de l'Anti-
997 Atlas (Maroc). Notes et Mém. Serv. géol. Maroc 240, 1-113.
- 998 Destombes, J., 2006a. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Paléozoïque
999 inférieur : Cambrien moyen et supérieur - Ordovicien - base du Silurien. Sommaire général
1000 sur les mémoires explicatifs des cartes géologiques au 1/200 000 de l'Anti-Atlas marocain.
1001 Notes & M. Serv. géol. Maroc 515, 1-150.
- 1002 Destombes, J., 2006b. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
1003 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur – Ordovicien – Base du
1004 Silurien. Feuille Zagora – Coude du Dra. Chap. A. Notes & M. Serv. géol. Maroc 273bis,
1005 1-54.
- 1006 Destombes, J., 2006c. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
1007 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
1008 Silurien. Feuille Bou Haiara- Zegdou. Chap. B. Notes & M. Serv. géol. Maroc 259bis, 1-
1009 30.
- 1010 Destombes, J., 2006d. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
1011 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
1012 Silurien. Feuille Jbel Saghro-Dadès. Chap. C. Notes & M. Serv. géol. Maroc 161bis, 1-41.
- 1013 Destombes, J., 2006e. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
1014 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
1015 Silurien. Feuille Todrha- Maïder. Chap. D. Notes & M. Serv. géol. Maroc 243bis, 1-58.

- 1016 Destombes, J., 2006f. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
 1017 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
 1018 Silurien. Feuille Tafilalt – Taouz. Chap. E. Notes & M. Serv. géol. Maroc 244bis, 1-69.
- 1019 Destombes, J., 2006g. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
 1020 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
 1021 Silurien. Feuille Telouet Sud, Ouarzazate, Alougoum, Agadir Tissinnt. Chap. F. Notes &
 1022 M. Serv. géol. Maroc 138bis, 1-43.
- 1023 Destombes, J., 2006h. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
 1024 explicative. Paléozoïque inférieur : Cambrien moyen et supérieur - Ordovicien - Base du
 1025 Silurien. Feuille Foug el Hassane-Assa. Chap. H. Notes & M. Serv. géol. Maroc 159bis ,
 1026 1-35.
- 1027 Destombes, J., 2006i. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
 1028 explicative. Paléozoïque inférieur : Cambrien moyen - Ordovicien - Base du Silurien.
 1029 Feuille Goulimine- Dra inférieur au 200 000°, feuille Fask au 100 000°. Chap. I. Notes &
 1030 M. Serv. géol. Maroc 90bis A, 1-34.
- 1031 Destombes, J., 2006j. Carte géologique au 1/200 000 de l'Anti-Atlas marocain. Notice
 1032 explicative. Paléozoïque inférieur. Cambrien moyen - Ordovicien - Base du Silurien.
 1033 Feuille région de Tan-Tan, Jbel Zini (Province de Tarfaya). Chap. J. Notes & M. Serv.
 1034 géol. Maroc 90bis B, 1-29.
- 1035 Destombes, J., Willefert, S., 1959. Sur la présence de *Dictyonema* dans le Trémadoc de l'Anti-
 1036 Atlas (Maroc). C. R. Acad. Sci. Paris 249, 1246-1247.
- 1037 Destombes, J., Hollard, H., Willefert, S., 1985. Lower Palaeozoic Rocks of Morocco. In:
 1038 Holland, C.H. (Ed.), Lower Palaeozoic Rocks of the World. 4. Lower Palaeozoic of North
 1039 Western - Central Africa. Wiley, New York, pp. 91-336.

- 1040 Deunff, J., 1968a. *Arbusculidium*, genre nouveau d'acritarche du Trémadocien marocain. C.
1041 R. somm. Soc. Géol. France 3, 101-102.
- 1042 Deunff, J., 1968b. Sur une forme nouvelle d'acritarche possédant une ouverture polaire
1043 (*Veryhachium miloni* n. sp.) et sur la présence d'une colonie de *Veryhachium* dans le
1044 Trémadocien marocain. C. R. Acad. Sci. Paris 267, 46-49.
- 1045 Donovan, S.K., Savill, J.J., 1988. *Ramseyocrinus* (Crinoidea) from the Arenig of Morocco. J.
1046 Paleont. 62, 283-285.
- 1047 Dorjes, J., 1972. Georgia coastal region, Sapelo Island, USA: sedimentology and biology.
1048 VIII. Distribution and zonation of macrobenthic animals. Senckenb. marit. 4, 183-216.
- 1049 Driscoll, E.G., Swanson, R.A., 1973. Diversity and structure of epifaunal communities on
1050 mollusc valves, Buzzards Bay, Massachusetts. Palaeogeogr., Palaeoclimatol., Palaeoecol.
1051 14, 229-247.
- 1052 Droser, M.L., Finnegan, S. 2003. The Ordovician radiation: a follow-up to the Cambrian
1053 explosion? Integr. Comp. Biol. 43, 178-184.
- 1054 Ebbestad, J.O.R., Lefebvre, B., in press. An unusual onychochilid mollusc from the
1055 Ordovician (Tremadocian) Fezouata Formation, Morocco. Geobios.
- 1056 Elaouad-Debbaj, Z., 1984. Acritarches et chitinozoaires de l'Arenig-Llanvirn de l'Anti-Atlas
1057 (Maroc). Rev. Palaeobot. Palyn. 43, 67-88.
- 1058 Elaouad-Debbaj, Z., 1988. Acritarches et chitinozoaires du Tremadoc de l'Anti-Atlas central
1059 (Maroc). Rev. Micropal. 31, 85-128.
- 1060 El Bourkhissi, M., Sarmiento, G.N., 1997. Primeros conodontos ordovicicos del Anti-Atlas
1061 (Marruecos). In: Grandal d'Anglade, A., Gutiérrez-Marco, J.C., Santos Fidalgo, L. (Eds.),
1062 Comunicaciones 13° Jornadas de paleontologia y 5° reunion internacional proyecto PICG
1063 351: Palaeozoico Inferior del Noroeste de Gondwana, 56-59.

- 1064 Farrell, U.C., Martin, M.J., Hagadorn, J.W., Whiteley, T., Briggs, D.E.G., 2009. Beyond
1065 Beecher's Trilobite Bed: Widespread pyritization of soft tissues in the Late Ordovician
1066 Taconic foreland basin. *Geology* 37, 907-910.
- 1067 Fatka, O., Lerosey-Aubril, R., Budil, P., Rak, S., 2013. Fossilised guts in trilobites from the
1068 Upper Ordovician Letná Formation (Prague Basin, Czech Republic). *Bull. Geosci.* 88, 95-
1069 104.
- 1070 Flotte de Roquevaire, R., de, 1897. Carte du Maroc à l'échelle du 1.000.000e. Barrère, Paris.
- 1071 Fortey, R.A., 2009. A new giant asaphid trilobite from the Lower Ordovician of Morocco.
1072 *Mem. Assoc. Austral. Palaeont.* 37, 9-16.
- 1073 Fortey, R.A., 2011. Trilobites of the genus *Dikelocephalina* from Ordovician Gondwana and
1074 Avalonia. *Geol. J.* 46, 405-415.
- 1075 Fortey, R. A. 2012. The first known complete lichakephalid trilobite, Lower Ordovician of
1076 Morocco. *Mem. Assoc. Austral. Palaeont.* 42, 1-7.
- 1077 Foucauld, C., de, 1888. Reconnaissance au Maroc (1883-1884). Challamel, Paris, 495 pp.
- 1078 Friend, D., Zhuravlev, A.Y., Solov'ev, I.A., 2002. Middle Cambrian *Eldonia* from the
1079 Siberian Platform. *Paleont. J.* 36, 22-26.
- 1080 Fritsch, K.W., von, 1879. Reisebilder aus Marokko. *Mitt. Vereins Erdkunde Halle* 1, 11-53.
- 1081 Frizon de Lamotte, D., Saint-Bezar, B., Bracène, R., Mercier, E., 2000. The main steps of the
1082 Atlas building and geodynamics of the western Mediterranean. *Tectonics* 19, 740-761.
- 1083 Gabbott, S.E., Hou, X.-G., Norry, M.J., Siveter, D.J., 2004. Preservation of Early Cambrian
1084 animals of the Chengjiang biota. *Geology* 32, 901-904.
- 1085 Gaines, R.R., Droser, M.L., Orr, P.J., Garson, D., Hammarlund, E.U., Qi, C.S., Canfield,
1086 D.E., 2012a. Burgess Shale-type biotas were not entirely burrowed away. *Geology* 40,
1087 283-286.

1088 Gaines, R.R., Briggs, D.E.G., Orr, P.J., Van Roy, P., 2012b. Preservation of giant
1089 anomalocaridids in silica-chlorite concretions from the Early Ordovician of Morocco.
1090 *Palaios* 27, 317-325.

1091 Gentil, L., 1905a. Observations géologiques dans le Sud marocain. C. R. somm. Soc. Géol.
1092 France 5, 521-523.

1093 Gentil, L., 1905b. Sur la présence de schistes à graptolithes dans le Haut-Atlas marocain. C.
1094 R. Acad. Sci. Paris 140, 1659-1660.

1095 Gentil, L. 1906. Contribution à la géologie et à la géographie du Maroc. *Ann. Géogr.* 15, 133-
1096 151.

1097 Gentil, L., 1912. La géologie du Maroc et la genèse de ses grandes chaînes. *Ann. Géogr.* 21,
1098 130-158.

1099 Gentil, L., 1920. Carte géologique provisoire du Maroc 1:1 500 000. Larose, Paris.

1100 Gentil, L., 1929. L'Anti-Atlas et le Bani (exploration de 1923). *Rev. géogr. phys. géol. dyn.* 2,
1101 1-66.

1102 Gould, S.J., 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. Norton,
1103 New York. 347 pp.

1104 Guensburg, T.E., Sprinkle, J., 1992. Rise of echinoderms in the Paleozoic evolutionary fauna:
1105 significance of paleoenvironmental controls. *Geology* 20, 407-410.

1106 Guensburg, T.E., Sprinkle, J., 2003. The oldest known crinoids (Early Ordovician, Utah) and
1107 a new crinoid plate homology system. *Bull. Amer. Paleont.* 364, 1-43.

1108 Gutiérrez-Marco, J.C., Sá, A.A., Garcia-Bellido, D.C., Rabano, I., 2014. The extent of the
1109 Middle Ordovician Dapingian Stage in peri-Gondwanan Europe and North Africa:
1110 stratigraphic record, biostratigraphic tools and regional chronostratigraphy. *GFF* 136, 90-
1111 94.

- 1112 Haug, J.T., Mayer, G., Haug, C., Briggs, D.E.G., 2012. A Carboniferous non-onychophoran
1113 lobopodian reveals long-term survival of a Cambrian morphotype. *Current Biol.* 22, 1673-
1114 1675.
- 1115 Havlíček, V., 1971. Brachiopodes de l'Ordovicien du Maroc. *Notes et Mém. Serv. géol.*
1116 Maroc 230, 1-135.
- 1117 Hodgkin, T., 1866. Narrative of a journey to Morocco in 1863 and 1864, with geological
1118 annotations. Cautley Newby, London, 183 pp.
- 1119 Hooker, J.D., Ball, J., 1878. Journal of a tour in Morocco and the Great Atlas with an
1120 appendix including a sketch of the geology of Morocco by G. Maw. McMillan, London,
1121 446 pp.
- 1122 Horny, R.J., 1997. Ordovician Tergomya and Gastropoda (Mollusca) of the Anti-Atlas
1123 (Morocco). *Sbor. Národ. Muz. Praze* 53, 37-78.
- 1124 Hou, X., Aldridge, J.J., Bergström, J., Siveter, D.J., Siveter, D.J., Feng, X., 2004. The
1125 Cambrian Fossils of Chengjiang, China: The Flowering of Early Animal Life. Blackwell
1126 Science, Oxford, 256 pp.
- 1127 Hu, S., Zhu, M., Steiner, M., Luo, H., Zhao, F., Liu, Q., 2010. Biodiversity and taphonomy of
1128 the early Cambrian Guanshan Biota, eastern Yunnan. *Sci. China Earth. Sci* 53, 1765-1773.
- 1129 Hübner, M., 2011. Highly significant statistical results for the location of Plato's Island of
1130 Atlas in the Souss plain in today's South Morocco. Abstracts, 3rd International Atlantis
1131 Conference, 25-26 June 2011, Santorini, Greece, 12 pp.
- 1132 Hunter, A.W., Lefebvre, B., Nardin, E., Régnault, S., Van Roy, P., Zamora, S., 2010. New
1133 echinoderm Lagerstätten from the Upper Ordovician of the eastern Anti-Atlas, Morocco.
1134 In: Harris, L.G., Böttger, S.A., Walker, C.W., Lesser, M.P. (Eds.), *Echinoderms*: Durham.
1135 Balkema, Leiden, pp. 23-30.

1136 Hupé, P., 1952. Contribution à l'étude du Cambrien inférieur et du Précambrien III de l'Anti-
 1137 Atlas marocain. Faunes de trilobites et zones paléontologiques du Cambrien inférieur de
 1138 l'Anti-Atlas. Notes et Mém. Serv. géol. Maroc 103, 1-402.

1139 Jackson, J.G., 1809. An account of the empire of Marocco and the district of Suse, compiled
 1140 from miscellaneous observations made during a long residence in, and various journies
 1141 through, these countries. To which is added, an accurate and interesting account of
 1142 Timbuctoo, the great emporium of central Africa. Bulmer, London, 287 pp.

1143 Klug, C., Kröger, B., Kiessling, C., Mullins, G.L., Servais, T., Fryda, J., Korn, D., Turner, S.,
 1144 2010. The Devonian nekton revolution. *Lethaia* 43, 465-477.

1145 Kröger, B., Lefebvre, B., 2012. Palaeogeography and palaeoecology of early Floian (Lower
 1146 Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco. *Fossil*
 1147 *Record* 15, 61-75.

1148 Kühl, G., Bergström, J., Rust, J., 2008. Morphology, paleobiology and phylogenetic position
 1149 of *Vachonisia rogeri* (Arthropoda) from the Lower Devonian Hunsrück Slate (Germany).
 1150 *Palaeontogr. Abt. A* 286, 123-157.

1151 Kühl, G., Briggs, D.E.G., Rust, J., 2009. A great appendage arthropod with a radial mouth
 1152 from the Lower Devonian Hunsrück Slate, Germany. *Science* 323, 771-773.

1153 Kühl, G., Rust, J., 2010. Re-investigation of *Mimetaster hexagonalis*: A marrellomorph
 1154 arthropod from the Lower Devonian Hunsrück Slate (Germany). *Paläont. Z.* 84, 397-411.

1155 Lefebvre, B., 2007. Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran
 1156 echinoderms. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 245, 156-199.

1157 Lefebvre, B., Botting, J.P., 2007. First report of the mitrate *Peltocystis cornuta* Thoral
 1158 (Echinodermata, Stylophora) in the Lower Ordovician of central Anti-Atlas (Morocco).
 1159 *Ann. Paléont.* 93, 183-198.

1160 Lefebvre, B., Fatka, O., 2003. Palaeogeographical and palaeoecological aspects of the
 1161 Cambro-Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan
 1162 Europe. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 195, 73-97.
 1163 Lefebvre, B., Ware, D., 2007. Abnormalities in the Lower Ordovician cornute *Phyllocystis*
 1164 Thoral, 1935 (Echinodermata: Stylophora) from Montagne Noire (southern France):
 1165 implications for plate homology and phylogeny. *J. Paleont.* 81, 779-787.
 1166 Lefebvre, B., Nardin, E., Hunter, A.W., Régnault, S., 2007. Les échinodermes de l'Ordovicien
 1167 supérieur de l'Anti-Atlas (Maroc): biostratigraphie et paléodiversité. *Afric. Geosci. Rev.*
 1168 14, 123-148.
 1169 Lefebvre, B., Noailles, F., Hunter, A.W., Nardin, E., Régnault, S., Franzin, B., Van Roy, P.,
 1170 El Hariri, K., 2008. Les niveaux à échinodermes de Bou Nemrou, un gisement à
 1171 préservation exceptionnelle de l'Ordovicien supérieur du Tafilalt occidental (Maroc).
 1172 *Mésogée* 64, 7-25.
 1173 Lefebvre, B., Noailles, F., Franzin, B., Régnault, S., Nardin, E., Hunter, A.W., Zamora, S.,
 1174 Van Roy, P., El Hariri, K., Lazreq, N., 2010. Les gisements à échinodermes de
 1175 l'Ordovicien supérieur de l'Anti-Atlas oriental (Maroc) : un patrimoine scientifique
 1176 exceptionnel à préserver. *Bull. Instit. Sci. Rabat* 32, 1-17.
 1177 Lefebvre, B., Sumrall, C.D., Shroat-Lewis, R.A., Reich, M., Webster, G.D., Hunter, A.W.,
 1178 Nardin, E., Rozhnov, S.V., Guensburg, T.E., Touzeau, A., Noailles, F., Sprinkle, J., 2013.
 1179 Palaeobiogeography of Ordovician echinoderms. In: Harper, D.A.T, Servais, T. (Eds.),
 1180 Early Palaeozoic Biogeography and Palaeogeography. *Geol. Soc. London, Mem.* 38, pp.
 1181 173-198.
 1182 Legg, D.A. & Hearing, T.W., 2015. A late surviving xenopod (Arthropoda) from the
 1183 Ordovician Period, Wales. *Geol. Mag.* 152, 942-948.

- 1184 Lemoine, P., 1905. Quelques résultats d'une mission dans le Maroc occidental. Bull. Soc.
1185 géol. France 5, 198-200.
- 1186 Lecointre, G., 1918. Sur la présence du Cambrien et du Silurien(?) à Casablanca (Maroc
1187 occidental). C. R. Acad. Sci. Paris 166, 173-174.
- 1188 Lecointre, G., 1929. Examen des fossiles paléozoïques rapportés par M. L. Gentil de l'Anti-
1189 Atlas, en 1923. Rev. géogr. phys. géol. dyn. 2, 67.
- 1190 Lenz, O., 1884. Timbuktu, Reise durch Marokko, die Sahara und den Sudan. Brockhaus,
1191 Leipzig, 838 pp.
- 1192 Lerosey-Aubril, R., 2015. *Notchia weugi* gen. et sp. nov.: a new short-headed arthropod from
1193 the Weeks Formation Konservat-Lagerstätte (Cambrian; Utah). Geol. Mag. 152, 351-357.
- 1194 Liu, H.P., McKay, R.M., Young, J.N., Witzke, B.J., McVey, K.J., Liu, X., 2006. A new
1195 Lagerstätte from the Middle Ordovician St. Peter Formation in northeastern Iowa, USA.
1196 Geology 34, 969-972.
- 1197 Marek, L., 1983. The Ordovician hyoliths of Anti-Atlas (Morocco). Sbor. Národ. Muz. Praha
1198 39, 1-36.
- 1199 Martin, E., Lefebvre, B., Pittet, B., Vannier, J., Bachnou, A., El Hariri, K., Hafid, A.,
1200 Masrour, M., Noailles, F., Nowak, H., Servais, T., Vandenbroucke, T., Van Roy, P., Vidal,
1201 M., Vizcaïno, D., 2014. The Fezouata Biota (Central Anti-Atlas, Morocco): biostratigraphy
1202 and associated environmental conditions of an Ordovician Burgess Shale. In: Rocha, R.,
1203 Pais, J., Kullberg, J.C., Finney, S. (Eds.), Strati 2013, First International Congress on
1204 Stratigraphy - At the Cutting Edge of Stratigraphy. Springer, Cham, Heidelberg, New
1205 York, Dordrecht, London, pp. 419-422.
- 1206 Martin, E., Lefebvre, B., Vaucher, R., 2015. Taphonomy of a stylophoran-dominated
1207 assemblage in the Lower Ordovician of Zagora area (central Anti-Atlas, Morocco). In:

1208 Zamora, S., Rabano, I. (Eds.), Progress in Echinoderm Palaeobiology. Cuadernos del
1209 Museo Geominero 19, pp. 95-100.

1210 Martin, E., Pittet, B., Gutiérrez-Marco, J.C., Vannier, J., El Hariri, K., Leroosey-Aubril, R.,
1211 Masrour, M., Nowak, H., Servais, T., Vandenbroucke, T., Van Roy, P., Vaucher, R.,
1212 Lefebvre, B., in press. The Lower Ordovician Fezouata Konservat-Lagerstätte from
1213 Morocco: age, environment and evolutionary perspectives. Gondwana Research.

1214 Medioni, R., 2011. L'œuvre des géologues français au Maroc. Trav. Com. fr. Hist. Géol. 25,
1215 1-52.

1216 Mergl, M., 1981. The genus *Orbithale* (Brachiopoda, Inarticulata) from the Lower Ordovician
1217 of Bohemia and Morocco. Vestn. Ustred. Ustav. Geol. 56, 287-292.

1218 Michard, A., 1976. Elements de géologie marocaine. Notes et Mém. Serv. géol. Maroc 252,
1219 1-408.

1220 Murlon, M., 1870. Esquisse géologique sur le Maroc. Bull. Acad. roy. Belgique 30, 42-57.

1221 Nardin, E., Lefebvre, B., David, B., Mooi, R., 2009. La radiation des échinodermes au
1222 Paléozoïque inférieur : l'exemple des blastozoaires. C. R. Palevol 8, 179-188.

1223 Neltner, L., 1929a. Etat des connaissances actuelles sur la géologie du Maroc. C. R. 15ème
1224 Congr. géol. internat. Pretoria 2(6), 550-556.

1225 Neltner, L., 1929b. Sur l'extension du Cambrien dans le sud marocain et la présence dans
1226 cette région de plissements précambriens. C. R. Acad. Sci. Paris 188, 871-873.

1227 Neltner, L., 1938. Etudes géologiques dans le Sud marocain (Haut-Atlas et Anti-Atlas). Notes
1228 et Mém. Serv. géol. Maroc 42, 1-435.

1229 Noailles, F., Lefebvre, B., Guensburg, T.E., Hunter, A.W., Nardin, E., Sumrall, C.D., Zamora,
1230 S., 2010. New echinoderm-Lagerstätten from the Lower Ordovician of central Anti-Atlas
1231 (Zagora area, Morocco): a Gondwanan perspective of the Great Ordovician

- 1232 Biodiversification Event. In: Reich, M., Reitner, J., Roden, V., Thuy, B. (Eds.),
 1233 Echinoderm Research 2010. Universitätsverlag Göttingen, pp. 77-78.
- 1234 Nowak, H., Akodad, M., Lefebvre, B., Servais, T., 2015. Discovery of the *messaoudensis*–
 1235 *trifidum* acritarch assemblage (upper Tremadocian–lower Floian, Lower Ordovician) in the
 1236 subsurface of Morocco. Est. J. Earth Sci. 64, 80–83.
- Ortega-Hernández, J., Lerosey-Aubril, R., Kier, C., Bonino, E., 2015. A rare non-trilobite
 artiopodan from the Guzhangian (Cambrian Series 3) Weeks Formation Konservat-
 Lagerstätte in Utah, USA. Palaeontology 58, 265-276.
- Ortega-Hernández, J., Van Roy, P., Lerosey-Aubril, R., in press. A new aglaspidid euarthropod
 with a six-segmented trunk from the Early Ordovician Fezouata Konservat-Lagerstätte,
 Morocco. Geol. Mag.
- 1237 Ortelius, A., 1570. Theatrum Orbis Terrarum. Coppers, Antwerp, 53 pp.
- 1238 Paterson, J.R., García-Bellido, D.C., Jago, J.B., Gehling, J.G., Lee, M.S.Y., Edgecombe, G.D.
 1239 in press. The Emu bay Shale Konservat-Lagerstätte: A view of Cambrian life from East
 1240 Gondwana. Journal of the Geological Society. Peel, J.S., Ineson, J.R., 2011. The Sirius
 1241 Passet Lagerstätte (early Cambrian) of North Greenland. Palaeont. Can. 31, 109-118.
- 1242 Potocki, J., 1792. Voyage dans l'Empire du Maroc fait en l'année 1791. Suivi du Voyage de
 1243 Hafez, récit oriental. Dufour, Varsovie, 333 pp.
- 1244 Rabano, I., 1990. Trilobites del Museo Geominero. I. *Platypeltoides magrebiensis* n. sp.
 1245 (Asaphina, Nileidae) del Ordovícico inferior del Anti-Atlas central (Marruecos). Bol. Geol.
 1246 y Minero 101, 21-27.
- 1247 Renou, E., 1844. Carte de l'Empire du Maroc. Bouffard, Paris. Robison, R.A., Babcock, L.E.,
 1248 Gunther, V.G. 2015. Exceptional Cambrian Fossils from Utah: A Window into the Age of
 1249 Trilobites. Miscellaneous Publication 15-1. Utah Geological Survey, Salt Lake City. 97 pp.

- 1250 Roch, E., 1930a. Etudes géologiques dans la région méridionale du Maroc occidental. Notes
1251 et Mém. Serv. géol. Maroc 9, 1-542.
- 1252 Roch, E., 1930b. Carte géologique provisoire de l'Atlas méridional. Notes et Mém. Serv. géol.
1253 Maroc, 12.
- 1254 Roch, E., 1939. Description géologique des montagnes à l'Est de Marrakech. Notes et Mém.
1255 Serv. géol. Maroc 51, 1-438.
- 1256 Roch, E., 1950. Histoire stratigraphique du Maroc. Notes et Mém. Serv. géol. Maroc 80, 1-
1257 435.
- 1258 Rohlf, G.F., 1868. Reise durch Marokko. Übersteigung des grossen Atlas. Exploration der
1259 Oasen von Tafilet, Tuat und Tidikelt und Reise durch die grosse Wüste über Rhadames
1260 nach Tripoli. Kühtmann, Bremen, 200 pp.
- 1261 Rohlf, G.F., 1874. Adventures in Morocco and journeys from the oases of Draa and Tafilet.
1262 Gilbert and Rivington, London, 371 pp.
- 1263 Sanson, N., 1655. Etats et royaumes de Fez et Maroc, Darha et Segelmesse. Mariette, Paris.
- 1264 Schnell, P., 1892. Das marokkanische Atlasgebirge. Petermanns Mitt. 103, 1-110.
- 1265 Ségaud, E., 1933. Le synclinal de Tiznit (Maroc sud-occidental). Chron. Mines Colon. 14,
1266 248-258.
- 1267 Ségaud, E., Termier, H., 1933. Sur l'Ordovicien du Djebel Tachilla (Maroc Sud-Ouest). C. R.
1268 somm. Soc. Géol. France 3, 33.
- 1269 Seilacher, A., 1970. Begriff und Bedeutung der Fossil-Lagerstätten. N. Jb. fü Geol. Paläont.
1270 Monat. 1970, 34–39.
- 1271 Service géologique du Maroc, 1956. Carte géologique de la terminaison occidentale de l'Anti-
1272 Atlas : région de Goulimine et du Dra inférieur : feuilles Plage Blanche, Goulimine, Cap
1273 Dra et Taïdalt au 200 000°. Notes et Mém. Serv. géol. Maroc 90.

- 1274 Service géologique du Maroc, 1969. Carte géologique du Maroc : Foum el Hassane - Assa au
1275 200 000°. Notes et Mém. Serv. géol. Maroc 159.
- 1276 Service géologique du Maroc, 1970a. Carte géologique de l'Anti-Atlas central et de la zone
1277 synclinale de Ouarzazate : feuilles Ouarzazate, Alougoum et Telouet Sud au 200 000°.
1278 Notes et Mém. Serv. géol. Maroc 138.
- 1279 Service géologique du Maroc, H., 1970b. Carte géologique du Maroc : Akka - Tafagount -
1280 Tata au 1/200 000. Notes et Mém. Serv. géol. Maroc 163.
- 1281 Service géologique du Maroc, 1971. Carte géologique du Maroc : Agadir Tissint - Oued
1282 Zemoul au 1/200 000. Notes et Mém. Serv. géol. Maroc 219.
- 1283 Service géologique du Maroc, 1977. Carte géologique du Maroc : Jbel Saghro - Dadès (Haut-
1284 Atlas central, sillon Sud-atlasique et Anti-Atlas central) au 1/200 000. Notes et Mém. Serv.
1285 géol. Maroc 161.
- 1286 Service géologique du Maroc, 1982. Carte géologique du Maroc : Bou Haïara - Zegdou (Anti-
1287 Atlas oriental, zone périphérique méridionale et Kem-Kem occidentaux) au 1/200 000.
1288 Notes et Mém. Serv. géol. Maroc 259.
- 1289 Service géologique du Maroc, 1986. Carte géologique du Maroc : Tafilalt - Taouz au 1/200
1290 000. Notes et Mém. Serv. géol. Maroc 244.
- 1291 Service géologique du Maroc, 1988. Carte géologique du Maroc : Todhra - Maïder au 1/200
1292 000. Notes et Mém. Serv. géol. Maroc 243.
- 1293 Service géologique du Maroc, 1989. Carte géologique du Maroc : Zagora - Coude du Dra -
1294 Hamada du Dra (p.p.) au 1/200 000. Notes et Mém. Serv. géol. Maroc 273.
- Smith, A.B., 1988. Patterns of diversification and extinction in Early Palaeozoic echinoderms.
Palaeontology 31, 799-828.
- 1295 Snape, M.G., 1993. A palynological study of the Ordovician to Devonian sediments of the
1296 Anti Atlas, Morocco. Unpubl. PhD thesis, University of Sheffield, 363 pp.

- 1297 Spjeldnaes, N., 1967. The palaeogeography of the Tethyan region during the Ordovician.
1298 Syst. Ass. Public. 7, 45-47.
- 1299 Sprinkle, J., Guensburg, T.E., 1995. Origin of echinoderms in the Paleozoic Evolutionary
1300 Fauna: the role of substrates. *Palaios* 10, 437-453.
- 1301 Sumrall, C.D., Zamora, S., 2011. Ordovician edrioasteroids from Morocco: faunal exchanges
1302 across the Rheic Ocean. *J. Syst. Palaeont.* 9, 425-454.
- 1303 Termier, G., Termier, H., 1950. Paléontologie marocaine 2 (4). Invertébrés de l'Ere Primaire.
1304 Annélides, arthropodes, échinodermes, conularides et graptolithes. Notes et Mém. Serv.
1305 géol. Maroc 79, 1-279.
- 1306 Termier, H., 1927. Observations nouvelles en Maroc central. C. R. somm. Soc. Géol. France
1307 9, 100-102.
- 1308 Termier, H., 1936. Etudes géologiques sur le Maroc central et le Moyen-Atlas septentrional.
1309 Notes et Mém. Serv. géol. Maroc 33, 1-1556.
- 1310 Termier, H., Termier, G., 1947. Les principaux niveaux paléontologiques dans l'Ordovicien
1311 marocain. C. R. somm. Soc. Géol. France 13, 254-256.
- 1312 Thomson, J., 1888. Map of Southwestern Morocco. Philip, London and Liverpool.
- 1313 Thomson, J., 1899. Geology of southern Morocco and the Atlas mountains. *Quart. J. geol.*
1314 *Soc.* 55, 190-213.
- 1315 Thorat, M., 1935. Contribution à l'étude paléontologique de l'Ordovicien inférieur de la
1316 Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire.
1317 Imprimerie de la Charité, Montpellier, 362 pp.
- 1318 Ubaghs, G., 1963. *Rhopalocystis destombesi* n. g., n. sp., éocrinoïde de l'Ordovicien inférieur
1319 (Trémadocien supérieur) du Sud marocain. Notes et Mém. Serv. géol. Maroc 172, 25-45.
- 1320 Ubaghs, G., 1970. Les Echinodermes "Carpoïdes" de l'Ordovicien inférieur de la Montagne
1321 Noire (France). Editions du CNRS, Paris, 110 pp.

- 1322 Ubaghs, G., 1983. Echinodermata. Note sur les échinodermes de l'Ordovicien inférieur de la
 1323 Montagne Noire (France). In: Courtessole, R., Marek, L., Pillet, J., Ubaghs, G., Vizcaïno,
 1324 D. (Eds.), Calymenina, Echinodermata et Hyolitha de l'Ordovicien inférieur de la
 1325 Montagne Noire (France méridionale). Mém. Soc. Et. Sci. Aude, pp. 33-35.
- 1326 Vandenbroucke, T.R.A., Armstrong, H.A., Williams, M., Zalasiewicz, J.A., Sabbe, K., 2009.
 1327 Ground-truthing Late Ordovician climate models using the paleobiogeography of
 1328 graptolites. *Paleoceanogr.* 24, 1-19.
- 1329 Van Roy, P., 2006. Non-trilobite arthropods from the Ordovician of Morocco. Unpubl. PhD
 1330 thesis, Ghent University, 230 pp.
- 1331 Van Roy, P., Briggs, D.E.G., 2011. A giant Ordovician anomalocaridid. *Nature* 473, 510-513.
- 1332 Van Roy, P., Tetlie, O.E., 2006. A spinose appendage fragment of a problematic arthropod
 1333 from the Early Ordovician of Morocco. *Acta Palaeont. Pol.* 51, 239-246.
- 1334 Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., El Hariri, K.,
 1335 Briggs, D.E.G., 2010. Ordovician faunas of Burgess Shale type. *Nature* 465, 215-218.
- 1336 Van Roy, P., Briggs, D.E.G., Gaines, R.R., 2015a. The Fezouata fossils of Morocco; an
 1337 extraordinary record of marine life in the Early Ordovician. *J. Geol. Soc. London* 172, 541-
 1338 549.
- 1339 Van Roy, P., Daley, A.C., Briggs, D.E.G., 2015b. Anomalocaridid trunk limb homology
 1340 revealed by a giant Ordovician filter-feeder with paired lateral flaps. *Nature* 522, 77-80.
- 1341 Vidal, M., 1996. Le modèle des biofaciès à trilobites : un test dans l'Ordovicien inférieur de
 1342 l'Anti-Atlas, Maroc. *C. R. Acad. Sci. Paris, Sci. Terre planètes* 327, 327-333.
- 1343 Vidal, M., 1998. Trilobites (Asaphidae et Raphiophoridae) de l'Ordovicien inférieur de l'Anti-
 1344 Atlas, Maroc. *Palaeontogr. Abt. A* 251, 39-77.
- 1345 Vinther, J., Van Roy, P., Briggs, D.E.G., 2008. Machaeridians are Palaeozoic armoured
 1346 annelids. *Nature* 451, 185-188.

1347 Vizcaïno, D., Lefebvre, B., 1999. Les échinodermes du Paléozoïque inférieur de Montagne
1348 Noire: biostratigraphie et paléodiversité. *Geobios* 32, 353-364.

1349 Vizcaïno, D., Alvaro, J.J., Lefebvre, B., 2001. The Lower Ordovician of the southern
1350 Montagne Noire. *Ann. Soc. géol. Nord* 8, 213-220.

1351 von Bitter, P.H., Purnell, M.A., Tetreault, D.K. & Stott, C.A. 2007. Eramosa Lagerstätte –
1352 Exceptionally preserved soft-bodied biotas with shallow-marine shelly and bioturbating
1353 organisms (Silurian, Ontario, Canada). *Geology* 35, 879-882.

1354 Washington, J., 1831. Geographical notice of the Empire of Morocco. *J. Roy. Soc. London* 1,
1355 123-155.

1356 Whittington, H.B., 1993. Anatomy of the Ordovician trilobite *Placoparia*. *Phil. Trans. R. Soc.*
1357 *London. B* 339, 109-118.

1358 Willefert, S., 2004. A la découverte des terrains à graptolithes (1727-1958). *Geobios mém. sp.*
1359 25, S1-S521.

1360 Young, G.A., Rudkin, D.M., Dobrzanski, E.P., Robson, S.P., Nowlan, G.S., 2007.
1361 Exceptionally preserved Late Ordovician biotas from Manitoba, Canada. *Geology* 35, 883-
1362 886.

1363 Yovanovitch, B., 1936. Carte géologique du Maroc au 1/1 500 000. *Notes et Mém. Serv. géol.*
1364 *Maroc* 47.

1365 Zamora, S., Zhu, X., Lefebvre, B., 2013. A new Furongian (Cambrian) echinoderm-
1366 Lagerstätte from the Sandu Formation (South China). *Cah. Biol. Mar.* 54, 565-569. Zhao,
1367 Y., Zhu, M., Babcock, L.E., Peng, J. 2011. The Kaili Biota: Marine Organisms from 508
1368 million Years Ago. Guizhou Publishing Group, Guiyang. 251 pp.

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Appendix

1372 List of taxa described in the Lower Fezouata Shale Formation from 1950 to 2000, compiled
1373 from Choubert et al. (1953, 1955), Destombes and Willefert (1959), Destombes (1960a, 1963,
1374 1967, 1970, 2006a), Ubaghs (1963), Chauvel (1966b, 1969, 1971a, 1978), Deunff (1968a,
1375 1968b), Havlíček (1971), Mergl (1981), Destombes et al. (1985), Chauvel and Régnault
1376 (1986), Elaouad-Debbaj (1988), Rabano (1990), El Bourkhissi and Sarmiento (1997):

- 1377 • **acritarchs:** *Acanthodiacrodium* cf. *achrasi*, *A. comptulum*, *A. divisa*, *A. formosum*, *A.*
1378 *hirtum*, *A. simplex*, *A. ubui*, *A. uniforme*, *A. sp.*, *Actinotodissus* sp., *Arbusculidium*
1379 *destombesii*, *A. frondiferum*, *Baltisphaeridium hirsutoides*, *B. cf. multipilosum*, *B.?*
1380 sp., *Baltisphaerosum* cf. *annelieae*, *B. granosum*, *Cymatiogalea bellicosa*, *C. cristata*,
1381 *C. cf. cristata*, *C. cuvillieri*, *C. cf. cuvillieri*, *C. velifera*, *Electoriskos zagoraensis*,
1382 *Eupoikilofusa squama*, *Glaucotesta latiramosa*, *Goniosphaeridium tener*, *G.*
1383 *uncinatum*, *Impliviculus miloni*, *Leiofusa simplex*, *Priscotheca complanata*, *P.*
1384 *prismatica*, *P. raia*, *Stelliferidium barbarum*, *S. cylindrata*, *S. distincta*, *S. cf. gautieri*,
1385 *S. cf. simplex*, *S. stelligerum*, *S. sp. 1*, *S. sp. 2*, *Trochosphaeridium annolavaense*,
1386 *Veryhachium miloni*, *V.?* sp., *Vulcanisphaera africana*, *V. britannica*, *V. frequens*.
- 1387 • **brachiopods:** *Acrothele* sp., *Lingulida* indet., *Plectorthis simplex*, *Ranorthis fasciata*.
- 1388 • **chitinozoans:** *Conochitina poumoti*, *Lagenochitina destombesi*, *L. esthonica*, *L.*
1389 *ventriosa*.
- 1390 • **conodonts:** *Drepanoistodus?* cf. *pervetus*.
- 1391 • **echinoderms:** *Aristocystitidae* indet., *Balantiocystis* sp., *Macrocystella bohémica*, *M.*
1392 cf. *mariae*, *Paleosphaeronites prokopi*, *Rhopalocystis dehirensis*, *R. destombesi*, *R.*
1393 *fraga*, *R. grandis*, *R. havliceki*, *R. lehmani*, *R. zagoraensis*, *R. sp. A*, *R. sp. B*, *R. sp. C*.
- 1394 • **graptolites:** *Anisograptus* cf. *matanensis*, *Bryograptus divergens*, *B. kjerulfi*
1395 *cumbrensis*, *B. lapworthi*, *Clonograptus flexibilis*, *C. rigidus*, *C. tenellus*,

- 1396 *Didymograptus* sp., *Rhabdinopora flabelliforme* cf. *anglica*, *R. flabelliforme*
 1397 *flabelliforme*, *R. flabelliforme multithecatum*, *R. flabelliforme norvegicum*.
- 1398 • **trilobites:** *Apatokephalus* sp., *Asaphellus* sp., *Asaphopsis* sp., *Bavarilla* sp., *Beltella*
 1399 sp., *Dikelocephalina* sp., *Orometopus* sp., *Parapilekia* sp., *Pharostomina?* sp.,
 1400 *Platypeltoides magrebiensis*, *Symphysurus* sp.
- 1401
- 1402 List of taxa described in the Upper Fezouata Shale Formation from 1950 to 2000, compiled
 1403 from Destombes (1960b, 1962a, 1963, 1967, 1970, 1972, 2006a), Chauvel (1966a, 1966b,
 1404 1969, 1971b, 1978), Havlíček (1971), Mergl (1981), Marek (1983), Elaouad-Debbaj (1984),
 1405 Destombes et al. (1985), Donovan and Savill (1988), Babin and Destombes (1990), Vidal
 1406 (1996, 1998), Horny (1997):
- 1407 • **bivalves:** *Babinka prima*, *B.* sp., *Ctenodonta escosurae*, *Praenucula* sp., *Redonia* cf.
 1408 *michela*.
- 1409 • **brachiopods:** *Angusticardinia* sp., *Lingula salteri*, *Orbithele vana*, *Paurorthis*
 1410 *tadristensis*, *Ranorthis fasciata*, *Tarfaya marocana*.
- 1411 • **chitinozoans:** *Conochitina* sp., *Eremochitinus baculata brevis*.
- 1412 • **conulariids:** *Conularia* indet.
- 1413 • **echinoderms:** *Anatifopsis escandei*, *Balantiocystis regnelli*, *Chauvelicystis ubaghsi*,
 1414 *Hemicystites* cf. *boehmi*, *Macrocystella bohémica*, *M.* cf. *mariae*, *M. tasseftensis*,
 1415 *Ramseyocrinus* sp., *Thoralicystis zagoraensis*.
- 1416 • **gastropods:** *Carcassonnella courtessolei*, *Lesueurilla prima*, *Thoralispira laevis*, *T.?*
 1417 cf. *occitana*.
- 1418 • **graptolites:** *Acrograptus nicholsoni*, *Adelograptus* sp., *Araneograptus murrayi*,
 1419 *Azygograptus* sp., *Clonograptus flexilis*, *C. persistens*, *C. rigidus*, *Didymograptus* cf.
 1420 *arcuatus*, *D. deflexus*, *D. extensus*, *D. v-fractus*, *D. intendus*, *D. pennatulus*, *D. nanus*,

1421 *D. nitidus*, *D. patulus*, *D. sparsus*, *Etagraptus putillus*, *Hermannograptus* sp.,
1422 *Isograptus caduceus arcuatus*, *I. caduceus gracilis*, *I. furcula*, *Pterograptus* sp.,
1423 *Schizograptus* sp., *Temnograptus multiflex*, *T. cf. noveboracensis*, *T. ramulus*,
1424 *Tetragraptus cf. approximatus*, *T. quadribrachiatus*, *T. reclinatus*, *T. serra*, *T.*
1425 *tornquisti*.

- 1426 • **hyolithids**: *Cavernolites senex*, *Elegantilites* sp., *Gamalites?* sp., *Gompholites* sp.,
1427 *Nephrotheca* sp., *Pauxillites* sp.
- 1428 • **rostroconchs**: *Ribeiria* sp.
- 1429 • **trilobites**: *Ampyx cf. priscus*, *Apatokephalus* sp., *Asaphellus fezouataensis*, *A. cf.*
1430 *fezouataensis*, *A. aff. jujuanus*, *A. tataensis*, *Asaphinae* indet., *Basilicus (Basiliella?)*
1431 *destombesi*, *B. (B.?) aff. destombesi*, *B. (B.?)* sp. A, *B. (B.?)* sp. B, *Bathycheilus*
1432 *gallicus*, *Bavarilla aff. zemmourensis*, *Ceraurinella?* sp., *Colpocoryphe thoralis*,
1433 *Euloma* sp., *Megalaspidea* sp., *Megistaspis (Ekeraspis) cf. filacovi*, *M. (E.)* sp. indet.,
1434 *Neseuretus aff. attenuatus*, *Platycoryphe* sp., *Pradoella tazzarinensis*, *Prionocheilus*
1435 *aff. languedocensis*, *Symphysurus angustatus sicardi*, *Toletanaspis aff. borni*.

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1438 **Figure captions**

1439

1440 Fig. 1. Correlation chart for Ordovician lithostratigraphic units of the Anti-Atlas (left
1441 columns) with the international (columns A-B, H) and the British Ordovician regional
1442 (columns C-G) time scales. Groups were defined by Choubert (1942) and formations, by
1443 Destombes (1970, 1971). Chronostratigraphy after: (A) Thomson (1888) and Gentil (1912,
1444 1920). (B) Gentil (1929). (C) Choubert and Termier (1947). (D) Choubert (1956). (E)
1445 Destombes (1962a). (F) Destombes (1970, 1971) and Destombes et al. (1985). (G)

1446 Gutierrez-Marco et al. (2003) and Destombes (2006b). (H) Lefebvre et al. (2008) and
1447 Martin et al. (in press).

1448

1449 Fig. 2. Late 19th century explorers of the Anti-Atlas. (A) Charles de Foucauld (1858-1916).
1450 (B) Friedrich Rohlf (1831-1896). (C) Oskar Lenz (1848-1925).

1451

1452 Fig. 3. (A) Gentil's 1920 geological map of Morocco. (B) Louis Gentil (1868-1925).

1453

1454 Fig. 4. The first three taxa reported and figured from the Lower Ordovician of the Anti-Atlas
1455 (and Morocco) in the early 1950s. (A) *Onchometopus?* sp. (Termier and Termier, 1950, pl.
1456 193 fig. 2), Jbel Kissane, late Tremadocian. (B) *Ogygia* cf. *desiderata* (Termier and
1457 Termier, 1950, pl. 193 fig. 1), Jbel Kissane, late Tremadocian. (C) *Macrocyrtella*
1458 *bohémica* (Choubert et al., 1953: fig. 1), Tansikht bridge, late Tremadocian. All scale bars:
1459 1 cm.

1460

1461 Fig. 5. The two main contributors to the geology and stratigraphy of the Lower Palaeozoic in
1462 the Anti-Atlas. (A) Jacques Destombes (1926-) in the Tafilalt (1959). (B) Georges
1463 Choubert (1908-1986) in the High-Atlas (1967).

1464

1465 Fig. 6. Choubert's 1956 geological map of Morocco.

1466

1467 Fig. 7. The collector who discovered the Fezouata Biota, Mohamed 'Ou Said' Ben Moula,
1468 photographed in the field in August 2014 while consolidating a central carapace element of
1469 the anomalocaridid *Aegirocassis benmoulai* in preparation of its removal from the rock.

1470

Fig. 8. The first exceptionally preserved Fezouata specimens discovered by Ben Moula: (A) the putative aglaspidid arthropod *Tremaglaspis* sp. (private museum of B. Tahiri); (B) the oldest cheloniellid arthropod (National Museums of Scotland, The Royal Museum NMS.G.2004.2.1)

Fig. 9. Ordovician outcrop map of the area N. of Zagora, southeastern Morocco. Areas yielding exceptionally preserved fossils are indicated in colour: red areas with yellow trim belong to the *Araneograptus murrayi* or *Hunnegraptus copiosus* Biozones; yellow areas with red trim fall in the Floian (Martin et al. in press; Gutiérrez-Marco pers. comm). A few additional sites farther to the W and N fall outside the area covered by the map. Insets show the study area within Morocco, and the stratigraphic context. The red arrow indicates the stratigraphic position of the Fezouata Biota.

Fig. 10. Some exceptionally preserved fossils from the Fezouata Biota. (A) The giant filter-feeding anomalocaridid *Aegirocassis benmoulai*, specimen showing the presence of two sets of lateral flaps, providing crucial information on arthropod limb evolution (Yale Peabody Museum of Natural History YPM 237172); (B) Marrellomorph arthropod, probably belonging to the genus *Furca* (Muséum d'Histoire naturelle de Toulouse MHNT PAL 2007.39.80.1); (C) halkieriid-like mollusk (YPM 227515); (D) the atypical aglaspidid *Brachyaglaspis singularis* (YPM 226552); (E) A subadult specimen of the oldest horseshoe crab (YPM 227586); (F) The fossil that solved machaeridian affinities: *Plumulites bengtsoni*, the first machaeridian annelid with preserved soft tissues (YPM 221134). The taxa shown in (A-C) are classical Burgess Shale-type fossils, while the specimens in (D-E) are typical of post-middle Cambrian faunas.

Figure 1

Groups	Formations	A	B	C	D	E	F	G	H			
2 nd Bani	U. 2 nd Bani	Lower Cretaceous (Neocomian)	Lower – Middle Devonian	Caradoc	Caradoc	Ashgill	Ashgill	Ashgill	Hirnantian			
	L. 2 nd Bani											
Ktaoua	U. Ktaoua			Llandeilo	Llandeilo		Caradoc	Caradoc	Katian			
	U. Tiouririne											
	L. Ktaoua											
1 st Bani	Izegguirène					Llandeilo	Llandeilo	Llandeilo	Llandeilo	Llandeilo	Llandeilo	Sandbian
	Ouine-Inirne											
	Guezzart											
	Bou Zeroual											
	Taddrist											
Outer Feijas	Tachilla			Llanvirn	Llanvirn	Llanvirn	Llanvirn	Llanvirn	Darriwilian			
	Zini					Arenig	Arenig			Arenig		
	U. Fezouata											
	L. Fezouata					Arenig	Tremadoc	Tremadoc		Tremadoc	Tremadoc	Tremadoc

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7

Figure 8

Figure 9

Figure 10