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

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A B S T R A C T

Exceptionally 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 utmost importance, for it demonstrates the extent in the fossil record of non-biomineralising 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.

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 the 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 aftermath have greatly benefited

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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 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 and 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 et al., 2010, 2015a,b; Van Roy and Briggs, 2011) 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 summarises 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 Foucauld, 1888; Gentil, 1929; Despujols, 1933; Choubert, 1952a; Willefert, 2004; Destombes, 2006a).

2.1. Beyond the High Atlas

The Atlas system is a 2500 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 [Hassan Al Wazzan], 1556).

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. Ortellius, 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 (Sijilmasa) 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). The map produced by Beaudouin (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 (Thomson, 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 Foum 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).

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

Fig. 1. Correlation chart for Ordovician lithostratigraphic units of the Anti-Atlas (left columns) with the international (columns A–B, H) and the British Ordovician regional (columns C–G) time scales. Groups were defined by Choubert (1942) and formations, by Destombes (1970, 1971). Chronostratigraphy after: (A) Thomson (1888) and Gentil (1912, 1920), (B) Gentil (1929), (C) Choubert and Termier (1947), (D) Choubert (1956), (E) Destombes (1962a), (F) Destombes (1970, 1971) and Destombes et al. (1985), (G) Gutiérrez-Marco et al. (2003) and Destombes (2006b), (H) Lefebvre et al. (2008) and Martin et al. (in press).

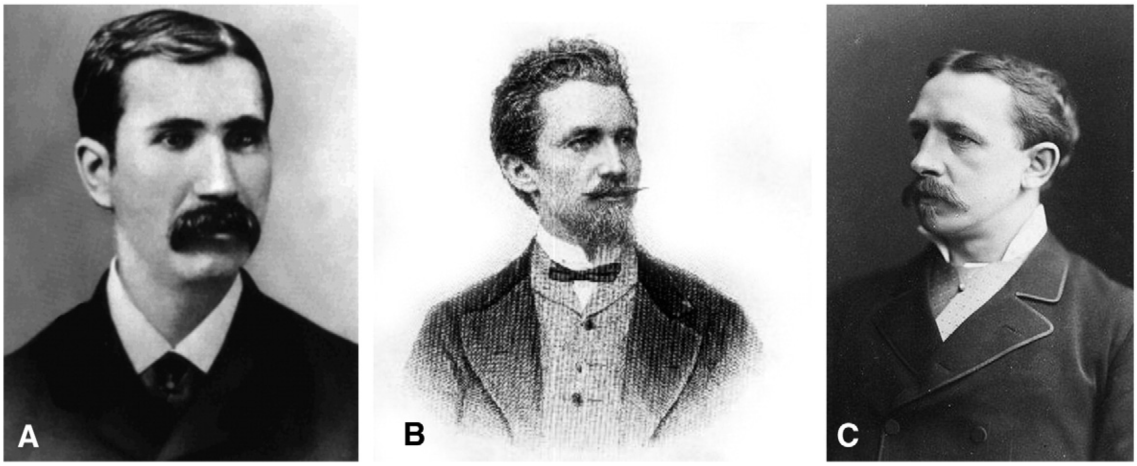

Fig. 2. Late 19th century explorers of the Anti-Atlas. (A) Charles de Foucauld (1858–1916). (B) Friedrich Rohlf (1831–1896). (C) Oskar Lenz (1848–1925).

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 (Hodgkin, 1866; Balansa, 1868; Mourlon, 1870; Brives, 1902, 1905, 1909; Gentil, 1905a,b, 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*).

At 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

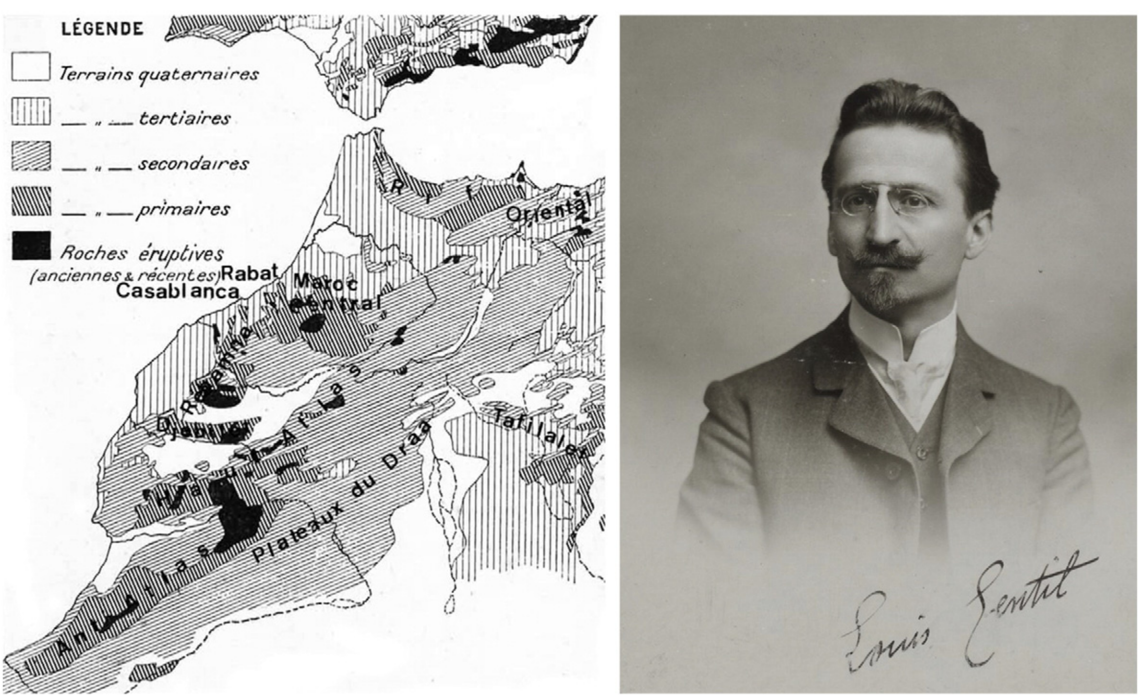

Fig. 3. (A) Gentil's (1920) geological map of Morocco. (B) Louis Gentil (1868–1925).

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,b; 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 Foum 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,b, 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 2000 m (Choubert, 1942) and 2850 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., 1952, 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 bohemica* (Fig. 4C) by Choubert et al. (1953) was the first

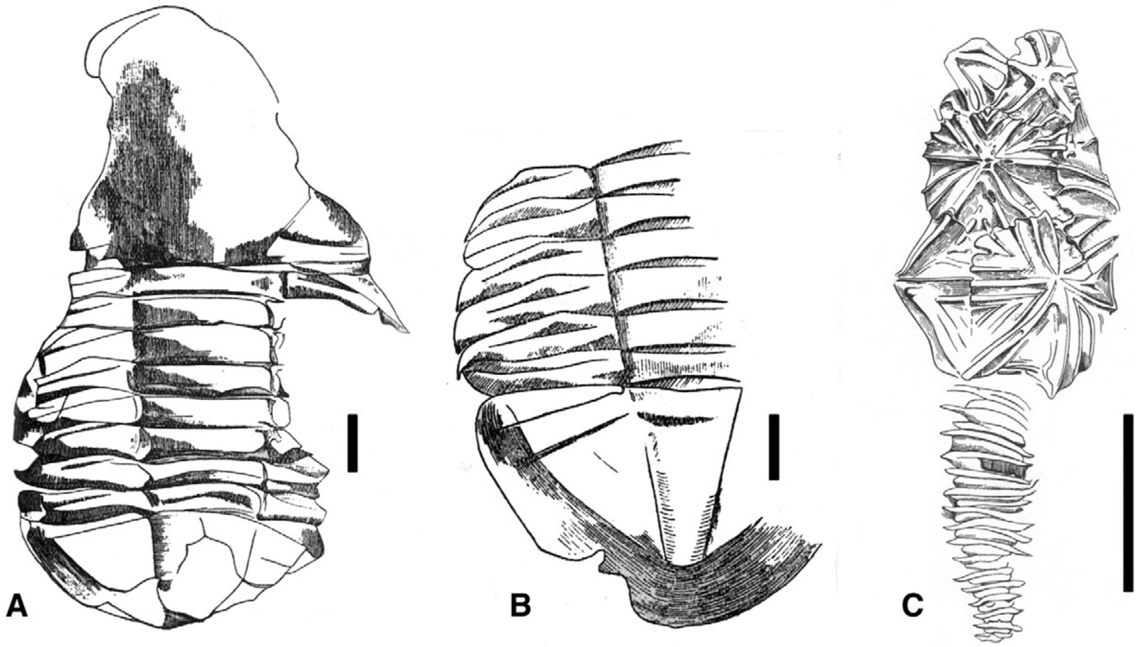

Fig. 4. The first three taxa reported and figured from the Lower Ordovician of the Anti-Atlas (and Morocco) in the early 1950s. (A) *Onchometopus*? sp. (Termier and Termier, 1950, pl. 193 Fig. 2), Jbel Kissane, late Tremadocian. (B) *Ogygia* cf. *desiderata* (Termier and Termier, 1950, pl. 193 Fig. 1),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

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,b; Bourcart and Le Villain, 1931), the distinction

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

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 subsiding, 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 bohemica* (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

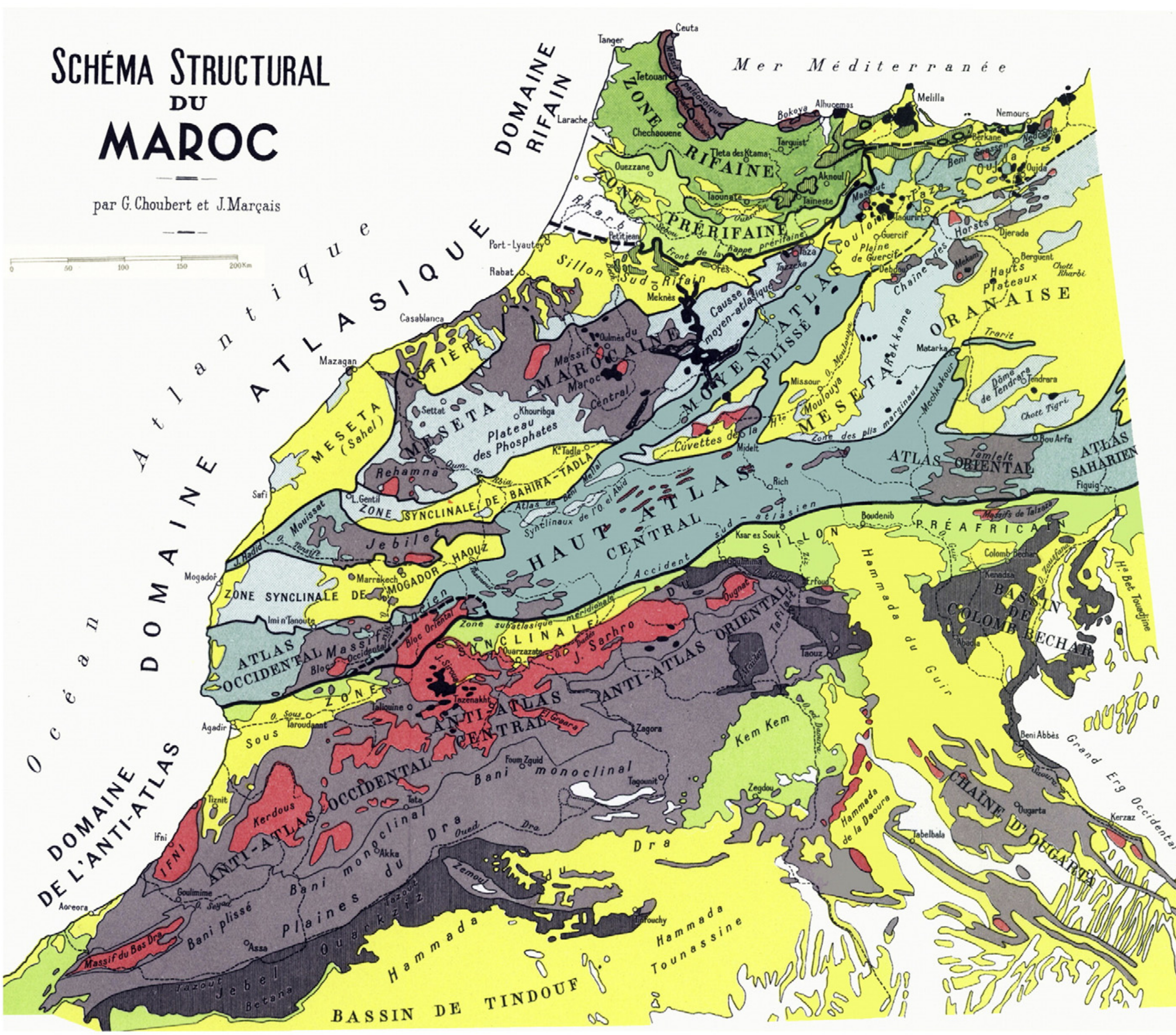

Fig. 6. Choubert's (1956) geological map of Morocco.

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. *homphrayi*, *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 bohemica*).

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 m below the estimated position of the Tansikht bridge level (late Tremadocian) yielding *Macrocystella bohemica* 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 oolithic 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' 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 lithostratographic 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 middle 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, 1970a, 1970b, 1971, 1977, 1982, 1986, 1988, 1989). His detailed descriptions of the Cambro-Ordovician series of the whole Anti-Atlas (written between 1983 and 2003) were finally published as a series of explanatory notes (Destombes, 2006a,b,c,d,e,f,g,h,i,j).

From the late 1950s to the late 1990s, Destombes discovered over 2000 Cambro-Ordovician localities throughout the whole Anti-Atlas (Destombes, 2006a). In the Lower Ordovician of the Zagora area, he identified and described 26 distinct fossiliferous horizons in the Lower Fezouata Shale Formation, and 22 levels in the Upper Fezouata Shale Formation (Destombes, 2006b). In this area, his reference section was located on the eastern side of Jbel Bou Dehir, about 20 km NE of Zagora. These localities yielded thousands of specimens, which were sent to various specialists for systematic description. Over 180 taxa of marine invertebrates and palynomorphs were described from the material collected by Destombes in both the Lower and the Upper Fezouata Shale formations (Destombes et al., 1985; Destombes, 2006a), including acritarchs (Deunff, 1968a,b; Elaouad-Debbaj, 1988; Snape, 1993), bivalves (Babin and Destombes, 1990), brachiopods (Destombes, 1970; Havlíček, 1971; Mergl, 1981), chitinozoans (Elaouad-Debbaj, 1984, 1988), conodonts (El Bourkhissi and Sarmiento, 1997), conulariids

(Destombes et al., 1985), echinoderms (Ubaghs, 1963; Chauvel, 1966a, b, 1969, 1971a,b, 1978; Chauvel and Régnault, 1986; Donovan and Savill, 1988), gastropods (Horny, 1997), graptolites (Destombes and Willefert, 1959; Destombes, 1960a,b, 1962a, 1963, 1970; Destombes et al., 1985), hyolithids (Marek, 1983), rostroconchs (Babin and Destombes, 1990), and trilobites (Destombes, 1967, 1970, 1972; Destombes et al., 1985; Rabano, 1990; Vidal, 1996, 1998). The complete list of all fossils collected from 1950 to 2000 is available in Appendix A.

Apparently only a single borehole crossed the Fezouata Shale Formation. This borehole, 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) in 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 c. 250 kilometre-long drive from Alnif to Bou Chrebeb, including the final c. 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 now requires 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).

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

Independently, on the 28th November 2001, several exquisitely preserved specimens of 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, had been 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.

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

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).

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

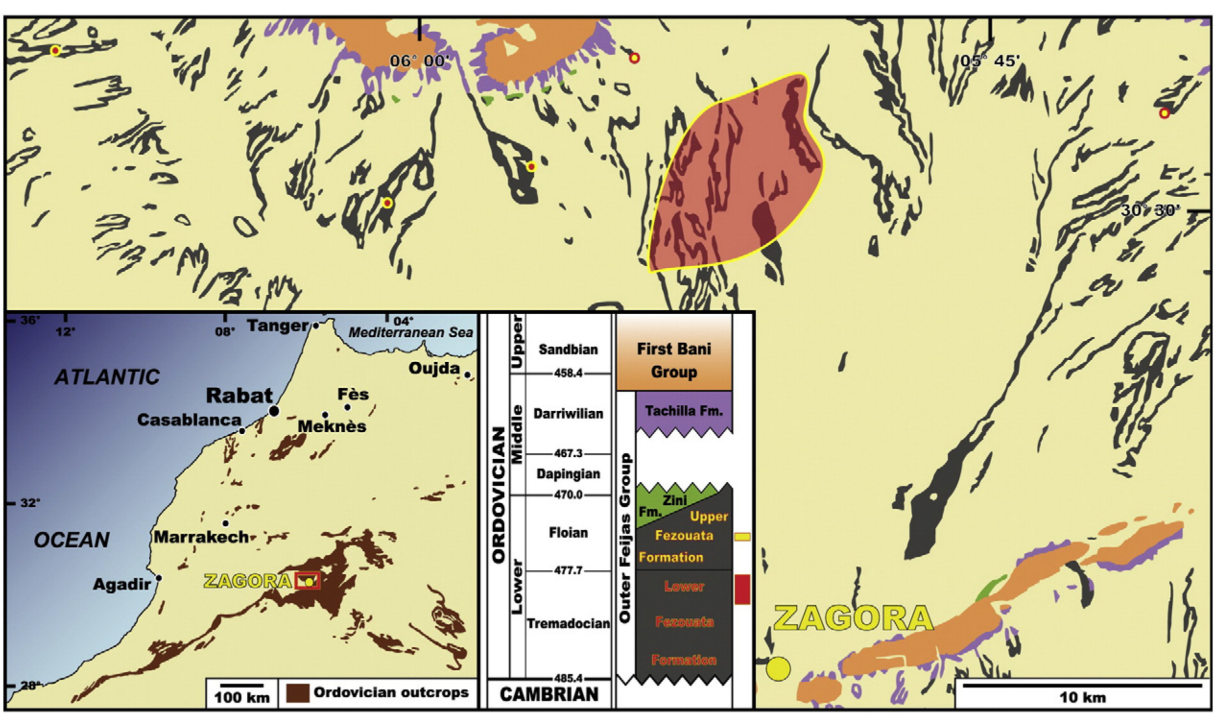

Fig. 9. Ordovician outcrop map of the area N. of Zagora, southeastern Morocco. Areas yielding exceptionally preserved fossils are indicated in colour: red areas with yellow trim belong to the *Araneograptus murrayi* or *Hunnegraptus copiosus* Biozones; yellow areas with red trim fall in the Floian (Martin 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.

exchanging information and specimens (Van Roy, 2006; Van Roy and Tetlie, 2006; Botting, 2007; Lefebvre and Botting, 2007; Van Roy et al., 2010).

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

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

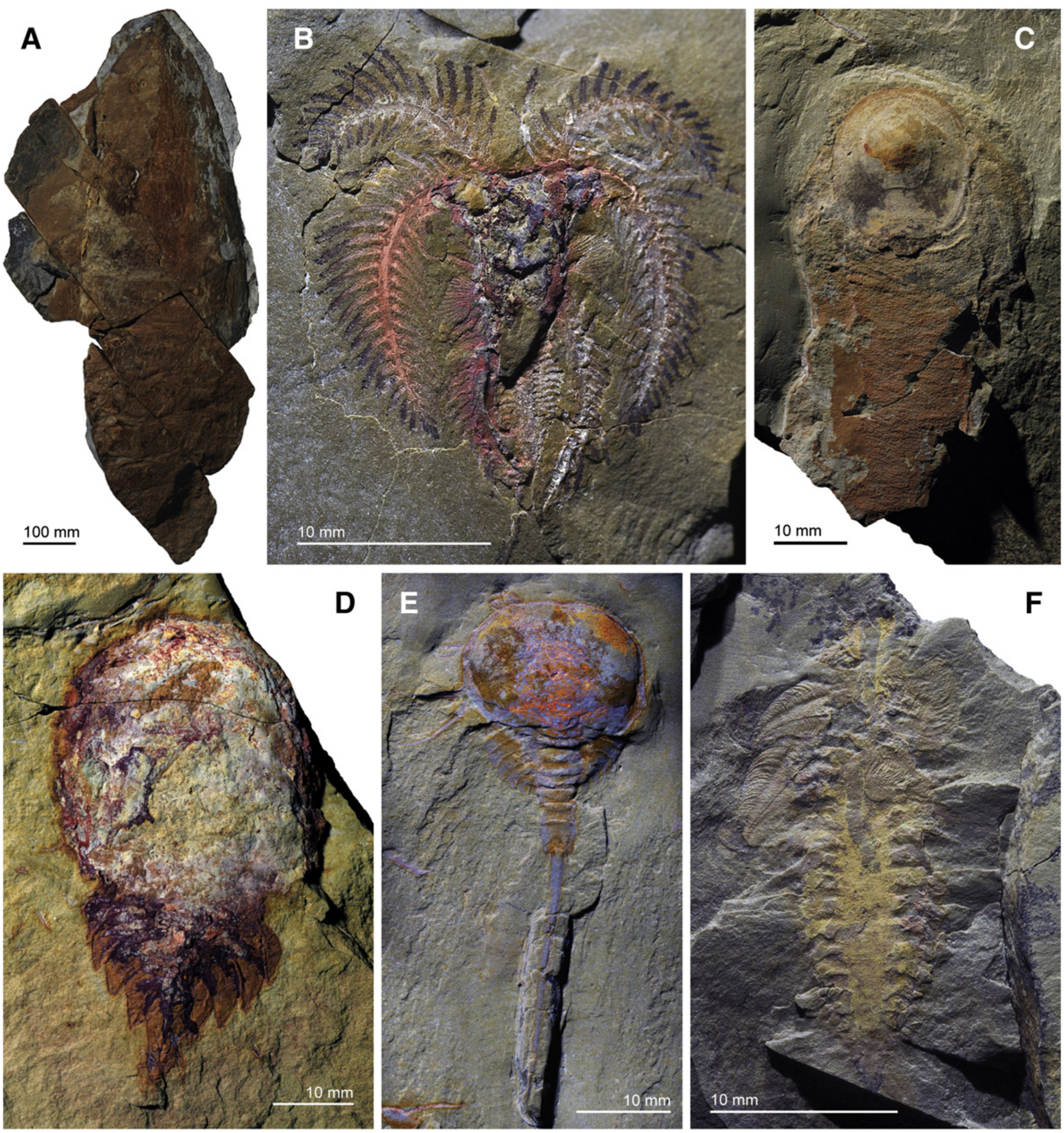

Fig. 10. Some exceptionally preserved fossils from the Fezouata Biota. (A) The giant filter-feeding anomalocaridid *Aegirocassis benmoulai*, specimen showing the presence of two sets of lateral flaps, providing crucial information on arthropod limb evolution (Yale Peabody Museum of Natural History YPM 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.

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, J. Botting, D. Briggs, L. Muir, 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), B. 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 3000 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 D. Briggs, Robert Gaines and P. Van Roy) and ANR (RALI) in France (primary team members B. 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 K. El Hariri, B. Lefebvre, Moussa Masrour and Muriel Vidal). All three projects were conceived to be complementary, with the NSF team focusing primarily on systematics, taphonomy and geochemistry (Van Roy and Briggs, 2011; Gaines et al., 2012b; Van Roy et al., 2015a,b; 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 m^2 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). This interpretation was challenged by a recent study led by B. Pittet, Romain Vaucher, Emmanuel Martin and B. Lefebvre, which suggested that in the area N of Zagora, exceptional preservation is restricted to only two stratigraphic intervals. Both intervals were originally believed to have a latest Tremadocian age, the lower was considered to be c. 25 m thick, falling in the *Araneograptus murrayi* graptolite biozone, while the upper was thought to have a thickness of c. 15 m and extend into the *Hunnegraptus copiosus* graptolite zone (Martin et al., in press). However, further detailed study of the graptolite faunas data indicates the presence of only one c. 60 m thick exceptional interval in the upper Tremadocian (*A. murrayi* graptolite biozone, possibly extending into the *H. copiosus* graptolite biozone), with a second, c. 15 m thick exceptional interval located considerably higher up, in the middle Floian (Gutiérrez-Marco and Martin, 2016–in this issue). This suggests that environmental conditions conducive to exceptional preservation in the late Tremadocian could briefly reoccur several Myr later. 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 may have been 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; 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 and Swanson, 1973). If *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: 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, characterised 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 *Lagerstätte* in the 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 *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; 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 c. 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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Appendix A

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

- **Acritarchs**: *Acanthodiacrodium* cf. *achrasi*, *A. comptulum*, *A. divisa*, *A. formosum*, *A. hirtum*, *A. simplex*, *A. ubui*, *A. uniforme*, *A.* sp., *Actinotodissus* sp., *Arbusculidium destombesii*, *A. frondiferum*, *Baltisphaeridium hirsutoides*, *B.* cf. *multipilosum*, *B.*? sp., *Baltisphaerosum* cf. *annelieae*, *B. granosum*, *Cymatiogalea bellicosa*, *C. cristata*, *C.* cf. *cristata*, *C. cuvillieri*, *C.* cf. *cuvillieri*, *C. velifera*, *Electoriskos zagoraensis*, *Eupoikilofusa squama*, *Glaucotesta latiramosa*, *Goniosphaeridium tener*, *G. uncinatum*, *Impliviculus miloni*, *Leiofusa simplex*, *Priscotheca complanata*, *P. prismatica*, *P. raia*, *Stelliferidium barbarum*, *S. cylindrata*, *S. distincta*, *S.* cf. *gautieri*, *S.* cf. *simplex*, *S. stelligerum*, *S.* sp. 1, *S.* sp. 2, *Trochosphaeridium annolavaense*, *Veryhachium miloni*, *V.*? sp., *Vulcanisphaera africana*, *V. britannica*, and *V. frequens*.
- **Brachiopods**: *Acrothele* sp., Lingulida indet., *Plectorthis simplex*, and *Ranorthis fasciata*.
- **Chitinozoans**: *Conochitina poumoti*, *Lagenochitina destombesi*, *L. esthonica*, *L. ventriosa*.
- **Conodonts**: *Drepanoistodus*? cf. *pervetus*.
- **Echinoderms**: Aristocystitidae indet., *Balantiocystis* sp., *Macrocystella bohemica*, *M.* cf. *mariae*, *Paleosphaeronites prokopi*, *Rhopalocystis dehirensis*, *R. destombesi*, *R. fraga*, *R. grandis*, *R. havliceki*, *R. lehmani*, *R. zagoraensis*, *R.* sp. *A*, *R.* sp. *B*, *R.* sp. *C*.
- **Graptolites**: *Anisograptus* cf. *matanensis*, *Bryograptus divergens*, *B. kjerulfi cumbrensis*, *B. lapworthi*, *Clonograptus flexibilis*, *C. rigidus*, *C. tenellus*, *Didymograptus* sp., *Rhabdinopora flabelliforme* cf. *anglica*, *R. flabelliforme flabelliforme*, *R. flabelliforme multithecatum*, and *R. flabelliforme norvegicum*.
- **Trilobites**: *Apatokephalus* sp., *Asaphellus* sp., *Asaphopsis* sp., *Bavarilla* sp., *Beltella* sp., *Dikelocephalina* sp., *Orometopus* sp., *Parapilekia* sp., *Pharostomina*? sp., *Platypeltoides magrebiensis*, *Symphysurus* sp.

List of taxa described in the Upper Fezouata Shale Formation from 1950 to 2000, compiled from Destombes (1960b, 1962a, 1963, 1967, 1970, 1972, 2006a), Chauvel (1966a, 1966b, 1969, 1971b, 1978), Havlíček (1971), Mergl (1981), Marek (1983), Elaouad-Debbaj (1984), Destombes et al. (1985), Donovan and Savill (1988), Babin and Destombes (1990), Vidal (1996, 1998), Horny (1997):

- **Bivalves**: *Babinka prima*, *B.* sp., *Ctenodonta escosurae*, *Praenucula* sp., and *Redonia* cf. *michelae*.
- **Brachiopods**: *Angusticardinia* sp., *Lingula salteri*, *Orbithele vana*, *Paurorthis tadristensis*, *Ranorthis fasciata*, and *Tarfaya marocana*.
- **Chitinozoans**: *Conochitina* sp., and *Eremochitina baculata brevis*.
- **Conulariids**: Conularia indet.
- **Echinoderms**: *Anatifopsis escandei*, *Balantiocystis regnelli*, *Chauvelicystis ubaghsi*, *Hemicystites* cf. *boehmi*, *Macrocystella bohemica*, *M.* cf. *mariae*, *M. tasseftensis*, *Ramseyocrinus* sp., *Thoralicystis zagoraensis*.
- **Gastropods**: *Carcassonnella courtessolei*, *Lesueurilla prima*, *Thoralispira laevis*, *T.*? cf. *occitana*.
- **Graptolites**: *Acrograptus nicholsoni*, *Adelograptus* sp., *Araneograptus murrayi*, *Azygograptus* sp., *Clonograptus flexilis*, *C. persistens*, *C. rigidus*, *Didymograptus* cf. *arcuatus*, *D. deflexus*, *D. extensus*, *D. v-fractus*, *D. intendus*, *D. pennatulus*, *D. nanus*, *D. nitidus*, *D. patulus*, *D. sparsus*, *Etagraptus putillus*, *Hermannograptus* sp., *Isograptus caduceus arcuatus*, *I. caduceus gracilis*, *I. furcula*, *Pterograptus* sp., *Schizograptus* sp., *Temnograptus multiflex*, *T.* cf. *noveboracensis*, *T. ramulus*, *Tetragraptus* cf. *approximatus*, *T. quadribrachiatus*, *T. reclinatus*, *T. serra*, and *T. tornquisti*.
- **Hyolithids**: *Cavernolites senex*, *Elegantilites* sp., *Gamalites*? sp., *Gompholites* sp., *Nephrotheca* sp., and *Pauxillites* sp.
- **Rostroconchs**: *Ribeiria* sp.
- **Trilobites**: *Ampyx* cf. *priscus*, *Apatokephalus* sp., *Asaphellus fezouataensis*, *A.* cf. *fezouataensis*, *A.* aff. *jujuanus*, *A. tataensis*, *Asaphinae indet.*, *Basilicus* (*Basiliella*?) *destombesi*, *B.* (*B.*?) aff. *destombesi*, *B.* (*B.*?) sp. A, *B.* (*B.*?) sp. B, *Bathycheilus gallicus*, *Bavarilla* aff. *zemmourensis*, *Ceraurinella*? sp., *Colpocoryphe thorali*, *Euloma* sp., *Megalaspidella* sp., *Megistaspis* (*Ekeraspis*) cf. *filacovi*, *M.* (E.) sp. *indet.*, *Neseuretus* aff. *attenuatus*, *Platycoryphe* sp., *Pradoella tazzarinensis*, *Prionocheilus* aff. *languedocensis*, *Symphysurus angustatus sicardi*, and *Toletanaspis* aff. *borni*.

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