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## Large trilobites in a stress-free Early Ordovician environment

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### Abstract :

Understanding variations in body size is essential for deciphering the response of an organism to its surrounding environmental conditions and its ecological adaptations. In modern environments, large marine animals are mostly found in cold waters. However, numerous parameters can influence body-size variations other than temperatures, such as oxygenation, nutrient availability, predation or physical disturbances by storms. Here, we investigate trilobite size variations in the Lower Ordovician Fezouata Shale deposited in a cold-water environment. Trilobite assemblages dominated by small- to normal-sized specimens that are a few centimetres in length are found in proximal and intermediate settings, while those comprising larger taxa more than 20 cm in length are found in the most distal environment of the Fezouata Shale. Drill core material from distal settings shows that sedimentary rocks hosting large trilobites preserved in situ are extensively bioturbated with a high diversity of trace fossils, indicating that oxygen and nutrients were available in this environment. In intermediate and shallow settings, bioturbation is less extensive and shallower in depth. The rarity of storm events (minimal physical disturbance) and the lack of predators in deep environments in comparison to shallower settings would also have helped trilobites attain larger body sizes. This highly resolved spatial study investigating the effects of numerous biotic and abiotic parameters on body size has wider implications for the understanding of size fluctuations over geological time.

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**Keywords** : Arthropod, body size, Palaeozoic, Fezouata Shale

## Introduction

Considered one of the most important aspects of animal biology (Bonner, 2006), body size results from numerous biotic and abiotic factors (Bell, 2014). Vertebrate size variations over geological time have received considerable attention (Sander & Clauss, 2008; Geiger et al., 2013). Comparatively, marine invertebrates have been less studied (Lamsdell & Braddy, 2009; Klug et al., 2015; Sigurdson & Hammer, 2016). For instance, it is well agreed that low temperatures can be responsible of the large sizes of modern marine invertebrates (i.e. Bergmann's rule; Timofeev, 2001; Moran & Woods, 2012). Nevertheless, if this was the sole parameter controlling body size, all taxa at high latitudes should be larger than genera found at lower latitudes. This is rarely the case because size variations occur locally in a specific paleoenvironment, owing to changes in water depth, oxygenation, predation, nutrient availability or even physical disturbances caused by storm events (Saleh et al., 2018).

During the Ordovician, Morocco was part of the Gondwana margins, at high latitudes, close to the South Pole. The Fezouata Shale was deposited near the Zagora region in Morocco, under cold waters at the transition between two major evolutionary events: the Cambrian Explosion and the Great Ordovician Biodiversification Event (Martin et al., 2016a). In this formation, two sedimentary intervals have yielded thousands of exceptionally preserved fossils belonging to different groups such as arthropods, echinoderms, mollusks, and sponges (Vinther et al., 2008, 2017; Van Roy et al., 2010, 2015a; Martí Mus, 2016; Lefebvre et al., 2019). A striking feature of this formation is extreme body size fluctuations at both taxon and assemblage scales between localities and even between different levels of the same locality (for further details see Ebbestad, 2016; Lefebvre et al., 2016; Martin, 2016; Saleh et al., 2018). Trilobites occur in all sites from the Fezouata Shale and show a large body-size range in this formation. Abundant and spectacular specimens of very large trilobites were found at Ouled Slimane near the Tanskhit bridge (Rábano, 1990; Fortey, 2009; Lebrun, 2018). In this study, the sedimentological and taphonomic contexts of levels with large trilobites from the Fezouata Shale are elucidated, in order to contribute to the understanding of body-size fluctuations in the geological record (see also Lamsdell & Braddy, 2009; Klug et al., 2015; Sigurdson & Hammer, 2016).

## 2. Geological and paleoenvironmental context

A long term transgression at the beginning of the Ordovician created epicontinental seas on the Gondwana margins in the Southern Hemisphere (Torsvik & Cocks, 2011; 2013). The Fezouata Shale Formation (Fig. 1a) was deposited in a cold water sea, at high latitudes (over 60°S) close to the South Pole (Fig. 1b) (Torsvik & Cocks, 2013; Martin et al., 2016b). Sedimentary rocks of this formation consist of blue-green to yellow-green siltstones (Destombes et al., 1985). The 900 m-thick succession of the Fezouata Shale (Fig. 1a) was deposited in a storm/wave dominated environment with a minor influence of tides (Vaucher et al., 2016). In this environment, sedimentological structures indicate a deepening trend from the SE to the NW (Fig. 1c) as shown in Vaucher et al. (2017). Thus, the most proximal settings in the Late Tremadocian (*A. murrayi* Zone) occur near Tamegroute (about 20 km ESE of Zagora; Fig. 1c) (see, Saleh et al., 2018). In this locality, sedimentary rocks are constituted of coarse siltstones to fine grained sandstones showing hummocky cross stratifications (HCS) of cm- to dm-scale wavelengths (Vaucher et al., 2016) (Fig. 1d). Intermediate settings of the Fezouata Shale occur in Bou Izargane in the Ternata plain about 20 km N of Zagora (Fig. 1c). In this setting, sedimentary rocks are characterized by finer siltstones and more abundant background sediments than in Tamegroute, in addition to the presence of storm events with up to cm-scale HCS (Saleh et al., 2019) (Fig. 1d). The average sedimentation rate in this area was estimated ~79 m/Ma (Saleh et al., 2019). The progradation

model proposed by Vaucher et al., (2017) suggests that the Ouled Slimane area is associated with more distal settings (Fig. 1c). A field campaign was organized in 2019 to better constrain the depositional environment of this locality (see section 3).

As for the faunal content of the different sites, all three sites yielded diverse assemblages of marine invertebrates (Saleh et al., 2018). However, Tamegroute is characterized by sessile epibenthic taxa (bivalves, brachiopods) that are about half the size of those in Bou Izargane (Saleh et al., 2018). Size variations in the Fezouata Shale between localities are not limited to brachiopods and bivalves. Trilobites also show body-size discrepancies between localities. The largest trilobites from the Fezouata Shale are found at Ouled Slimane (Rábano, 1990; Fortey, 2009; Lebrun, 2018).

<insert figure 1>

### 3. Material and methods

Two successive field campaigns were carried out in the Zagora region in 2018 and 2019 and two cores were obtained. The first core (~13m) was drilled in the intermediate settings of Bou Izargane. The second core (~2.5m) was made in Ouled Slimane, crossing the interval in which large trilobites were discovered. Both cores correspond strictly to the same stratigraphic interval in the *Araneograptus murrayi* biozone (see Vaucher et al., 2016; Saleh et al., 2018; and references therein for correlations). Cores were described for their lithology, grain size, depositional sedimentary structures and bioturbation intensity and size at the University of Lausanne, Switzerland, and are currently deposited at the University of Brest. All levels crossed by cores were repeatedly sampled from 2004 to 2017, and yielded a large number of fossils (most of them are deposited in the collections of the Cadi-Ayyad University, Marrakesh). Trilobite taxa and assemblages discovered in these levels are determined at the specific or at the generic level. Size distribution of trilobites was investigated between localities by measuring the full length of individuals from the anterior margin of the cephalon to the posterior margin of the pygidium. The sizes of representatives of the trilobite genus *Platypeltoides*, which occurs in all localities (Table 1), were measured based on the sagittal length of the pygidium including articulation half ring.

<insert table 1>

The current taxonomy of *Platypeltoides* is uncertain. *Platypeltoides magrebiensis* Rábano, 1990, was the only species of this genus reported from the Fezouata Shale (Rábano, 1990; Martin et al., 2016a). Recently, Corbacho et al. (2018) described four species of *Platypeltoides* from Morocco. The differences between these species are based on genal spine morphologies, the position of the eyes and the presence/absence of an anterior border (Corbacho et al., 2018). There are several issues with the definition of the new species. First, the morphology of the genal spine changes remarkably during ontogeny (Chatterton, 1980; Chatterton & Speyer, 1997; Park & Choi, 2009; Laibl et al., 2015) and differences in the position of eyes can be an effect of taphonomic compression (see Hughes & Rushton, 1990 for detailed explanation). Second, genal spines in Moroccan trilobites are often artificially modified by local collectors (Gutiérrez-Marco & García-Bellido, in press). Most importantly, species other than *P. magrebiensis* are based on the description of a single specimen (*P. hammondi* Corbacho & López-Soriano, 2016; *P. carmenae* Corbacho et al., 2017), or four specimens (*P. cuervoae* Corbacho & López-Soriano, 2012). Consequently, until more material is found and a comprehensive revision of the genus is performed, we consider *P. magrebiensis* as the only valid species and refer all our material to it.

## 4. Results

### 4.a. Trilobite size and preservation

The most diverse trilobite assemblage is found in the intermediate setting locality, Bou Izargane (i.e. 7 taxa; Table 1). Four of these taxa are also found in the more proximal site of



Tamegroute. *Platypeltoides magrebiensis* is the only taxon that is found across the proximal-distal axis (Table 1). The mean total sagittal length of all trilobite taxa recorded in the distal site of Ouled Slimane is 32.4 cm (median = 31.9; standard deviation sd = 1.41; n = 31), which is four times larger than the mean total sagittal length of all trilobites recorded in Bou Izargane (mean = 7.37 cm; median = 5.9 ; sd = 1.21; n = 14), and eight times larger than the mean total sagittal length of all trilobites recorded in Tamegroute (mean = 3.78 cm; median = 3.7 ; sd = 1.24; n = 15) (Fig. 2a; and Tab. 1 in supplementary material for detailed measurements). Total sagittal lengths of trilobite forming the assemblages in Ouled Slimane, Bou Izargane, and Tamegroute are statistically normally distributed (Shapiro-Wilk test,  $p$ -value= 0.97,  $p$ -value =0.23,  $p$ -value =0.4 respectively). Trilobite size variations between two contiguous localities (i.e. Ouled Slimane and Bou Izargane, Bou Izargane and Tamegroute) are significantly different (t-test,  $p$ -value =  $3.85 \cdot 10^{-14}$ ,  $p$ -value = 0.006 respectively; cf. Tab. 4 in supplementary material). The increase in size between proximal and distal sites is not only evidenced between assemblages but also between different species belonging to the same group (e.g. *Asaphellus* belonging to asaphids, and both *Platypeltoides* and *Symphysururs* belonging to nileids; Table 1).

The mean pygidial sagittal length including axial half ring of *Platypeltoides* in Ouled Slimane is 6.3 cm (median = 6.2; sd = 0.5; n = 9), which is twice longer than the mean pygidial sagittal length recorded in Bou Izargane (mean = 3.3 cm; median = 3.5 ; sd = 0.84; n = 5), and four times larger than the mean mean pygidial sagittal length recorded in Tamegroute (mean = 1.29 cm; median = 1.32 ; sd = 0.35; n = 5) (Fig. 2b, see supplementary material for detailed measurements). Pygidial sagittal length measurements for *Platypeltoides* are normally distributed in Ouled Slimane, Bou Izargane, and Tamegroute (Shapiro-Wilk test,  $p$ -value= 0.39,  $p$ -value =0.76,  $p$ -value =0.19 respectively; cf. Tab. 7 in supplementary material). Pygidial sagittal length variations for *Platypeltoides* between Ouled Slimane and Bou Izargane, in addition to those between Bou Izargane and Tamegroute are statistically significantly different (t-test,  $p$ -value = 0.0012,  $p$ -value =  $3.5 \cdot 10^{-6}$  respectively).

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Trilobites from Ouled Slimane are preserved in silicified, quartz-rich concretions. Some are disarticulated and other are complete (Fig. 3a–e). Trilobites from the two other localities are preserved in shales (Fig. 3f–h).

<insert figure 3>

#### 4.b. Sedimentological context

The background sediments of both cores from Bou Izargane and Tamegroute in the Fezouata Shale consist of very fine siltstones to claystones (Fig. 4a–d). In Bou Izargane, coarse siltstone event deposits are abundant (Fig. 4e). Event deposits have an erosive base and show occasionally HCS (Fig. 4e). In Ouled Slimane, event deposits are rare and consist of quartz silts that are finer than in Bou Izargane (generally < 40  $\mu$ m) (Fig. 4a). When they occur, they do not exceed 1 cm in thickness and lack HCS (Fig. 4a). Bioturbation occurs in all cores but it shows variations in both depth and intensity. Some intervals are only lightly bioturbated with a bioturbation depth of around 1 mm, while others are highly bioturbated with a bioturbation depth of few centimeters (Fig. 4f). Intensity of bioturbation varies from light (less than 10% of sedimentary rocks showing evidence of biological activity) to moderate (between 10 and 30% of sedimentary rocks showing evidence of biological activity), high (between 30 and 70% of sedimentary rocks affected by biological activity), and extreme (over 70% of sedimentary rocks reworked by biological activity). The used scale for the studied cores is simplified after the bioturbation index in Taylor & Goldring, 1993. However, there is no direct correlation between bioturbation depth and intensity. Some intervals can be extremely bioturbated with a bioturbation depth that does not exceed few millimeters (Fig. 4c). Generally, sediments from Ouled Slimane are more extensively bioturbated than in Bou

Izargane in terms of both traces intensity and depth (Fig. 4f). In Bou Izargane, bioturbation is generally less than 1 cm in depth (Fig. 4f).

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## 5. Interpretation and discussion

### 5.a. Depositional environment and preservation

In marine settings, grain sizes are indicative of the distance from the source traveled by sediments (Nichols, 2009). In the Fezouata Shale, coarse grains are found towards the south east, closer to the source, when compared to finer sediments that are mainly deposited in the basin (Vaucher et al., 2016, 2017). Furthermore, the abundance of storm events is indicative of the energy of the depositional environment (Nichols, 2009; Perillo et al., 2014). Stacked storm events designate a shallow unstable environment that is constantly agitated by waves (Nichols, 2009). In these agitated settings, waves generate orbitals in the water column that decrease in size with depth leaving oscillation traces such as HCS on the sea floor (Vaucher et al., 2016, 2017). The deeper the water column is, the smaller these HCS are. Thus, the presence in the Fezouata Shale of very fine siltstones to claystones with a scarce presence of storm events and an absence of HCS, all indicate that the sedimentary succession at Ouled Slimane was deposited relatively far from the source, in a stable environment that was rarely agitated by storm waves. In the Fezouata Shale, Ouled Slimane is the most distal locality. Despite being distal in position, an abundant bioturbation (i.e. light, high, and extreme) with variable depth (from a few millimeters to 4 cm) and a high diversity of trace fossils are observed in the sedimentary succession in Ouled Slimane. This validates that this environment was colonized by benthic organisms and shows that little to no chemical stress (i.e. related to nutrients and oxygen availability) occurred in the bottom of the water column but also, at least, in surface sediments.

In the Fezouata Shale, two modes of preservation have been evidenced. The first one, consisting of the preservation of both mineralized and soft bodied taxa in shales, is well understood (Martin et al., 2016b; Saleh et al., 2019). Living organisms of the Fezouata Biota colonized the sea floor and were repeatedly buried *in situ* by event deposits (Vaucher et al., 2017). The second mode consists of preservation in concretions, and the processes underlying it are more complex (McCoy et al., 2015a,b). Siliceous concretions similar to the ones preserving large trilobites at Ouled Slimane have been described from distal settings of the Fezouata Shale by Vaucher et al. (2017) and Gaines et al., (2012). The original siliceous material for the formation of these concretions comes from more proximal localities (Vaucher et al., 2017). However, the growth of these concretions was controlled by the decay rates of dead animals covered by event deposits (Gaines et al., 2012). When a large carcass is decaying, permissive anoxic conditions are established leading to mineral overgrowth around decaying carcasses (Gaines et al., 2012). This model was used to explain the preservation of giant and complete invertebrates *in situ* in the Fezouata Shale (i.e. radiodonts such as *Aegirocassis*; Gaines et al., 2012; Van Roy and Briggs, 2011; Van Roy et al., 2015b). The presence of partially articulated and complete large trilobites in the concretions from Ouled Slimane argue, in a similar way to *Aegirocassis*, in favor to an autochthonous preservation. If transport occurred, it was most likely limited and from the same distal setting (i.e. few meters only).

### 5.b. Body-size fluctuations

Many trilobite genera included in this study have been also discovered from other high latitude (peri)Gondwanan localities. For instance, the Třenice and Mílina formations (late Tremadocian; Czech Republic) have yielded a large number of trilobites comparable in size to those found in Tamegroute and Bou Izargane (i.e. total sagittal length of *Anacheirurus* ~ 3.5cm; *Euloma* ~ 2.5cm; *Platypeltoides* ~ 5.5cm; *Geragnostus* ~ 0.6cm; see e.g. Mergl, 2006). Other assemblages of similarly sized trilobites are known in the late Tremadocian

Saint-Chinian Formation, France (i.e. total sagittal length of *Euloma* ~ 3.3cm, *Geragnostus* ~ 1.1cm ; *Megistaspis* ~ 3.9cm ; *Symphysurus* ~ 3.4cm; Thoral, 1935; Capéra et al., 1975, 1978; Courtessole & Pillet, 1975; Courtessole et al., 1981). *Euloma* was also found in the late Tremadocian Vogtendorf Formation of Germany with a total sagittal length of size ~ 5.5cm (Sdzuy et al., 2001).

Although rare in the fossil record, occurrences of large trilobites are not restricted to the lower part of the Fezouata Shale. Other known occurrences include e.g. the Cambrian Series 2 Emu Bay Shale, Australia (Holmes et al., 2020), the Cambrian Series 2 to Miaolingian Jbel Wawrmast Formation of Morocco (Geyer, 1993), the Early Ordovician ‘Schistes à Gâteaux’ Formation, France (Thoral, 1946; Bérard, 1986), the Middle Ordovician Valongo Formation, Portugal (Rábano, 1990; Gutiérrez-Marco et al., 2009), the Late Ordovician Churchill River Group, Canada (Rudkin et al., 2003), and the Middle Devonian Onondaga Limestone, NY USA (Whiteley et al., 2002). In general, the largest trilobites occur in a wide array of environments. Some of them were reported from low latitude nearly equatorial areas, in shallow-water carbonates (Whiteley et al., 2002; Rudkin et al., 2003) or deeper, but still nearshore siliciclastic deposits (Paterson et al., 2016). Others come from high latitudes (over 60°S) of the West Gondwana margin, where they are preserved either in distal mudstones (Gutiérrez-Marco et al., 2009), fine grained sandstones and shales (Geyer, 1993), and concretions (Thoral, 1946; Bérard, 1986). The best analog for the Ouled Slimane assemblage is thus probably the Early Ordovician fauna described in the ‘Schistes à Gâteaux’ of the Cabrières area (eastern-most part of the southern Montagne Noire; Berard, 1986). In this region, similarly sized concretions (70 to 100 cm in diameter) formed under comparable depositional settings yielded abundant remains of both disarticulated and fully articulated large trilobites belonging to Asaphidae and Nileidae (Bérard, 1986). During the Early Ordovician, the Montagne Noire area was situated at relatively high latitudes, not far away from the Anti-Atlas area, on the western margin of Gondwana. In general, high latitudes, and consequently low temperatures are often considered as the main explanatory factor for trilobite gigantism (Gutiérrez-Marco et al., 2009; Klug et al., 2015). Given the widespread distribution of large trilobites in various latitudes and facies, it is unlikely that there is only one single controlling mechanism of trends toward larger sizes. Indeed, the trilobite size fluctuations within the Fezouata Shale in a comparatively restricted area suggest, that despite high latitudes, other factors must be taken into consideration.

In the Fezouata Shale, differences in size distribution between localities can be the result of numerous mechanisms and conditions (ontogeny, size sorting due to transport, oxygenation, nutrient availability; Saleh et al., 2018). Transport-induced size sorting is unlikely to explain size discrepancies of trilobites in general and *Platypeltoides* in particular. When current-related sorting happens in marine environments, small individuals are more easily transported than large ones, and they are consistently displaced towards more distal settings (Johnson, 1960; Fagerstrom, 1964). The opposite pattern for trilobites is observed in the Fezouata Shale. Furthermore, all previous surveys made on brachiopods, bivalves, echinoderms, and trilobites from this part of the Fezouata Shale have concluded that most fossils were preserved *in situ* (with occasional limited transport), because delicate anatomical structures were preserved (Saleh et al., 2018 and references therein). Brachiopods of the Fezouata Shale have frequently their setae preserved (Saleh et al., 2018) and in many cases, the most fragile skeletal elements of stylophoran echinoderms remained connected to the rest of the body (Martin et al. 2015; Lefebvre et al., 2016, 2019). As trilobites had a chitinous, partially biomineralized exoskeleton (Teigler & Towe, 1975), their remains are frequently preserved in marine Paleozoic deposits (Speyer & Brett, 1986). Given that post-mortem processes are insufficient to explain the size distribution seen in the Fezouata Shale (this study; Saleh et al., 2018), the presence of large trilobites in only the most distal paleoenvironments is taken as representing

the original size distribution of organisms. The increase in trilobite size from shallow proximal to deep distal localities in the Fezouata Shale is consistent with observations of crustacean body size fluctuations in modern marine environments, in which large animals are found in deep-water settings (Horikoshi, 1986; Timofeev, 2001).

The increase in size between proximal and distal localities may be related to ontogeny (e.g. Laibl et al., 2014), with younger -and therefore smaller- developmental stages favoring shallower environments, and older and larger ones preferring deeper settings. If this was the case, all taxa should be found in all localities, which is not true for the Fezouata Shale. For instance, Ouled Slimane seems to entirely lack small and medium-sized taxa (e.g. *Bavarilla*, *Anacheirurus*, *Euloma*), with the exception of *Platypeltoides magrebiensis* (Tab. 1). *Dikelokephalina* and *Ogyginus* are present in Ouled Slimane, but are absent in more proximal sites (Tab. 1). Ontogeny alone does not explain size discrepancies observed for *Platypeltoides magrebiensis*, because the material measured here consistently excluded juvenile stages (defined by the number of thoracic segments). Even if future work shows a correlation between changes in habitats and developmental stages of some trilobites, this fails to explain why older and bigger individuals preferred deeper environments. Therefore, there must have been external biotic and abiotic conditions that selected for larger bodies in deeper setting and smaller bodies in more proximal environments.

Oxygen availability is an abiotic parameter that can influence the body-size distribution of marine taxa (Zeuthen, 1953). It is suggested that large sizes are dictated by oxygen availability rather than by temperature in modern polar ecosystems (Chapelle & Peck, 1999). Oxygen concentration correlates with the general trend in marine gigantism during the Paleozoic (Vermeij, 2016), and a direct connection (i.e. in magnitude) between Paleozoic gigantism and atmospheric hyperoxia was also established using a mathematical model based on oxygen transport limitation (Payne et al., 2012). In contrast, benthic individuals tend to have smaller sizes in oxygen minima zones (i.e. Lilliput effect; Twitchett, 2007). However, for instance in Tamegroute, the bottom of the water column was oxic, leading to the development of diverse assemblages on the sea floor (Saleh et al., 2018).

Another abiotic factor that can limit size growth is nutrient availability (Booth et al., 2008). Nutrients are generally more abundant in proximal sites near the source (Rowe et al., 1975; Philippart et al., 2000; Wang et al., 2003). The occurrence of a relatively high and diverse bioturbation in Ouled Slimane (Fig. 4a-d) suggests that nutrients were not a limiting parameter. This interpretation is in accordance with the presence of diverse planktonic microorganism assemblages in the deepest settings of the Fezouata Shale (Nowak et al., 2016).

Storm turbulences generate another abiotic stress in shallow environments (Barry & Dayton, 1991; McAlister & Stancyk, 2005). Storms transport sediments that can cause the suffocation of both sessile and mobile invertebrate taxa in proximal sites (Tabb & Jones, 1962). Storms can also increase the input of fresh water to the sea, with the resulting change in water column salinity causing heavy mortalities (Tabb & Jones, 1962; Barry & Dayton, 1991). Furthermore, although exoskeleton formation in arthropods is mainly constrained by biotic parameters, the major source of calcium used for exoskeleton calcification is exogenous, and comes from from the waters where the organisms live (Luquet, 2012). In seawater, the concentration of calcium is generally very high (Luquet, 2012), but fresh water input during a storm may alter calcium availability for biomineralization in shallow waters, inhibiting marine arthropods from attaining large sizes. However, in the Ordovician, even the shallowest settings from the Fezouata Shale in Morocco were extremely far from the shore (more than 1000 km away; Guiraud et al., 2004). Thus, it is more likely that the impact of storms on living organisms was more related to transport of sediment and obrution events rather than calcium and salinity fluctuations. This sediment-induced stress was evidenced in proximal localities of the

Fezouata Shale, regularly killing sessile epibenthic taxa and thus inhibiting them from attaining large sizes (Saleh et al., 2018). This stress decreased from proximal to distal localities, allowing organisms to attain larger sizes in deeper environments (Saleh et al., 2018). However, mass mortality is not generally the trend for arthropods in storm-dominated modern shallow marine environments, except in the cases of supercritical events (Conner et al., 1989). In regions that are seasonally affected by storms, arthropods are able to migrate to more stable environments (Conner et al., 1989). Pink shrimp individuals are known to leave shallow waters to deeper environments about 60 miles offshore during a hurricane (Tabb & Jones, 1962), and similar shelter-seeking behavior is observed during the storms season in spiny lobsters (Hunt et al., 1994). It is likely that trilobites, similarly to modern vagile arthropods, were able to adapt against physical instabilities and were little affected by storm turbulences. Some of them even showed collective behavior by migrating during storm seasons, in a similar way to extant spiny lobsters (Vannier et al., 2019).

The occurrence of large trilobite individuals in deep waters may also indicate a lack of predators in these settings (Rex, 1976), as heavy predation is known to limit body size (Horikoshi, 1986). Cephalopods, major predators in both Ordovician and modern marine ecosystems (Cherel & Hobson, 2005; Kröger et al., 2009a), are absent in Ouled Slimane, although they are relatively common in more proximal localities of the Fezouata Shale (Kröger & Lefebvre, 2012). Their absence from the distal setting preserved at Ouled Slimane is in good accordance with the observation that their initial Furongian–Early Ordovician diversification was restricted to relatively shallow environments (Kröger et al., 2009b). The lack of predation pressure from cephalopods in distal marine environments in general during the Cambrian to Early Ordovician period may explain the numerous occurrences of large trilobites in distal settings globally during this time interval (e.g. Fezouata Shale, ‘Schistes à Gâteaux’, see also introduction), and the rarity of large trilobites in younger deposits more or less coincides with the paleoecological diversification of cephalopods into deeper settings during the Middle Ordovician (Kröger et al., 2009a). Thus, the environmental conditions of the distal Fezouata Shale setting were characterized by a lack of storms and predators, and an abundance of oxygen and nutrients, all of which are conducive to the local occurrence of large trilobites.

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## Figure captions

Figure 1. (Colour online) General geographical context of the Fezouata Shale. (a) Stratigraphic sequence of the Fezouata Shale with the studied interval. (b) Location of Morocco in the Early Ordovician near the South Pole (modified from Vaucher *et al.*, 2017). (c) Deepening trend in the Fezouata Shale from the SE to the NW (modified from Vaucher *et al.*, 2017), with the study localities Ouled Slimane, Bou Izargane, and Tamegroute indicated. (d) Proximal to distal relative position of the three localities

studied here: Ouled Slimane, Bou Izargane, and Tamegroute.

Figure 2. (Colour online) Trilobite size fluctuations in the Fezouata Shale. (a) General body size patterns, all taxa included, in Ouled Slimane, Bou Izargane, and Tamegroute. (b) Differences in the pygidial sagittal length of *Platypeltoides magrebiensis* between localities.

Figure 3. (Colour online) Trilobites from the Fezouata Shale, Morocco. (a-e) Large trilobites from Ouled Slimane preserved in concretions. (a) External moulds of trilobites non picked up by collectors. (b) Thorax and pygidium of *Platypeltoides magrebiensis*. (c) Incomplete cranidium of *Platypeltoides* sp. (d) Part of the thorax and pygidium of *Dikelocephalina brenchleyi* (e) Pygidium of *Asaphellus stubbsi*. (f) Normal-sized *Symphysurus* sp. from Bou Izargane. (g-h) Normal sized *Platypeltoides magrebiensis* from Bou Izargane (g) and Tamegroute (h) preserved in shales.

Figure 4. (Colour online) Drilled sedimentary rocks from Ouled Slimane and Bou Izargane. (a) Core sediments from Ouled Slimane showing the dominance of background clayey to silty sediments with rare, coarser grain event deposits. Bioturbation intensity variations between intervals at Ouled Slimane from light (a) to high (b) and extreme (c). (d) Bioturbation depth of few centimeters in Ouled Slimane. (e) Core sediments from Bou Izargane are less bioturbated and more affected by storm deposits. (f) Bioturbation intensity and depth along the core in Ouled Slimane and Bou Izargane. All scale bars are 1cm in length.

Table 1. Trilobite diversity, abundances and sizes in the studied localities from the Lower Ordovician of the Fezouata Shale.

Locality	Trilobite	N	Size range (cm)
<b>Tamegroute</b>	<i>Anacheirurus adserai</i> (Vela, & Corbacho, 2007)	2	4-4.8
	<i>Asaphellus</i> sp. aff. <i>jujuanus</i> Harrington, 1937	2	3.7-4.1
	<i>Bavarilla</i> sp.	4	2.2-2.8
	<i>Euloma</i> sp.	2	3.1
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	5	3.3-6.2
<b>Bou Izargane</b>	<i>Asaphellus</i> sp. aff. <i>jujuanus</i> Harrington, 1937	2	3.9-6.2
	<i>Bavarilla</i> sp.	2	3.7-4.1
	<i>Euloma</i> sp.	1	3.8
	<i>Geragnostus</i> sp.	1	0.9
	<i>Megistaspis</i> sp.	1	5.6
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	5	8.5-16.1
	<i>Symphysurus</i> sp.	2	3.9-4.2
<b>Ouled Slimane</b>	<i>Asaphellus stubbsi</i> Fortey, 2009	7	24.1-38
	<i>Dikelokephalina brenchley</i> Fortey, 2010	1	24.2-33.7
	<i>Ogyginus</i> sp.	3	39.2-49.1
	<i>Platypeltoides magrebiensis</i> Rábano, 1990	7	18-23
		4	

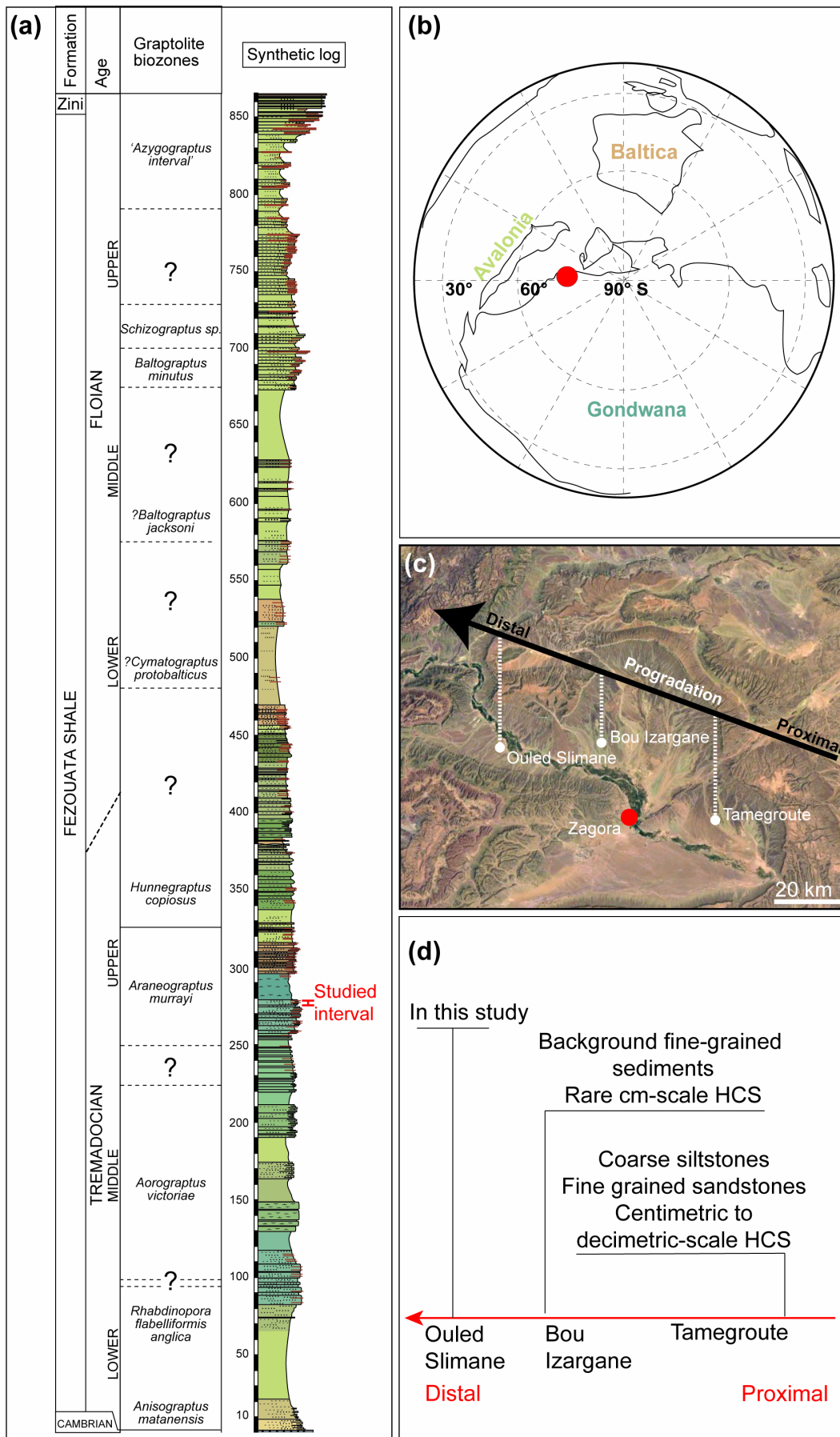


Figure 1

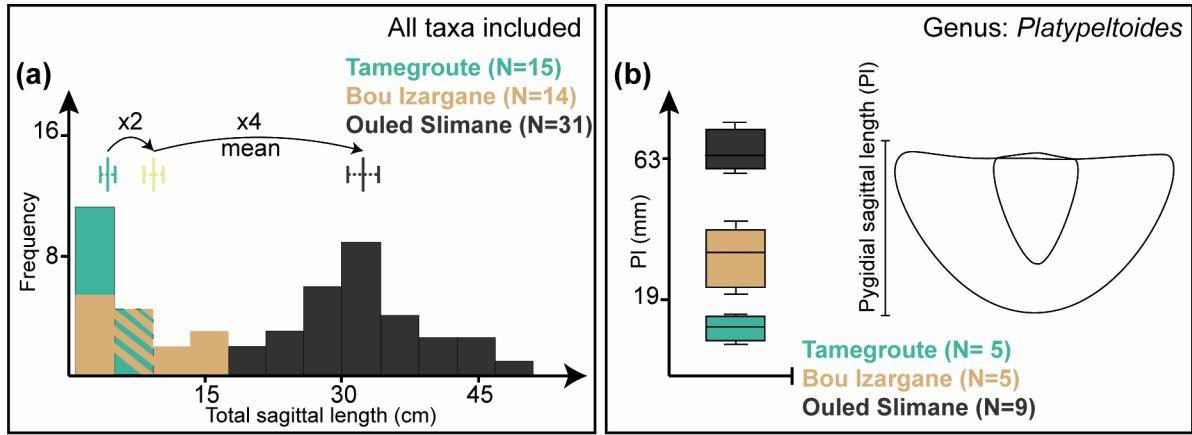
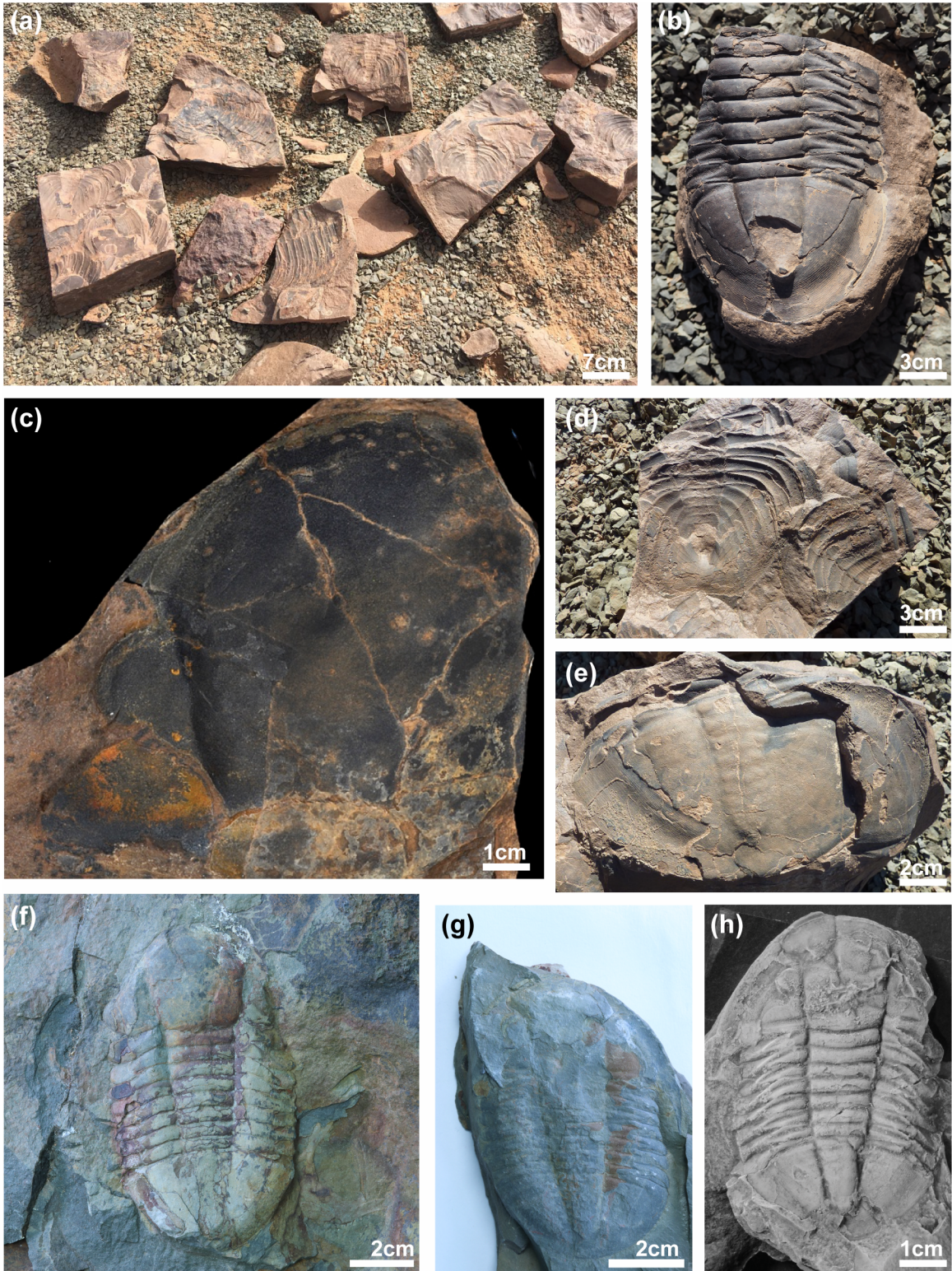


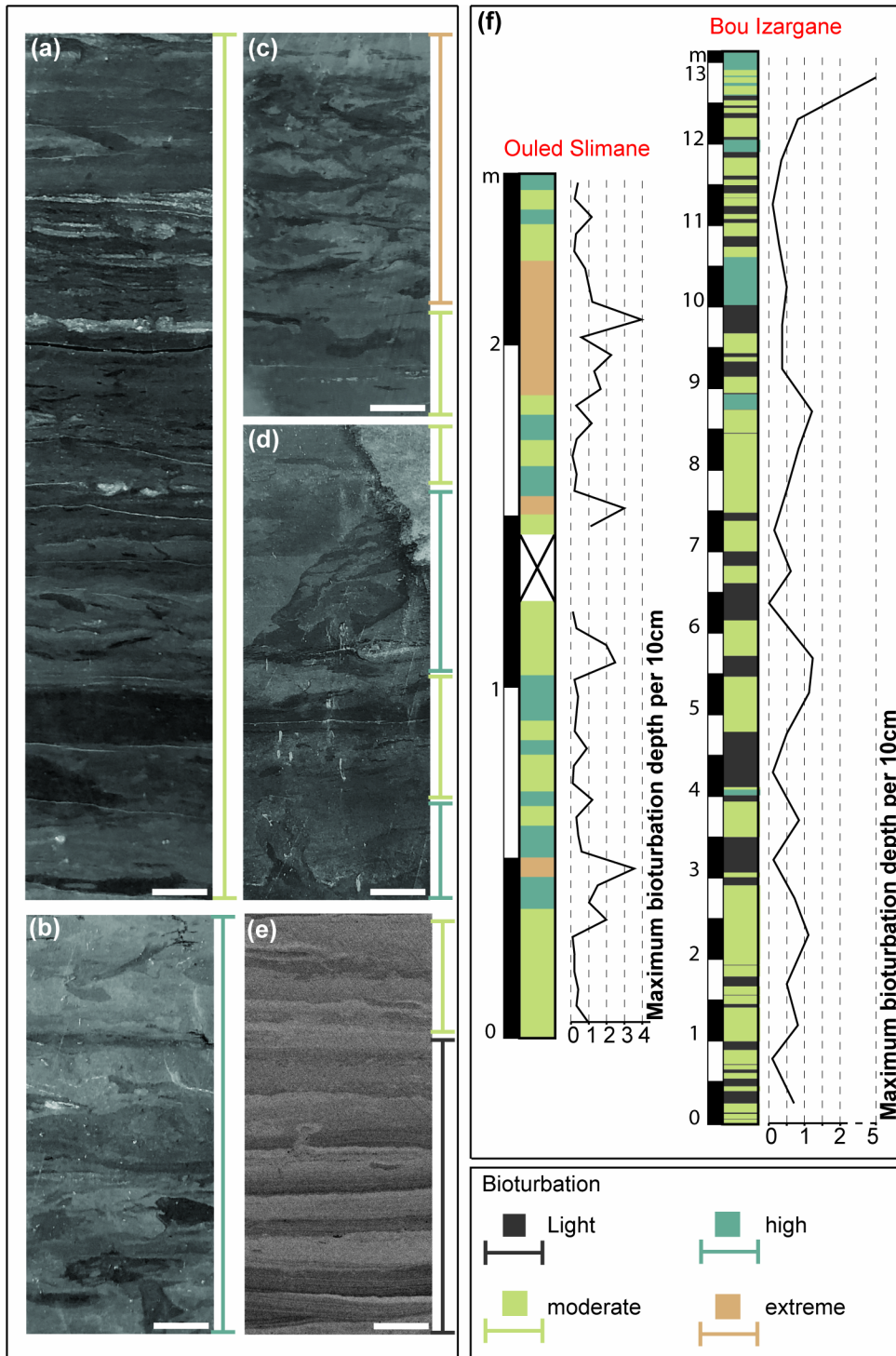
Figure 2





**Figure 3**





**Figure 4**