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# Trilobite biodiversity trends in the Devonian of North Africa

 The corrections made in this section will be reviewed and approved by a journal production editor.

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## Abstract

Taking advantage of the exceptional record of Devonian trilobites in North Africa, a new dataset was compiled in order to reveal their long-term evolutionary history leading to their extinction. This dataset comprises 1171 trilobite occurrences from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals (substage temporal scale), representing 556 species, 179 genera, and 15 families scattered among nine North African basins. The reconstructed palaeobiodiversity trajectories by means of various biodiversity estimators of taxonomic richness are consistent and highlight a progressive and continuous diversification throughout the Early Devonian to reach a maximum of diversity at the end of the Emsian. Most families encountered in North Africa contribute to this increase of diversity. This regional diversification shows the same trends as the global one. Thereafter, the trilobite diversity began to decline due to extinction rates higher than origination rates during the Eifelian (Middle Devonian). From the middle Givetian to the late Frasnian, the trilobite diversity remained low. After this major decline, and the Frasnian events, a faunal change occurred, especially in phacopid and proetid trilobites, which were the only two families crossing the Frasnian/Famennian boundary. Indeed, the Kellwasser Event impacted an already impoverished diversity leading to a major faunal renewal associated with quick taxonomic changes at the genus level. A larger proportion of deeper water and reduced-eye/blind trilobites who acted as opportunists characterized the Famennian recovery. Finally, these palaeobiodiversity trends are compared to those of ammonoids from the same area.

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**Keywords:** Arthropods; Palaeozoic; Morocco; Palaeobiodiversity; Extinction; Macroevolution

## 1 Introduction

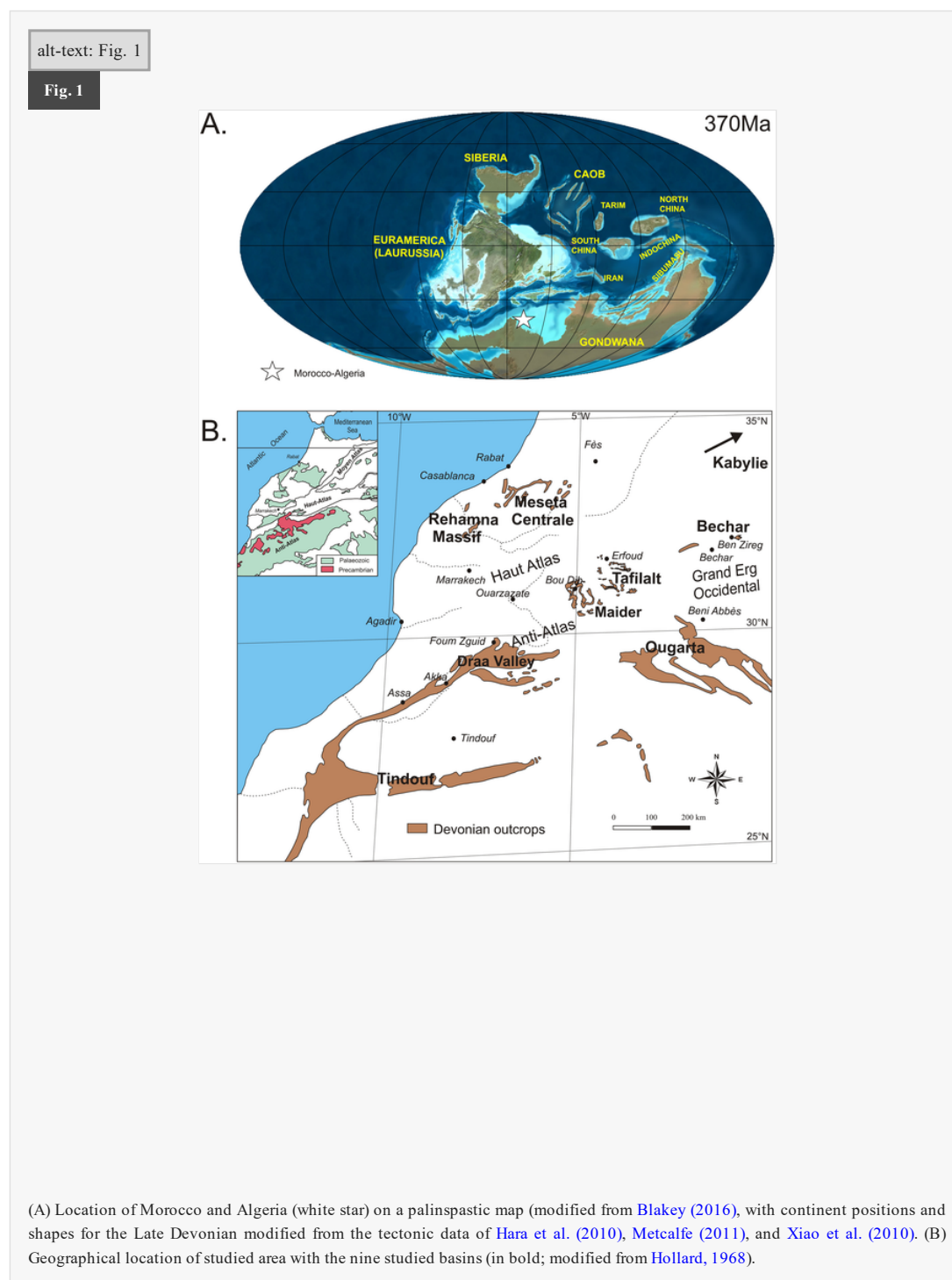
During the Cambrian Explosion, trilobites diversified rapidly at a low taxonomic level to become a dominant macrobenthic fauna thanks to several novelties ([Clarkson, 1975](#); [Clarkson et al., 2006](#); [Hughes, 2007](#); [Esteve et al., 2018](#)), which evolved during the ‘Great Ordovician Biodiversification Event’ (GOBE; [Harper, 2006](#); [Servais et al., 2010](#); [Harper et al., 2015](#)). They invaded both nektic and benthic zones ([Fortey, 1985](#)), shallow and deep waters ([Fortey, 1975](#)) and were present at many different latitudes ([Cocks and Fortey, 1990](#); [Adrain, 2013](#)).

Whereas the diversity of trilobites have been well-studied and documented during the GOBE ([Westrop and Adrain, 1998](#); [Adrain et al., 2004](#); [Adrain, 2013](#)), much less attention has been accorded to their late evolutionary history; a period marked by important environmental changes, i.e., important temperature variations ([Joachimski et al., 2009](#)) and palaeogeographic changes causing volcanism ([Ziegler et al., 1979](#)). Only a few works ([Feist, 1991](#); [Lerosey-Aubril and Feist, 2012](#)) focused on the diversity of Devonian trilobites and on the related events, which led to their decline from the Middle Devonian. [Chlupáč \(1994\)](#) identified general trends in diversity for the Devonian as a whole.

The ‘Devonian Nekton Revolution’ ([Klug et al., 2010](#)) was an important event, which led to another major diversification of trilobites, especially during the Early Devonian. At the beginning of the Devonian, five orders and nearly eighteen families were present worldwide ([Crônier and van Viersen, 2007](#)). They experienced a great diversification during the sea-level rise of the basal Pragian Event ([House, 2002](#)) and the related climate warming ([Vacek, 2011](#)). This sea-level rise probably contributed to the widening of shallow marine carbonate realms favourable for the development of trilobite communities ([Chlupáč, 1994](#); [Crônier and van Viersen, 2007](#); [Khaldi et al., 2016](#)), and led to the maintenance of family-level diversity, which persisted with some minor changes until the early Eifelian. Their

subsequent diversity decreased dramatically and high taxonomic levels disappeared due to a series of biological events (they were strongly affected by the Kacák and Taghanic events in the late Eifelian and the middle Givetian, respectively; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). These biotic events were associated with major rises in sea level and led to more widespread extinctions (Chlupáč, 1994; Crônier and van Viersen, 2007; McKellar and Chatterton, 2009).

Devonian trilobites are especially well represented and diverse in North Africa (Fig. 1). Originally part of a regionally continuous Gondwana passive margin, the North African platform experienced an increase of epeirogenic activity during Devonian times, reflecting the initial collision between Gondwana and Euramerica and the progressive creation of Pangaea (Boote et al., 1998). During this episode, intracratonic basins were created, such as the Tindouf, Maider and Tafilalt basins of Morocco, and the Ougarta Basin of Algeria. In these basins, carbonate production led to carbonate-dominated facies and brought favourable conditions for the settlement and the development of trilobites (McKellar and Chatterton, 2009). Devonian outcrops are mainly composed of limestones with shale intercalations and correspond to a temperate platform environment of the Rheic Ocean. This platform was progressively flooded until the Givetian, which corresponds to the maximal transgression before the latest Devonian regression (Conrad et al., 1986; Hollard, 1967).



In this context, we focused our investigations on biodiversity analyses of trilobite data gathered from this emblematic North African area, i.e., Morocco and Algeria, famous for their exceptional record of Silurian and Devonian trilobites, both qualitatively and quantitatively (Errami et al., 2015; Bonino and Kier, 2010). The aim of this study is to better understand the impact of the biological events occurring through the Devonian on macrobenthic organisms. Although the Silurian and Devonian trilobites from North Africa have been widely documented since the pioneer works of

Richter and Richter (1943), Termier and Termier (1950), Alberti (1964, 1966a, 1966b, 1966c, 1967a, 1967b, 1969, 1970a, 1970b, 1981a, 1981b, 1982, 1983), and the subsequent studies of Morzadec (1997, 2001), Chatterton et al. (2006), McKellar and Chatterton (2009), Gibb and Chatterton (2010), van Viersen and Prescher (2011, 2014), van Viersen and Heising (2015), van Viersen et al. (2017), Johnson and Fortey (2012), Feist and Chatterton (2015), Feist et al. (2016), Khaldi et al. (2016), van Viersen and Holland (2016), Feist and Belka (2018), and Crônier et al. (2013, 2018a, 2018b), among others; but no analysis based on a substantial occurrence database has been performed at a regional scale for this area.

A new dataset of trilobite occurrences is used and modern biodiversity metrics are applied to quantify the biodiversity fluctuations characterizing the evolution of trilobites throughout the Silurian and the Devonian, and to better document the Devonian extinction events in North Africa. Our investigations focus on the representative trilobite-bearing areas of Morocco and Algeria (North Africa) and on the taxonomic component of biodiversity (taxonomic richness, composition, and similarities), at the substage temporal scale. To understand their fluctuations in time and space, their distribution patterns are assessed thanks to diversity curves and by considering the palaeogeographic and palaeoenvironmental context.

## **2.2 Data**

### **2.1.2.1 Occurrences**

To analyse accurately the fluctuations in biodiversity, a dataset has been compiled to list all occurrences of Silurian and Devonian trilobites documented in Morocco, Algeria, Mauritania and Libya from the available literature (Appendix A). Only studies published after 1943 have been included, because the former publications either present an outdated taxonomy in need of revision, and/or a poor temporal resolution. This selection represents 98 publications (Appendix B) which cover the end of the Silurian and the Devonian from North Africa (Fig. Suppl. A). Our dataset contains all identified taxa at the species rank in a revised taxonomy and temporal framework, and is as much representative as possible of the current state of research concerning the knowledge of the Silurian and the Devonian trilobites from North Africa. All in all, this dataset (Appendix A) comprises 4324 trilobite specimens, i.e., 1171 trilobite bed-occurrences in total from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals from the Homerian to the Famennian. Only the highest number of either cephalo/cranidia, pygidia or complete exoskeletons per occurrence was kept to avoid duplicates. This number represents 556 species, 179 genera, and 15 families scattered among nine North African basins (Fig. Suppl. B). For each trilobite bed-occurrence, the dataset also contains the following information: source study (reference), location (locality, basin, country), stratigraphic position at different resolutions (stage and substage; their numerical ages are derived from the ICS International Chronostratigraphic Chart v2016/10; Cohen et al., 2013; updated), abundance, taxonomic information including the classification, taxonomic qualifiers (such as '?', 'cf.' and 'aff.') if relevant for genus and/or species, authorship, and original identification if it has been revised. In order to create a taxonomic framework reflecting the current state of research with as much consistency as possible, we relied on the identification and age-assignment in the original studies or subsequent published revisions and considered the intending synonymies. Without intention to validate or revise the taxonomy, the names used follow the last usage. Throughout our data compilation, genera and species were considered, but only the diversity fluctuations at the generic level are presented and discussed herein. The diversity changes at the specific level are presented in a supplemental figure (Fig. Suppl. F). The stratigraphic intervals or bins used in the database corresponds to the last three Silurian series and to the 18 Devonian substages. The duration of a substage varies from 1.6 Myr (lower and upper Pragian) to 8.6 Myr (lower Emsian) for a total duration of  $68.5 \pm 0.5$  Myr.

### **2.2.2.2 Trilobite vision and palaeoenvironments**

In order to highlight the potential environmental/ecological affinities or morphological adaptation of trilobites, two additional sets of information are recorded in the dataset. First, we considered the visual system of studied trilobites, which can be inferred directly from the eyes preserved as calcite lenses on a visual surface (Clarkson et al., 2006). Each taxon has been assigned to one of the three categories: blind, reduced-eye, or well-developed-eye. The diagnostic features related to the eye size or to the number of lenses were considered to establish these categories.

Second, we considered the marine environment of studied trilobites, for which associations are well-known to reflect relatively precise palaeoenvironmental indicators of different depths across shelves (Fortey, 1975; Speyer and Brett, 1986; Turvey, 2005; Crônier and van Viersen, 2007; Crônier and François, 2014). Four major environments can be recognized along a bathymetric profile: (1) the shoreface environment characterized by shallow, proximal and agitated deposits including trilobites as fragmented exoskeletons in sandstones; (2) the inner shelf environment characterized by mudstones intercalated with sandstones including trilobites as disarticulated and fragmented exoskeletons and/or as coquinas; (3) the middle shelf environment characterized by relatively deep deposits including moderately to highly diverse assemblages with trilobites with well-developed eyes, clumped or dispersed sclerites commonly articulated in mudstones; and (4) the outer shelf environment located below the effective storm wave-base including rare trilobites, as articulated exoskeletons, often blind or with reduced-eyes, in shales. Consequently, according to its depositional

environment and to the observed faunal assemblages, each genus has been assigned to only one of these four categories. Trilobites considered to have habitat specificity are found almost exclusively in their specific environment.

Blind or reduced-eye trilobites often indicate a dark and relatively deep environment, i.e., outer shelf/external platform, near or below the photic zone (Clarkson, 1967; Feist, 1991). By contrast, trilobites with well-developed eyes often indicate a shallow (i.e., inner platform) or a mid-depth (i.e., middle shelf) environment. For example, it has been demonstrated that Late Devonian phacopid trilobites, in the context of a deepening ocean, were subject to such evolutionary changes, i.e., a gradual reduction of the visual complex leading to blindness (Crônier and Courville, 2003; Crônier et al., 2004, 2011; Crônier and François, 2014). Only, the state of preservation and/or the nature of sediments and the associated fauna allow us to determine roughly the palaeoenvironmental/palaeoecological position along a bathymetric profile.

### **3.3 Methods (biodiversity metrics)**

The estimation of palaeobiodiversity and its variation through geological time is a major issue in macroevolution. Major biases (rock/fossil preservation, facies/ecology, sampling, ...) affect taxonomic richness reconstruction (Foote, 2000; Smith, 2001). For Morocco in particular, the biases concern also the issues due to the trade of valuable trilobites. Throughout the past decades, some beds that yield complete, articulated and well-preserved trilobites have often been the focus of investigations (e.g. Chatterton et al., 2006; van Viersen and Holland, 2016; among others). Even if major biases exist, the last decades have seen substantial progress in the knowledge of the Phanerozoic biodiversity (Sepkoski Jr. et al., 1981; Benton, 1993; Alroy et al., 2008; Fan et al., 2020), notably thanks to the use of resampling methods (Alroy, 2010a; Chao et al., 2012, 2014; Close et al., 2018).

Palaeobiodiversity can be measured in different ways and for any taxonomic rank. To produce reliable biodiversity trajectories through time close to the true diversity of coexisting taxa at a given time (i.e., 'standing diversity', Cooper, 2004), taxonomic approaches based on the count of distinct names for a given taxonomic rank (species, genera, families) and known as 'taxonomic richness' indices were used. Taxonomic richness indices were calculated by computing traditional incidence-based binning approaches, as well as modern occurrence-based resampling methods.

Classical binning approaches estimate taxonomic richness according to different biostratigraphic categories (e.g., single-interval, ranging through, originating, and disappearing; see Foote, 2000) based on the synthetic incidence (i.e., binary presence) range of the taxa considered in a moving "window" covering three time bins (for additional details and discussion, see Foote, 2000; Alroy, 2010b; Nowak et al., 2015): the sampled-in-bin diversity (SIB), which is the raw count of actually documented taxa; the range-through diversity (RT), which includes or excludes single-interval taxa, but interpolates discontinuous taxon ranges; the normalized diversity (NORM), which weights differently the various biostratigraphic categories; the boundary-crosser diversity (BC), which focuses at the chronostratigraphic limits and not within these time bins; and the single-interval diversity (SGL). All these traditional metrics can be biased by various effects such as heterogeneous sampling, but they are still useful in highlighting peculiarities in the dataset. Cooper (2004) evaluated the normalized diversity as a good approximation of the mean standing diversity. Additionally, the recent stochastic uniform-time-bin diversity (UTB) of Gibert and Escarguel (2017) has been applied: this approach is a back-transformation into a virtually continuous-time averaged time series of the time-discretized dataset constructed from the fossil record; the period of time under study was split into 2 Myr time bins, and each specimen was assigned multiple times at random to one of the bins between its maximum and minimum age brackets. This method has been shown to provide more accurate estimates of standing diversity than binning approaches, even when the origination and extinction are biased towards coinciding with the boundaries of bins (Gibert and Escarguel, 2017). Finally, origination and extinction rates are calculated based on range-through diversity excluding single-interval taxa. More precise and accurate methods of calculating origination/extinction rates such as the gap fillers method (Alroy, 2014, 2015) cannot be applied to our dataset because of the high proportion of taxa documented in less than four time intervals.

Although taxonomic richness is an intuitive measure of biodiversity, it is an elusive quantity to measure properly, because as more individuals are sampled, more species will be recorded (the so-called sampling intensity/effort problem) (Simpson, 1949; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001; Chao et al., 2014). Therefore, because the robustness of estimated curves of taxonomic richness depend on sample size, modern biodiversity metrics based on the resampling of abundance and/or collection data were also performed in this study: size-based rarefaction (CR) and coverage-based rarefaction (SQS), which are two interpolation methods, and richness estimated using a Poisson sampling model (TRiPS), which is an extrapolation approach (see Close et al., 2018). First, the conventional size-based rarefaction estimates taxonomic richness by repeated random down-sampling of data to a user-defined sample size (Sanders, 1968; Hurlbert, 1971; Foote, 1992; Shimadzu, 2018) to enable comparison of the time intervals considered at equal sampling effort. Second, the coverage-based rarefaction (shareholder quorum subsampling, SQS; Alroy, 2010a-b, Alroy, 2013) repeatedly randomly draws taxa from compiled in-bin occurrence lists, until a summed proportion of these taxa relative occurrence frequency reaches a certain 'quorum' to finally sum the taxa sampled. Coverage, as a measure of sampling quality, is defined as the proportion of the frequency distribution of taxa within a sample. In this study, diversity was estimated at various levels of coverage at intervals of 0.1 and by including dominant and single-interval taxa. Coverage-based rarefaction has been shown by both simulation studies and empirical data to

be a robust method of correcting for preservation and sampling heterogeneity (Alroy, 2010a-b; Chao and Jost, 2012; Close et al., 2018). Finally, TRiPS (Starrfelt and Liow, 2016) aims to estimate true richness by modelling per-interval sampling rates (inferred by maximum likelihood using observed taxon occurrence frequencies and interval durations) for extinct lineages as a homogeneous Poisson process.

Additional insights on the biodiversity of the Devonian trilobite fauna from North Africa were completed by investigating their evenness component (Smith and Wilson, 1996; Tuomisto, 2012; Kvålseth, 2015). Taxonomic evenness ('equitability') refers to how equal in numbers (relative abundance) each taxon in a (space/time) bin is, and is typically derived by rescaling a diversity measure to the interval from 0 to 1. Two measures of evenness are here computed: the Simpson index of dominance (D; Simpson, 1949) and the Pielou's equitability (E; Pielou, 1966) derived from the Shannon–Wiener index (Shannon and Weaver, 1949). Low values of dominance indicate taxa rather evenly represented, and conversely the index will be close to 1 if there is a single very dominant taxon. Inversely, values of equitability close to 0 reflect an overabundant taxon, while high values indicate almost equally distributed taxa.

In this work, the various biodiversity indices and methods were computed with the scientific environment R (version 3.5.2; R Core Team, 2019) using the package 'epaleo' (version 0.8.27; Monnet C., unpublished, University of Lille; for applications using this package, see e.g., Tétard et al., 2017; Shen et al., 2020), and with the software PAST (version 3.24; Hammer et al., 2001).

## 4.4 Results

### 4.1:4.1 Genus richness

The reconstructed biodiversity curves of the trilobite genera from North Africa during the Silurian and the Devonian substages are illustrated in Fig. 2 and Suppl. C and D, for both raw binning and collection resampling methods. As indicated by the various biodiversity estimates and notably the coverage-based rarefaction (SQS), the generic richness shows important fluctuations during the Silurian and the Devonian in North Africa (Fig. 2). The local diversity was characterised by low to moderate values from the Ludlow to the Lochkovian, followed by peaks of highest diversity in the second part of the Early Devonian and at the beginning of the Middle Devonian, i.e., from the Pragian to the Eifelian. This period constituted a plateau of high diversity. During this period, the diversity still fluctuated with a decrease of diversity in the early Emsian before the major peak at the late Emsian. After this high diversity period, the generic richness strongly decreased until the middle Givetian and stayed low until the late Frasnian. After a small diversification phase observed at the end of the Frasnian, there was a moderate decrease of diversity in the early Famennian, then, another small diversification phase occurred in the late Famennian (Fig. 2). However, the Late Devonian diversity remained low compared to the Early Devonian plateau.

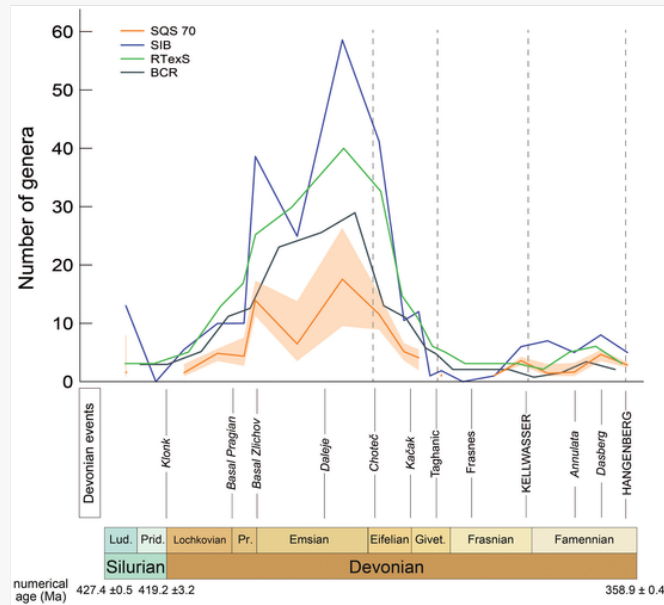
The taxonomic richness evaluated by the boundary-crosser diversity (BC) shows similar trends to the SQS, such as the initial protracted increase of diversity from the Ludlow to the early Eifelian (Fig. 2). The major difference is the absence of a diversity decrease in the early Emsian. Next, a huge decrease took place and the diversity reached low values during the middle Givetian, and stayed relatively low until the end of the Famennian. The range-through diversity excluding single-interval taxa (RTexS) shows as the boundary crosser diversity, a continuous Early Devonian diversification from the Lochkovian to the Emsian (Fig. 2). This period is followed by a relatively regular decrease of the diversity until the early Famennian. No increase was spotted in the late Frasnian contrary to the SQS method. Then, an increase happened in the middle and late Famennian as shown by the SQS curve. The sampled-in-bin diversity (SIB) and the uniform-time-bin diversity (UTB) show the same trends as the SQS diversity (Figs. 2, Suppl. C and D). This method also suggests a slight increase of the generic richness throughout the Frasnian. Most discrepancies observed between these various biodiversity estimates were due to episodic increases of single-interval taxa (e.g., late Pragian, late Emsian, late Frasnian and early Famennian; Fig. Suppl. D) or to increases of virtual ranges (e.g., early Emsian), depending on the importance given to these parameters by each index.

The size-based rarefaction (CR, Fig. Suppl. E2) analysis shows that some substages are under-sampled and require a higher number of individuals to achieve robust diversity estimates. Therefore, additional studies and fieldworks are required to complete the knowledge of trilobites especially for the early Lochkovian, the Givetian and the Frasnian. Nevertheless, the size-based rarefaction analysis confirms the trends observed with the other indices: a high diversity from the late Pragian to the late Emsian followed by a decrease during the Eifelian.

### 4.2:4.2 Origination and extinction

With regard to taxonomic changes, i.e., extinctions ( $E_{RT}$ ) and originations ( $O_{RT}$ ) (Fig. 3), the observed evolutionary pattern shows a global increase of the number of originations with moderately high values from the late Lochkovian to the late Emsian, interrupted by two major decreases occurring during the early Pragian and the early Emsian. Then, the number of originations decreased drastically during the Eifelian and the early Givetian. Thereafter, a small peak of originations occurred during the early and the middle Famennian (Fig. 3).

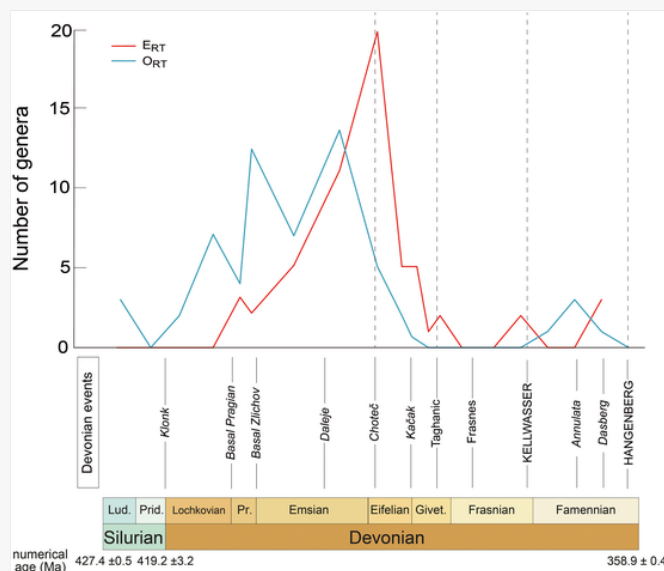
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Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Shareholder Quorum Subsampling (SQS) diversity, estimation for a quorum of 70; Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Range-through diversity excluding single-interval taxa (RTextS), which estimates diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Boundary-Crosser diversity (BC), count of all taxa present in two successive intervals. Stratigraphic position of the extinction events according to [Becker et al. \(2016b\)](#); first-order events in capital, second-order events in bold and third-order events in italic. Ages from [Cohen et al. \(2013, updated\)](#).

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Fluctuations of the number of extinctions ( $E_{RT}$ ) and originations ( $O_{RT}$ ) of trilobites from North Africa during the Silurian and the Devonian, at the generic level. Stratigraphic position of the extinction events according to [Becker et al. \(2016b\)](#); first-order events in capital, second-order events in bold and third-order events in italic. Ages from [Cohen et al. \(2013, updated\)](#).

Concerning extinctions, the evolutionary pattern shows a major increase during the Early Devonian, with a maximum reached in the early Eifelian. This peak of extinction followed the high origination period observed during the Early

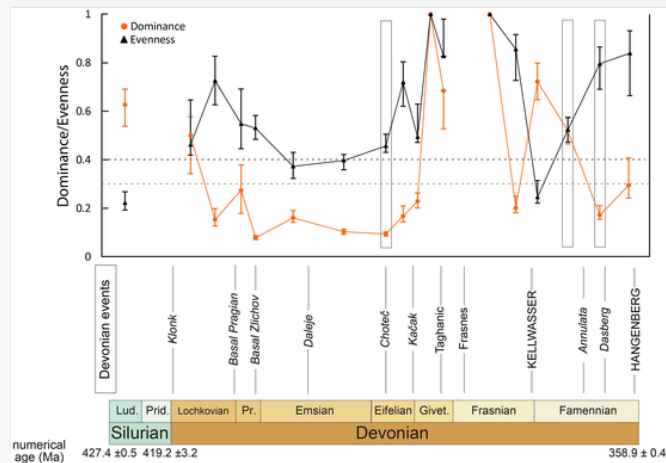
Devonian. During the Middle and Late Devonian, four other moderate extinction peaks occurred (early and late Givetian, late Frasnian and late Famennian; Fig. 3).

#### 4.3.4.3 Evenness and dominance

In North Africa, the dominance was generally low (less than 0.3) during the Early and Middle Devonian (Fig. 4). Only the Ludlow, the early Lochkovian and the late Givetian were characterized by a dominance above 0.4, and the middle Givetian was characterized by a dominant taxon ( $D = 1$ ) in a very depauperate assemblage (Fig. 4). Throughout this period, a relatively high evenness (more than 0.4) is recorded except for the Emsian. The transition from the late Frasnian to the late Famennian was characterized by a sharp decrease of evenness (from 0.82 to 0.23) and a distinct increase of dominance (from 0.23 to 0.72). After these important changes, the evenness increased gradually during the Famennian to reach high values, and conversely, the dominance decreased until the late Famennian before a slight increase at the end of the Devonian.

alt-text: Fig. 4

Fig. 4



Variations of two diversity indices (dominance and evenness) during the Silurian and the Devonian, computed for the trilobites from North Africa at the generic level. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

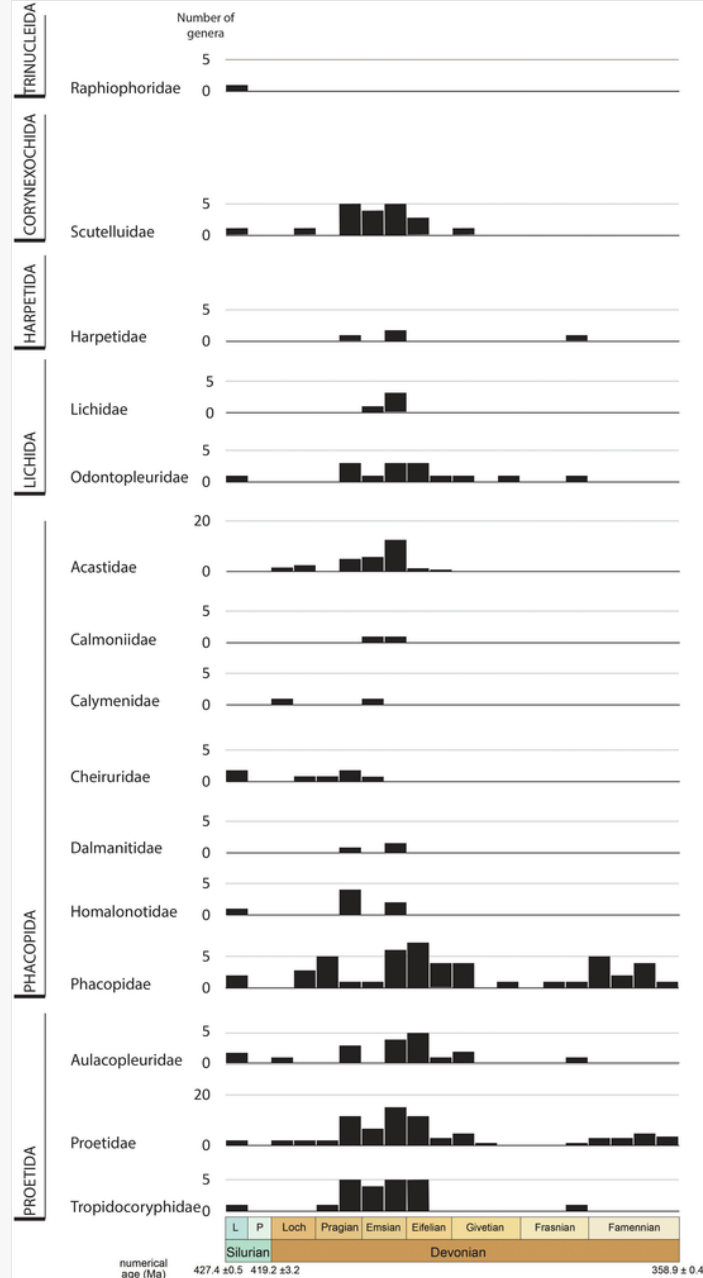
#### 4.4.4.4 Richness per family

Six orders of trilobites (Trinucleida, Lichida, Harpetida, Corynexochida, Proetida, Phacopida) are documented in North Africa from the Ludlow to the latest Famennian (Fig. 5). Trinucleida (see Bignon et al., 2020) did not reach the Devonian, Corynexochida disappeared in the Middle Devonian, and Lichida and Harpetida did not cross the Frasnian/Famennian Boundary. Only Proetida and Phacopida were present until the Famennian.

alt-text: Fig. 5

Fig. 5





Number of genera for each trilobite family during the Silurian and the Devonian in North Africa. Families are ordered by order. Ages from Cohen et al. (2013, updated).

Sixteen families are documented in North Africa during the studied period (Fig. 5). The Raphiophoridae (Trinucleida) were only present during the end of the Silurian. Among Phacopida, Calmoniidae, Calymenidae, Cheiruridae, Dalmanitidae and Homalonotidae did not cross the Early Devonian. During the maximum diversity period characterizing the late Emsian, 12 families coexisted in North Africa. After the major decrease of the diversity observed during the Eifelian, the middle Givetian records the presence of only one family (Proetidae). In comparison to the Emsian and Eifelian stages, the Frasnian is relatively poor in both phacopids and proetids. The odontopleurids and the harpetids were present until the late Frasnian, where they are both represented by only one genus. Then, only two

families managed to survive the Kellwasser Crisis, proetids and phacopids, which experienced a new diversification in the Famennian.

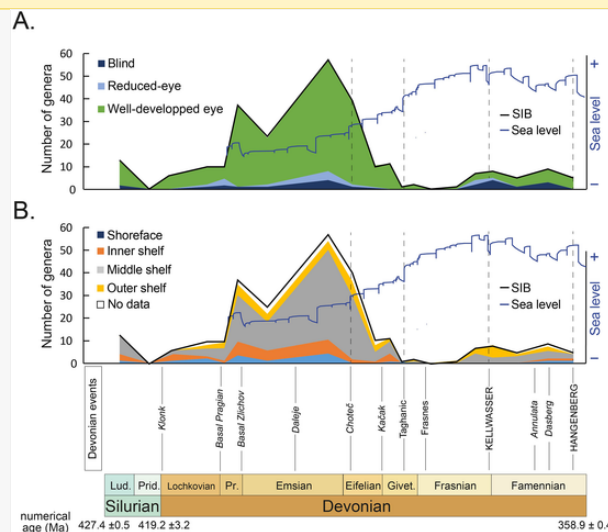
#### 4.5.4.5 Vision of trilobites and palaeoenvironments

The variations of the relative genus diversity according to the visual capabilities (blind, reduced-eye or well-developed-eye taxa) and to the living environment (shoreface, inner shelf, middle shelf, outer shelf) are reported in Fig. 6. Three time intervals were marked by peaks of presence of reduced-eye and blind taxa: the Pragian, the late Emsian and the Famennian (Fig. 6A). Compared to the total taxonomic richness, the early Famennian was characterized by the greatest proportion of reduced-eye or blind taxa. The Pragian showed a relatively substantial number of reduced-eye and blind trilobites. The increase of trilobites with a reduced vision in the late Emsian corresponded to a global and regional diversity peak, whereas the two other peaks of reduced-eye taxa occurred in the Famennian were associated to low diversity values (Fig. 6A).

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Fig. 6

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Fluctuations of the relative genus diversity of trilobites from North Africa during the Silurian and the Devonian, according to (A) three visual capabilities (blind, reduced-eye or well-developed-eye taxa), and (B) four depositional environments, i.e., bathymetric depth (shoreface; upper offshore or inner shelf; median offshore or middle shelf; lower offshore or outer shelf located below effective storm wave-base environments; and not allocated or ubiquitous genera). Each genus is attributed to its main environment even if it could live in other environment. Sea level from Johnson et al. (1985). Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

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Regarding the depositional environments and faunal assemblages, trilobites encountered in shallow environments (shoreface) were present especially during medium to high diversity periods, i.e., during the entire Early Devonian, the early Givetian and the latest Famennian (Fig. 6B). In contrast, the trilobites encountered in deeper environments (outer shelf) were present throughout the Devonian but in higher proportion in the late Frasnian and the Famennian.

## 5.5 Discussion

The palaeobiodiversity trends of the North African trilobites reconstructed using various biodiversity indices are consistent and highlight significant diversity changes throughout the end of the Silurian and the Devonian. In summary (Fig. 2), North African trilobites were characterised by a low diversity, slightly increasing during the Lochkovian. A sharp increase was recorded during the Pragian, leading to a plateau of maximum diversity during the Emsian and the early Eifelian. An abrupt diversity decrease occurred subsequently during the late Eifelian, from which the diversity stayed low until the end of the Devonian, with only small changes observed.

### 5.1.5.1 End of the Silurian and Lochkovian

The comparison of the regional diversity with the global diversity patterns described in the literature shows marked similarities and differences. At the global scale, the trilobite diversity that is characterized by numerous genera that belongs to conservative and long-ranging genera, was documented from the Silurian to the Lochkovian with few changes due to only minor extinctions (Chlupáč, 1994). A decrease of diversity occurred in the Ludlow and the Pridoli in some places (e.g., Prague Basin; Manda and Frýda, 2014) and especially in North Africa. The Lau Event (Jeppsson and Aldridge, 2000) which took place during this interval with faunal changes concerning conodonts and graptolites among others, at the global scale. This event was not clearly identified in North Africa but could be associated to this decrease. No trilobites are found in the shale and black limestone deposits of the eastern Anti-Atlas because of the deep-water conditions, which are not favourable to the development of benthic fauna (Morzadec, 2001). Thus, in North Africa, a low trilobite diversity was documented from the Silurian to the Lochkovian. Only few trilobite taxa dominated these communities as shown by the high dominance index in the Ludlow and the Lochkovian (Fig 4).

### 5.2.5.2 Pragian and Emsian

At a global scale, the major regressive Basal Pragian Event (Chlupáč and Kukul, 1986) contributed to the widening of shallow marine environments with carbonate sedimentation favourable for trilobites, and led to an increase of the genus diversity (Chlupáč, 1994) associated with the proliferation of many benthic species on the continental shelves (Morzadec, 2001). There was a protracted diversification throughout the Early Devonian, with a diversity maximum recorded during the late Emsian. Meanwhile, the long-term gradual transgressive Daleje Event occurring at the beginning of the late Emsian (House, 1985; García-Alcade, 1997; Becker et al., 2018) contributed to the installation of siliciclastic environments and led to strengthening the trilobite diversity increase. As a result of the preceding Daleje Event, offshore trilobites also proliferated worldwide, with numerous blind and reduced-eyes taxa (Chlupáč, 1994). The fauna composed of *Plagiolaria* associated with other small-eyed or blind trilobites (*Piriproetus*, *Leonaspis*) encountered in the Pragian, represents a specialized group of trilobites inhabiting a muddy and rather deep water environment (Chlupáč, 1977, 1983). Hence, the generic richness reached its maximum level (Adrain, 2008).

In North Africa, the Pragian diversification is also documented (Hollard, 1967; Morzadec, 2001; Ouali Mehadji et al., 2011). However, whereas the peak of diversity was recorded in the early Pragian at the global scale (Chlupáč, 1994), the African regional diversity showed a peak rather in the late Pragian. This difference can be explained by the fact that most studies concerning Pragian trilobites from North Africa lack enough chronostratigraphic resolution to be included in our analysis. However, our study is the only one with a substage chronostratigraphic resolution, contrary to previous ones with a stage chronostratigraphic resolution. The increase of diversity is not explained by the proliferation of a few genera but corresponds to a general trend: the diversification (Fig. 6) is also observed at the family level (Fig. 5). The majority of Pragian genera persisted through the Emsian, both in North Africa (Fig. 2, see BC curve) and at the global scale, therefore, contributing to the richest interval, i.e., the Emsian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012).

A decrease of diversity occurred in the early Emsian. However, the poor preservation of trilobites with no commercial opportunities limits their sampling and their subsequent analyses despite the notified presence of dalmanitids (odontochilines) for instance in the Draa valley (Becker et al., 2004). After this decrease of diversity, the transgressive Daleje Event led to an increase of the abundance of trilobites encountered in deeper environments in North Africa (Fig 6). Blind and reduced-eye trilobite genera were better adapted to live in this environment and become more numerous in the late Emsian (Fig 6). Additionally, trilobite taxa from shallow siliciclastic environments such as asteropygins were also well diversified in Morocco (Morzadec, 2001). All these diversification phases led to the Devonian peak of diversity recorded in the late Emsian (Fig. 2) in North Africa but also at the global scale (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). The evenness decreased with the Early Devonian diversification to reach a minimum in the late Emsian, which corresponds to the substage with the highest diversity (Fig 4). This decrease shows that even if no genera dominate the community, some of them took advantage of the environment (e.g., proetids, acastids and phacopids; Fig 5).

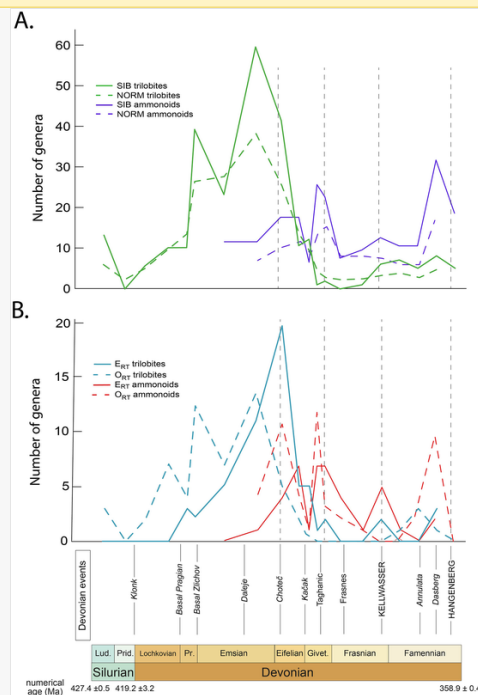
In the context of the progressive colonization of the water column by predators during the 'Devonian Nekton Revolution' (Klug et al., 2010, 2017), potential connections especially with ammonoids can be evaluated. Indeed, the ammonoids which appeared during the early Emsian worldwide, were efficient nektic predators during the Devonian, as the jawed fishes (Klug et al., 2017). A comparison with the ammonoids from Morocco (data from Allaire, 2017, unpublished PhD; the same methods as those used in this study were performed to obtain these data) has been done in order to evaluate differences and similarities between trends. Evolutionary novelties within the trilobites may be a direct

response of the development of passive morphological defences (as spinose skeletons) or active behavioural defences (as infaunal moulting or other cryptic behaviours) against durophagous predators such as nektic ammonoids. During the Devonian, the highly diverse Emsian and Eifelian trilobites from Morocco and from North America show a high frequency of spinose genera in several lineages (Brett and Walker, 2002). Such spinose skeletons may have had a selective advantage against durophagous predators (Brett and Walker, 2002). The ammonoids from Morocco showed a relatively low diversity during the Emsian, while the trilobites were characterized by a very high diversity (Fig. 7A). This trend suggests a nekton-benthos decoupling as proposed by Ebbighausen et al. (2011) for the Draa Valley in Morocco. These low diversity values represent the first step of the Nekton Revolution (Klug et al., 2010) which is underway and has not yet reached its acme. The subsequent increase of the ammonoid diversity (see following section) could be a consequence of the development of benthos such as trilobites in oxic zones.

alt-text: Fig. 7

Fig. 7

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Diversity dynamics of trilobites from North Africa and ammonoids from Morocco during the Silurian and the Devonian, at the generic level. See text for the definition of indices. Data for trilobites: this study; data for ammonoids from Allaire (2017, unpublished PhD). (A) Taxonomic richness: Sampled-in-Bin diversity (SIB) and normalized diversity (NORM). (B) Extinctions (ERT) and Originations (ORT).

Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

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### 5.3.5.3 Eifelian and Givetian

In contrast to the Silurian and Early Devonian, the diversity patterns observed during the Middle Devonian were somewhat different considering regional and global scales. Lerosey-Aubril and Feist (2012) noted a global diversity

loss from the Eifelian to the Frasnian, but without an examination at a substage resolution. Trilobite faunas were rather diverse and locally abundant, and often distributed in geographically restricted biofacies. As underlined by [Lerosey-Aubril and Feist \(2012\)](#), this period was affected repeatedly by environmental disturbances generating large restructuration within marine ecosystems at a global scale ([Walliser, 1996](#)).

Although only a small faunal turnover occurred at the global scale during the Choteč Event ([Barnes et al., 1996](#)), a sharp decrease of the diversity occurred at the regional scale in North Africa in the early Eifelian. Indeed, a transgression occurred in the Western Sahara Platform ([Ouali Mehadji et al., 2004](#)) leading to biotic and abiotic changes. These changes were not favourable for trilobites and led to extinctions such as the genus *Paralejurus*, which disappeared both at the regional and global scales ([Chlupáč, 1994](#)). Additionally, this event strongly affected the Proetida with the regional extinction of some representatives of the Proetidae and Aulacopleuridae. [Morzadec \(2001\)](#) noted that because of the high sea level, trilobites living in shallow environments such as Asteropyginae remained scarce even if, at a global scale, they were able to adapt in deep environments ([Bignon and Crônier, 2015](#)). In North Africa, numerous taxa were impacted by this event; after the crisis, the diversity and the evenness remained relatively low and the dominance index suggests the presence of barely dominant taxa ([Fig. 4](#)).

The Choteč Event, which particularly affected trilobites in North Africa, did not affect all organisms in the same way. Indeed, as pelagic and nektic organisms, the ammonoids were less impacted by this transgressive event than the trilobites. The generic richness of the Moroccan ammonoids showed a progressive increase from the late Emsian to the late Eifelian; no drop down is recorded after the Choteč Event ([Fig. 7A](#); [Allaire, 2017](#), unpublished PhD).

The Kacák and Taghanic events (late Eifelian and middle Givetian, respectively) mark the end of the sharp decrease of the trilobite diversity already underway at all taxonomic ranks, and lead to a stepwise diversity drop ([Chlupáč, 1994](#); [Lerosey-Aubril and Feist, 2012](#)). The major transgressive Taghanic Event initiated in the middle Givetian led to a worldwide development of a deep-sea/pelagic cephalopod environment ([Johnson, 1970](#); [House, 1985](#)) not favourable for trilobites; the disappearance of numerous families is observed (Calmoniidae, Cheiruridae, Lichidae) due to the disappearance of the near-shore neritic and peri-reefal environments. Only, a few taxa survived this worldwide deepening and successfully adapted to deeper and more homogeneous environmental conditions which characterise the late Givetian. The surviving faunas exhibited a pronounced reduction in generic and specific diversity concomitant with an increasing cosmopolitanism ([Lerosey-Aubril and Feist, 2012](#)).

At the regional scale, the Kacák Event was underlined by an increasing number of extinctions in trilobites. As the Choteč Event, the Kacák Event corresponds to a global eustatic rise combined to oxygenated-depleted conditions in benthic environments ([Lerosey-Aubril and Feist, 2012](#)) not favourable to trilobites ([Fig. 6A](#)). This deepening ([House, 1985](#)) affected the North African faunas ([Beřka et al., 1999](#)). The low trilobite diversity recorded after the Kacák Event corresponds to assemblages dominated by one genus (i.e., *Gerastos*).

For ammonoids, the early Givetian is poorly documented in the literature; only a few genera have been reported in Morocco. Consequently, the ammonoid diversity characterising the early Givetian is certainly underestimated ([Fig. 7B](#)) and so the impact of the Kacák Event is difficult to evaluate. [Aboussalam and Becker \(2011\)](#) noted a remarkable near absence of trilobites (and also brachiopods) in south-eastern Tafilalt in comparison to the similar reefal environments observed in Germany for the middle Givetian. [Kaufmann \(1998\)](#) highlighted that significant faunal and lithological changes affected the eastern Anti-Atlas from the early Eifelian to the early Givetian, and documented the replacement of benthic faunas (trilobites) by pelagic ones (ammonoids). Our results seem to confirm such patterns: for trilobites, the diversity continues to decrease dramatically, while for ammonoids, the diversity reaches high values and the number of originations significantly increases during the Givetian ([Fig. 7B](#)).

After the Choteč and Kacák events, the trilobite diversity remained very low in North Africa and the middle Givetian Taghanic Event ([Johnson, 1970](#); [House, 1985](#)) impacted already impoverished trilobite faunas. [Aboussalam and Becker \(2011\)](#) noted that the Taghanic Event affected trilobites, in particular those of the Tafilalt basin and the Draa Valley; this extinction phase is immediately followed by a radiation in the Tafilalt basin only. They reported only the presence of phacopids and proetids in the Givetian of Morocco. Moreover, [McKellar et al. \(2012\)](#) reported an exceptional occurrence of *Pedinopariops* (*Hypsipariops*) in the Givetian coarsely siliciclastic facies from Libya. Such occurrence suggest a shift away from carbonate environment in which phacopids prospered during much of the Lower to early Middle Devonian.

For ammonoids, the Taghanic Event seems to have not sharply affected the communities: the late Givetian record high diversity values ([Fig. 7A](#)). However, when regarding the fluctuations at a higher time resolution (i.e., biozone temporal scale), the diversity recorded through the Taghanic interval is particularly low and the impact of the Taghanic Event in ammonoids can be seen ([Allaire, 2017](#), unpublished PhD). Thus, the Taghanic Event seems to have more impacted nektic organisms as ammonoids.

As it was demonstrated in the Ardenne Massif (Belgium) by [Bignon and Crônier \(2015\)](#) during the Middle Devonian, the trilobite biodiversity was more influenced by the global events than the local environmental changes. However, due

to regional peculiarities, the global events may have different consequences at the local scale compared to the global scale.

#### 5.4.5.4 Frasnian

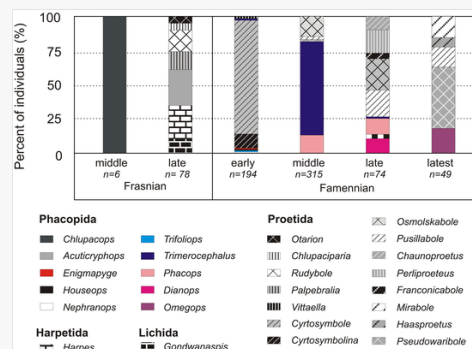
At a global scale, the trilobite diversity was low during the early Frasnian and the Frasnian Event (*sensu* House, 1985), called also the *Manticoceras* Event (*sensu* Walliser, 1985), was marked by few extinctions of trilobites, and showed the appearance of two subfamilies, the Pteropariinae and Drevermanniinae (Feist, 1991).

During the late Frasnian, the pronounced eustatic deepening became maximal just before the upper Kellwasser event (Girard et al., 2005), leading to the development of pelagic and euxinic facies. The Kellwasser Event, leading to one of the five major extinctions (Raup, 1986; Raup and Sepkoski, 1982), was characterized by an eustatic instability and hypoxic/anoxic depositional conditions in the deeper outer-shelf environment, affecting especially benthic trilobites adapted to life in deep environments. In these offshore depositional environments beyond the light penetration limit, the visual complex regression leading to blindness in trilobites was an evolutionary trend observed in various independent lineages (phacopids and proetids). This evolutionary trend may result from an ‘opportunistic’ and adaptive strategy correlative with environmental constraints, insofar as it leads to a good match between organisms and their environment (Crônier, 1999; Crônier and Courville, 2003). However, such a link led them to a subsequent evolutionary impasse resulting in their extinction. Moreover, the late Frasnian *Acuticryphops* showed a morphological intra-specific drift inducing a variability of the visual complex (Crônier et al., 2004; Feist et al., 2009), which would be located at speciation boundaries. These disturbances that occurred during the development seem to be linked to environmental stress, which can be induced by the rapid sea-level fluctuations recorded at the end-Frasnian (Feist and Schindler, 1994). The Kellwasser Event led also to the extinction of almost all reefs and their associated trilobite faunas (Odontopleuridae), and to a significant decrease of diversity for other trilobite taxa (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Otherwise, the late Frasnian trilobites from shallow/near-shore deposits remain poorly known (Lerosey-Aubril and Feist, 2012). Only few data are available; they concern the trilobite faunas from the Canning Basin in Australia (Feist et al., 2009), where well-oxygenated conditions prevailed throughout the Frasnian–Famennian transition (George and Chow, 2002).

In North Africa, only four trilobite orders (Fig. 5) were present during the Frasnian (Lichida represented by Odontopleuridae, Harpetida, Phacopida, and Proetida). For phacopids, among the seven genera known during the Frasnian at the global scale (Crônier et al., 2013; Crônier and François, 2014; van Viersen and Vanherle, 2018), only two were present in North Africa (*Chlupacops* originated in the middle Frasnian and *Acuticryphops* in the late Frasnian; Fig. 8). Phacopids were also rare elsewhere and only one genus (i.e., *Eldredgeops*) was reported so far in North America for example (Crônier and François, 2014). No Proetida were present during the early and the middle Frasnian (Fig. 8). The Drevermanniinae (*Palpebralia*) appeared in the late Frasnian at the same time as other genera (Fig. 8), implying an increase in diversity (Fig. 2). Additionally, the low dominance and the high evenness observed during the late Frasnian suggest a balanced ecosystem for benthic trilobite faunas for this period (Fig 4).

alt-text: Fig. 8

Fig. 8



Relative diversity of trilobite genera in percent of individuals, for the Late Devonian in North Africa.

Unlike trilobites, ammonoids experienced a severe extinction during the Frasnian Event, both in North Africa (Fig 7) and at the global scale (Walliser, 1996). The generic richness of the Moroccan ammonoids shows a sharp decrease around the Givetian–Frasnian boundary, and the values stayed low throughout the Frasnian. Although the ammonoids diversity shows low values during this stage, their diversity was significantly higher than the trilobite diversity (Fig. 7 A). This difference reflects a global trend. In the Frasnian deposits, the trilobites as well as the majority of the benthic faunas remain scattered, the nektonic and planktonic faunas were more widespread (Wendt and Beřka, 1991).

For the North African trilobites, the impact of the Late Devonian mass extinction remains elusive because the taxonomic richness is already low during the Frasnian (Fig. 2). Nevertheless, the coverage-based rarefaction and the boundary-crosser diversities show a small decrease during this event (Fig. 2). For the Moroccan ammonoids, an increasing number of extinctions was recorded and no origination has so far been reported (Fig. 7B; Allaire, 2017; unpublished PhD). However, this interval needs to be better documented to assess robust and precise conclusion concerning the impact of the Frasnian–Famennian biocrisis on the ammonoids from Morocco.

### 5.5.5.5 Famennian

The Famennian was punctuated by several global events (i.e., the Condroz–Enkeberg events in the early Famennian, the *annulata* event in the middle Famennian, and the Dasberg and Hangenberg events in the late Famennian), which impacted the trilobite diversity (Walliser, 1996; Lerosey-Aubril and Feist, 2012). Of the five orders present during the Frasnian (Corynexochida, Harpetida, Lichida, Phacopida, and Proetida), only the Phacopida and Proetida persisted into the Famennian (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) by surviving to the Kellwasser Event. The post-Kellwasser recovery was slow, and no trilobite was found in the first Famennian conodont zone (Lerosey-Aubril and Feist, 2012). The earliest Famennian trilobite encountered was a blind phacopid (*Nephranops*) from European offshore environments and in North Africa, the oculated phacopid (*Houseops*), earlier than the reappearance of proetids (Lerosey-Aubril and Feist, 2012). The recovery occurring during the early Famennian was due to the development of blind phacopids. At the global scale, they even have the highest origination rate (Feist, 2019). Apart from these blind phacopids, the other taxa present in the Famennian were mainly blind or small eyed, both in North Africa (Fig. 6) and at a global scale (Feist, 1991; Becker et al., 2016a); except in the Americas where no phacopid are reported (Chlupáč, 1975; Lerosey-Aubril and Feist, 2012; Crônier and François, 2014) and in the Central Asian Orogenic Belt where phacopids have well-developed eyes (Crônier et al., 2020). A new turnover occurred during the late Famennian (Crônier et al., 2013) and the late Famennian Dasberg Event witnessed a major diversification of both phacopids and proetids at the global scale (Lerosey-Aubril and Feist, 2012). Phacopids originated and diversified in the deeper offshore environments and were mostly blind or reduced-eyed, reflecting the ultimate evolutionary step of the visual complex regression leading to blindness. On the shallow carbonate platforms, the phacopids *Omegops*, *Rabienops*, and *Phacops sensu lato* and the proetids *Pseudowaribole* and *Perliproetus*, which were oculate taxa, were widely distributed, exhibiting a high degree of cosmopolitanism (from eastern to western of the North Peri-Gondwanan margin), except in the Americas and in Australia (Lerosey-Aubril and Feist, 2012; Crônier et al., 2013; Crônier and François, 2014). The global Hangenberg Crisis which was caused by a complex pattern of palaeoenvironmental changes (Kaiser et al., 2015) seriously impacted the diversity of pelagic and hemipelagic environments (Walliser, 1996) including trilobites. The disappearance of Phacopida strongly impoverished and several genera of Proetida including all reduced-eyed and blind taxa suggests a significant eustatic lowering (Lerosey-Aubril and Feist, 2012). The reason why the widespread phacopids died out in the neritic environments whilst the associated brachymetopids managed to survive remains unexplained (Kaiser et al., 2015).

In North Africa, the very high dominance and the low evenness (Fig. 4) show that the Kellwasser Event had an impact on the trilobite community and a few opportunistic taxa such as Cyrtosymbolinae took advantage of the extinction event and became dominant during the early Famennian (Fig. 4). Thus, the post-Kellwasser recovery marked a new step for biodiversity and occurred during the middle Famennian leading to a new turnover. A relative increase in taxonomic richness is observed for trilobites, linked to increasing origination (Fig. 7). This pattern is also observed at the global scale in trilobites (Lerosey-Aubril and Feist, 2012) and largely results of the diversification of Cyrtosymbolinae fostered by the development of shallow outer-shelf in northern Gondwanan margins (Feist, 1991; Wendt, 1993). Proetida and Phacopida remained the only trilobite component in the Famennian (Fig. 5). For proetids, of the 11 genera present in North Africa, all were new and dominated by two Cyrtosymbolinae: *Cyrtosymbolina* and *Cyrtosymbole*, which represent 100% of the proetids and 95% of all the trilobites (Fig. 8). Apart from these well-developed eye proetids, other taxa present in the Famennian were mainly blind or small eyed taxa both in North Africa (Figs. 6, 8) and at a global scale (Feist, 1991; Becker et al., 2016a). For phacopids, of the eight genera present in North Africa, seven were new and dominated by the blind *Trimerocephalus* taxa until the middle Famennian; *Trimerocephalus* represented almost 70% of the phacopid generic diversity during the middle Famennian (Fig. 8). The development of blind and reduced-eye trilobites after the Frasnian–Famennian crisis partially explain the rise of the diversity during the Famennian. Another peak of blind trilobites occurred, after their diversity decrease in the middle Famennian. Two blind phacopid genera, i.e., *Dianops* and *Trifoliops*, occurred and persisted during the late Famennian (Fig. 8). No reduced-eyed phacopid taxa has so far been encountered in North Africa (but newly sampled in the Famennian of the Saoura Valley, a work in progress). From the middle to the latest Famennian in North Africa, the reappearance of trilobites inhabiting shallow habitats (*Omegops*, *Phacops*, *Pusillabole*, *Osmolskabole*) in north-west Gondwana is coherent with the wide distribution of well-developed-eyed phacopids and proetids in contemporaneous shallow shoal environments (Lerosey-Aubril and Feist, 2012; Crônier and François, 2014). *Omegops*, a well-developed-eyed taxon replaced another well-developed-eyed taxon, i.e., ‘*Phacops*’. *Phacops* known in the Early and Middle Devonian were different from those known in the Late Devonian such as ‘*Phacops*’ *granulatus* widely distributed geographically all around the world (Crônier and François, 2014). In North Africa, this diversification initiated during the Dasberg Event (late Famennian) was followed by a decrease of the diversity which led to the lower

values recorded during the latest Famennian (Fig. 2). The same pattern affected the ammonoids. Throughout the Famennian, the evenness increased and the dominance decreased and tended to reach the late Frasnian values, symbol of a balanced community. Finally, at the Devonian–Carboniferous boundary, the rise of the sea-level trapped the deep sea trilobites and for this reason, blind taxa and/or outer shelf trilobites almost disappeared. Phacopida died out without leaving any Carboniferous descendants.

## 6.6 Conclusions

Based on a substantial compilation of published data on North African trilobites during the end of the Silurian and throughout the Devonian, the taxonomic diversity of these organisms has been accurately estimated at the genus level.

The reconstructed regional diversity follows the patterns observed at a global scale, except an important diversification in the Early Devonian (from the Lochkovian to the Emsian) in North Africa. The sharp decrease of the trilobite diversity observed through the Middle Devonian at a global scale, occurred earlier in North Africa (Eifelian) than in other localities where this important decrease was generally recorded during the Givetian. In North Africa, the diversity remained very low in the Givetian and the early Frasnian before a slight increase in the late Frasnian. Then, the well-known Kellwasser Event (one of the big five mass extinction) at the Frasnian–Famennian boundary also affected the North African trilobites with a decrease in diversity which is associated to an increasing number of extinctions. Only two orders crossed this limit: Phacopida and Proetida. Then, the trilobites recovered in the early Famennian thanks to the development of opportunistic taxa. This recovery was accompanied by morphological and habits changes. Indeed, a high fraction of blind, reduced eyes and/or deep-water trilobite genera proliferated after the Kellwasser Crisis. Afterward, another increase of diversity occurred in the late Famennian, then, the diversity decreased again, at the end of the Devonian. This decrease in diversity is followed by the occurrence of the Hangenberg Event, which led to the disappearance of the Phacopida. All these diversity fluctuations through the Devonian seems to reflect the rapid reaction of trilobites facing abrupt sea level changes and hypoxic/anoxic events. This review concerning a famous region for its trilobites highlights a lack of data for the Lochkovian, Givetian and Frasnian stages, for which more studies will help to better estimate the regional diversity of North African trilobites.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2020.110208>.


## Declaration of Competing Interest

For our manuscript entitled “Trilobite biodiversity trends in the Devonian of North Africa” by Bault, Allaire, Monnet and myself that we wish to submit for publication in the *Palaeogeography, Palaeoclimatology, Palaeoecology*, there is no conflict of interest.

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 The corrections made in this section will be reviewed and approved by a journal production editor. The newly added/removed references and its citations will be reordered and rearranged by the production team.

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## Footnotes

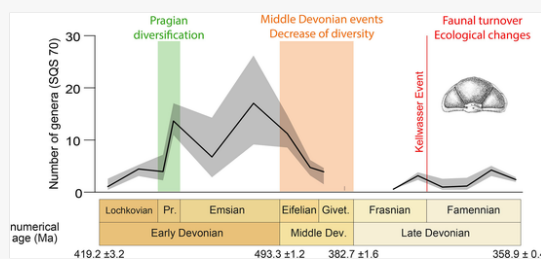
### Text Footnotes

[1] This part (Multimedia Component 8 = Supplementary material 1) correspond to the Appendix A

[2] I do not see the Appendix B: **Appendix B**. Compilation of 98 selected publications with sufficient chronostratigraphic information to calibrate occurrences at the stage and substage levels and taxonomic information to up-to-date taxonomy; set of references constituting a relatively complete fossil record of the Silurian and Devonian in North Africa.

## Graphical abstract

alt-text: Unlabelled Image



## Highlights

- Taxonomic richness underlying a diversification until the late Emsian.
- Extinction rates higher than origination rates during the Eifelian.
- Kellwasser Event impacting an already impoverished diversity.
- Mainly reduced-eye/blind taxa as opportunist taxa during the Famennian recovery.

To analyse accurately the fluctuations in biodiversity, a dataset has been compiled to list all occurrences of Silurian and Devonian trilobites documented in Morocco, Algeria, Mauritania and Libya from the available literature (Appendix A). Only studies published after 1943 have been included, because the former publications either present an outdated taxonomy in need of revision, and/or a poor temporal resolution. This selection represents 98 publications (Appendix B) which cover the end of the Silurian and the Devonian from North Africa (Fig. Suppl. A). Our dataset contains all identified taxa at the species rank in a revised taxonomy and

temporal framework, and is as much representative as possible of the current state of research concerning the knowledge of the Silurian and the Devonian trilobites from North Africa. All in all, this dataset (Appendix A) comprises 4324 trilobite specimens, i.e., 1171 trilobite bed-occurrences in total from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals from the Homerian to the Famennian. Only the highest number of either cephalo/cranidia, pygidia or complete exoskeletons per occurrence was kept to avoid duplicates. This number represents 556 species, 179 genera, and 15 families scattered among nine North African basins (Fig. Suppl. B). For each trilobite bed-occurrence, the dataset also contains the following information: source study (reference), location (locality, basin, country), stratigraphic position at different resolutions (stage and substage; their numerical ages are derived from the ICS International Chronostratigraphic Chart v2016/10; Cohen et al., 2013; updated), abundance, taxonomic information including the classification, taxonomic qualifiers (such as '?', 'cf.' and 'aff.') if relevant for genus and/or species, authorship, and original identification if it has been revised. In order to create a taxonomic framework reflecting the current state of research with as much consistency as possible, we relied on the identification and age-assignment in the original studies or subsequent published revisions and considered the intending synonymies. Without intention to validate or revise the taxonomy, the names used follow the last usage. Throughout our data compilation, genera and species were considered, but only the diversity fluctuations at the generic level are presented and discussed herein. The diversity changes at the specific level are presented in a supplemental figure (Fig. Suppl. F). The stratigraphic intervals or bins used in the database corresponds to the last three Silurian series and to the 18 Devonian substages. The duration of a substage varies from 1.6 Myr (lower and upper Pragian) to 8.6 Myr (lower Emsian) for a total duration of  $68.5 \pm 0.5$  Myr.

The reconstructed biodiversity curves of the trilobite genera from North Africa during the Silurian and the Devonian substages are illustrated in Fig. 2 and Suppl. C and D, for both raw binning and collection resampling methods. As indicated by the various biodiversity estimates and notably the coverage-based rarefaction (SQS), the generic richness shows important fluctuations during the Silurian and the Devonian in North Africa (Fig. 2). The local diversity was characterised by low to moderate values from the Ludlow to the Lochkovian, followed by peaks of highest diversity in the second part of the Early Devonian and at the beginning of the Middle Devonian, i.e., from the Pragian to the Eifelian. This period constituted a plateau of high diversity. During this period, the diversity still fluctuated with a decrease of diversity in the early Emsian before the major peak at the late Emsian. After this high diversity period, the generic richness strongly decreased until the middle Givetian and stayed low until the late Frasnian. After a small diversification phase observed at the end of the Frasnian, there was a moderate decrease of diversity in the early Famennian, then, another small diversification phase occurred in the late Famennian (Fig. 2). However, the Late Devonian diversity remained low compared to the Early Devonian plateau.

The taxonomic richness evaluated by the boundary-crosser diversity (BC) shows similar trends to the SQS, such as the initial protracted increase of diversity from the Ludlow to the early Eifelian (Fig. 2). The major difference is the absence of a diversity decrease in the early Emsian. Next, a huge decrease took place and the diversity reached low values during the middle Givetian, and stayed relatively low until the end of the Famennian. The range-through diversity excluding single-interval taxa (RTexS) shows as the boundary crosser diversity, a continuous Early Devonian diversification from the Lochkovian to the Emsian (Fig. 2). This period is followed by a relatively regular decrease of the diversity until the early Famennian. No increase was spotted in the late Frasnian contrary to the SQS method. Then, an increase happened in the middle and late Famennian as shown by the SQS curve. The sampled-in-bin diversity (SIB) and the uniform-time-bin diversity (UTB) show the same trends as the SQS diversity (Figs. 2, Suppl. C and D). This method also suggests a slight increase of the generic richness throughout the Frasnian. Most discrepancies observed between these various biodiversity estimates were due to episodic increases of single-interval taxa (e.g., late Pragian, late Emsian, late Frasnian and early Famennian; Fig. Suppl. D) or to increases of virtual ranges (e.g., early Emsian), depending on the importance given to these parameters by each index.

The size-based rarefaction (CR, Fig. Suppl. E2) analysis shows that some substages are under-sampled and require a higher number of individuals to achieve robust diversity estimates. Therefore, additional studies and fieldworks are required to complete the knowledge of trilobites especially for the early Lochkovian, the Givetian and the Frasnian. Nevertheless, the size-based rarefaction analysis confirms the trends observed with the other indices: a high diversity from the late Pragian to the late Emsian followed by a decrease during the Eifelian.

The following are the supplementary data related to this article.

[Multimedia Component 1](#)

**Suppl. Fig. A**

alt-text: Suppl. Fig. A

Devonian stratigraphic scheme and stratigraphic ranges of source studies used for the diversity analyses. Ages from Cohen et al. (2013, updated).

[Multimedia Component 2](#)

**Suppl. Fig. B**

alt-text: Suppl. Fig. B

Synthetic occurrence range chart; genera are ordered by family. (1) Proetida. (2) Phacopida. (3) Other orders.



### [Multimedia Component 3](#)

#### Suppl. Fig. C

alt-text: Suppl. Fig. C

Fluctuations of the Shareholder Quorum Subsampling (SQS) diversity of trilobites from North Africa during the Silurian and the Devonian, computed at the generic level (estimations for quorums of 30, 40, 50, 60 and 70). See text for the definition of indices. Ages from [Cohen et al. \(2013, updated\)](#).

### [Multimedia Component 4](#)

#### Suppl. Fig. D

alt-text: Suppl. Fig. D

Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Poisson-based resampling diversity (TRiPS), computes the approach of ‘true richness estimation using Poisson sampling’ based on an abundance range chart and a timescale; Uniform time bin diversity (UTB), quantifies the length of uniform time bins to reconstruct time series by using the mean time interval duration; Range-through diversity including single-interval taxa (RTinS; aka. total diversity), estimates the diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Normalized diversity (NORM), corresponds to the number of taxa ranging from the interval below to the interval above, plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself; Single-interval diversity (SGL), corresponds to the number of single-interval taxa known from only one bin; Crossover diversity (COV), counts the number of taxa known before and after the considered stratigraphic interval. Ages from [Cohen et al. \(2013, updated\)](#).

### [Multimedia Component 5](#)

#### Suppl. Fig. E

alt-text: Suppl. Fig. E

Rarefaction methods. (1) Rarefaction curves per substages. Arrows indicate the comparative individual number for substages of same size (50 or 100). (2) Size-based rarefaction (CR). Ages from [Cohen et al. \(2013, updated\)](#).

### [Multimedia Component 6](#)

#### Suppl. Fig. F

alt-text: Suppl. Fig. F

Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the specific level per substages. Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Normalized diversity (NORM), number of taxa ranging from the interval below to the interval above,

### [Multimedia Component 7](#)

plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself. Stratigraphic position of the extinction events according to [Becker et al. \(2016b\)](#); first-order events in capital, second-order events in bold and third-order events in italic. Ages from [Cohen et al. \(2013, updated\)](#).

alt-text: Image 1

### [Multimedia Component 8](#)

Supplementary material 1<sup>1</sup>

alt-text: Image 2

### [Multimedia Component 9](#)

Supplementary material 2<sup>2</sup>

alt-text: Image 3

Q1

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