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1 Post-Ordovician trilobite diversity and evolutionary faunas

2

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18

19 Highlights

- 20 • Trilobites were highly diversified in the Devonian
- 21 • Four post-Ordovician trilobite evolutionary faunas existed
- 22 • Environmental and ecological changes strongly affected post-Ordovician trilobites
- 23 • The Devonian was a key-period for trilobites regarding diversification and extinctions

24

25 ABSTRACT

26 Trilobites were the most successful clade of marine invertebrates during the Cambrian, as
27 highlighted by Sepkoski's Cambrian Evolutionary Fauna. After the Cambrian they were
28 abundant, widespread and highly diversified. Previous analyses show that trilobite diversity
29 dynamics during the Ordovician can be summarized by several trilobite evolutionary faunas.
30 Trilobites, however, were severely affected by the end-Ordovician extinction event, and never
31 again reached such a high diversity. Here we aim to investigate the evolutionary history of
32 trilobites after this crisis. We aim to evaluate how their diversity dynamics are structured in
33 evolutionary faunas and environmental controls on these faunas. Using occurrences from the
34 Paleobiology Database, we estimate the post-Ordovician palaeobiodiversity of trilobites by
35 coverage rarefaction (SQS) and identify trilobite evolutionary faunas by means of factor
36 analysis. During the Silurian, trilobite taxonomic richness was relatively high and the Silurian
37 Fauna was dominated by the families that appeared in the Ordovician and survived the end-
38 Ordovician extinction, such as Odontopleuridae and Encrinuridae. A Devonian Fauna
39 established progressively from the end of the Silurian as other families diversified, such as
40 Acastidae and Tropicoryphidae. The Early Devonian records the highest post-Ordovician
41 diversity, probably favoured by the spreading of epicontinental shallow seas. Abrupt sea-level
42 changes and anoxic events during the Middle Devonian strongly reduced trilobite diversity
43 and brought both Silurian and Devonian Faunas close to their disappearance. During the Late
44 Devonian, trilobite diversity was low and dominated by phacopids and proetids, which
45 characterize a Kellwasser Fauna. Finally, the Hangenberg event (end-Devonian) affected all
46 existing trilobite clades and the following Tournaisian diversification led to the Late
47 Palaeozoic Fauna, composed of phillipsiids and brachymetopids. Despite an important
48 diversity decrease in the Visean–Serpukhovian, this fauna was the only one to persist until the
49 extinction of trilobites at the end of the Permian.

50

51 **Keywords:**

52 Trilobites

53 Palaeozoic

54 Evolutionary faunas

55 Palaeobiodiversity

56 Extinction

57 Environmental events

58

59 **1. Introduction**

60

61 Trilobites appeared in the **early** Cambrian at the same time as several other metazoan
62 clades (Fortey et al., 1996, 1997; Paterson et al., 2019). They quickly **became** abundant in the
63 early Palaeozoic with a maximum diversity between the late Cambrian and the Late
64 Ordovician (Foote, 1993; Westrop and Aldrain, 1998). In addition to this taxonomic
65 diversification, trilobites showed an increase **in** morphological disparity until a maximum
66 disparity during the Ordovician (Foote, 1991, 1993; Webster, 2007). These arthropods also
67 developed a wide range of feeding habits (Fortey and Owens, 1999) and various
68 palaeoecological adaptations (Fortey, 2004, 2014, Hopkins, 2014), highlighting their capacity
69 for adaptation and **they were present** in all fully marine habitats, and even brackish
70 **environment by** the Early Ordovician (Mángano et al., 2021; Serra et al., 2021). These
71 ecological adaptations contributed to a resilience against extreme environmental changes **in**
72 **the Palaeozoic** and thus, the trilobites survived two of the five biggest mass extinction events,
73 i.e., the Late Ordovician and the Late Devonian mass extinctions (Raup and Sepkoski, 1982;
74 Raup, 1986; Bambach et al., 2004). However, about 250 million years ago, trilobites became
75 extinct at the end of the Permian (Owens, 2003; Lerosey-Aubril and Feist, 2012).

76 Early Palaeozoic trilobite faunas and their co-evolutionary diversity trends have been well
77 studied. Originally, Adrain et al. (2004) identified three evolutionary faunas from the
78 Ordovician to the early Silurian, which are characterized by different families showing a
79 similar pattern of diversity. These faunas were identified according to
80 geographical/environmental features such as latitude or marine habitats (Adrain et al., 2000,
81 2004). However, the trilobite evolutionary faunas of the Silurian–Permian interval remain
82 undefined, although important compositional changes occurred.

83 In the Silurian, although considered relatively stable from an environmental point of view
84 (Calner, 2008; Melchin et al., 2020), environmental changes took place including temperature
85 variations and transgressive events associated with anoxia. Silurian environmental conditions
86 were favourable for trilobites, which recovered from the end-Ordovician mass extinction and
87 became diverse (Adrain et al., 2000). The Early Devonian records a diversity peak (Chlupáč,
88 1994; Adrain, 2008; Alroy, 2010b) followed by a sharp decrease in the Middle and Late
89 Devonian, to the extent that only one order persisted in the Carboniferous (Feist, 1991;
90 Lerosey-Aubril and Feist, 2012). The Early Devonian is the only important period of
91 diversification after the Late Ordovician. This period was characterized by several
92 environmental changes, including the displacement of Gondwana towards lower latitudes
93 leading to the increase of carbonate deposits (Scotese and McKerrow, 1990; Scotese, 2021)
94 and important temperature fluctuations (Scotese et al., 2021). Repeated and rapid sea-level
95 changes and anoxic/hypoxic events also affected oceans at this time (House, 1985, 2002;
96 Johnson et al., 1985), leading to the Kellwasser events (Buggisch, 1991; Bond and Wignall,
97 2008; Carmichael et al., 2019). The late Palaeozoic was also a period of major ecological
98 changes with the proliferation of nektonic organisms during the Devonian Nekton Revolution
99 (Klug et al., 2010), the colonisation of land by vascular plants (Gerrienne et al., 2016; Capel
100 et al., 2021) and the invasion of continents by animals (Selden, 2016; Van Straalen, 2021).

101 Because trilobites responded differently to the various environmental changes over the
102 Silurian–Permian interval, it is important to identify which taxa had similar diversity
103 dynamics in order to identify the causes influencing trilobite taxonomic richness, including
104 their diversifications and declines. Therefore, the goal of this study is to review the
105 evolutionary trends in the paleobiodiversity of Silurian–Permian trilobites and possibly
106 identify their evolutionary faunas, as well as their potential influencing biotic and abiotic
107 factors.

108

109 **2. Material and methods**

110

111 2.1. Dataset

112

113 Trilobite occurrences were downloaded from the Paleobiology Database (PBDB,
114 www.paleobiodb.org) on May 21st 2021 (see Supplementary material). Data were then
115 cleaned using the following protocol: (1) selection of all trilobite genera (field
116 “accepted_name”) present in each stage from the Silurian to the Permian; (2) subgenera were
117 not treated as genera and thus discarded; (3) number of occurrences per stage for each genus
118 counted. The resulting dataset comprised 13,802 occurrences and 570 genera belonging to 23
119 families and 6 orders, from the Silurian to the Permian.

120 To better understand the relationship between environments, palaeogeography, and
121 taxonomy, we also collected data on habitat affinities and palaeolocation from the PBDB. For
122 each occurrence with available additional data, we collected lithological data from the
123 “lithology1” and “lithology2” fields, environmental data from the “environment” field and
124 latitudinal data from “paleolat” field. Among the 13,802 occurrences, 66% record lithological
125 data, 37% environmental data, and 68% latitudinal data. Lithological data were simplified into

126 three categories (Fig. SUPPL. A): siliciclastic, carbonate and mixed. Bathymetrical data occur
127 in four categories, i.e., shallow, inner platform, outer platform and slope/basin, and latitudinal
128 data in three categories, i.e., low, middle and high latitudes (Fig. SUPPL. A). We followed the
129 International Chronostratigraphic Chart (Cohen et al., 2013) as the geochronological
130 framework.

131

132 2.2. Systematic considerations

133

134 As the taxonomic assignments in the PBDB are not always updated, a revision of the
135 taxonomy was conducted. Trilobite systematics and phylogenetic relationships remain
136 debated, especially between major post-Cambrian trilobite clades and their Cambrian
137 ancestors (Paterson, 2020). The latest studies carried out at the class level were those of
138 Fortey (1997) and Adrain (2011). For more robust analyses, some studies have focused on
139 smaller subsets such as the recent analyses on asteropygins (Bignon and Crônier, 2014),
140 calmoniids (Abe and Lieberman, 2009), phacopids (McKellar and Chatterton, 2009; Oudot et
141 al. 2019), or the recent redefinition of the order Trinucleida (Bignon et al., 2020). We chose to
142 base our analyses on the taxonomic framework described by Adrain (2011) with some
143 updates. First, we follow Bignon et al (2020) in separating the newly erected order
144 Trinucleida from the Asaphida. Secondly, although Adrain (2011) separated the order
145 Aulacopleurida from Proetida, we considered them as a subdivision of Proetida following
146 Lamsdell and Selden (2015). Indeed, the monophyly of the order Proetida has been regularly
147 questioned and the superfamily Aulacopleuroidea is included as one of the three super-
148 families with Proetoidea and Bathyuroidea. Consequently, we considered Aulacopleuroidea as
149 a super-family of Proetida, not as an order. We followed Adrain (2013) in considering, within
150 the order Proetida, the family Phillipsiidae as a subfamily of Proetidae.

151 Eleven orders are recognized within trilobites across their evolutionary history (Fig. 1). All
152 of them appeared in the Cambrian–Ordovician. Eodiscida, Ptychopariida, Asaphida, Olenida
153 and Redlichiida were extinct before the Silurian; Trinucleida in the Silurian; and Harpetida,
154 Odontopleurida, Lichida and Corynexochida in the Middle–early Late Devonian. Only
155 Phacopida and Proetida survived to the Kellwasser events, and Phacopida disappeared with
156 the Hangenberg event at the Devonian/Carboniferous boundary (Feist, 1991; Chlupáč, 1994;
157 Lerosey-Aubril and Feist, 2012).

158 Some subfamilies have been reassigned to families. In this study, Tropicocoryphidae has
159 been considered as a distinct family, including Eremiproetinae, as in recent studies (Helling
160 and Schöllmann, 2018; Feist and Belka, 2018), although this subfamily has sometimes been
161 assigned to Proetidae. Some post-Ordovician styginids are inventoried in the PBDB.
162 However, we considered that the Scutelluidae are different from the exclusively Ordovician
163 Styginidae (Holloway, 2007). Therefore, the trilobites assigned to the Styginidae in the
164 database were assigned to the Scutelluidae. Some genera have been reassigned to families and
165 subfamilies and some issues of junior synonyms were also solved, following the statements of
166 Jell and Adrain (2002) and subsequent updating. The proetid genera *Constantina* Cisne, 1970,
167 *Ormistonina* Maksimova, 1978, *Pseudoproetus* Poulsen, 1934 and *Schaderthalaspis* Alberti,
168 1983 not assigned to a subfamily were not used in the Factor Analysis.

169

170 2.3. Palaeobiodiversity

171

172 Estimating past taxonomic richness faces several biases (Smith, 2001; Alroy, 2010b) but
173 the development of modern resampling methods helps palaeontologists to estimate diversity
174 from the fossil record (Alroy, 2010a; Close et al., 2018). Here, trilobite diversity is estimated
175 at genus level from the Silurian to the Permian using two different methods. First, we

176 calculated the range-through diversity (RT), including single-interval taxa, also known as the
177 total diversity, which is the count of actually documented taxa per stage plus interpolated
178 discontinuous taxon ranges (Foote, 2000). Second, we computed the shareholder quorum
179 subsampling (SQS) diversity (Alroy, 2010a). This subsampling method aims to overcome
180 uneven sampling among considered time intervals. We further estimated net changes, which
181 correspond to the difference between originations and extinctions of each time bin. Net
182 changes of faunas has been estimated as the difference in logged total diversity between
183 successive intervals, which enable highlighting periods of gain or loss of genera.
184 Palaeobiodiversities were computed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.)
185 using the R statistical environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>).

186

187 2.4. Evolutionary faunas

188

189 Post-Ordovician trilobites were distributed into the 23 families used for this work. Within the
190 family Proetidae, there are many subfamilies with different diversity dynamics and temporal
191 distribution: Cornuproetinae, Crassiproetinae, Cyrtosymbolinae, Dechenellinae,
192 Drevermanniinae, Eodrevermanniinae, Mirabolinae, Proetinae and Warburgellinae. We used
193 trilobite families and proetid subfamilies as variables in our analyses.

194 Factor analysis (FA), a multivariate explorative method of data mining, was used to
195 describe the covariance in taxonomic richness of fossils’ clades through the Phanerozoic and
196 to extract so-called “evolutionary faunas” (Sepkoski, 1981). It has been further applied for
197 more specific time intervals and faunas or floras (Figueirido et al., 2012; Cleal and Cascales-
198 Minana, 2014; Morales et al., 2015; Capel et al., 2021). This method allows modeling
199 observed variables, and their covariance structure, in terms of a smaller number of underlying
200 latent “factors”. We conducted Sepkoski’s (1981) approach by applying a CABFAC Q-mode

201 factor analysis (Mulaik 1972; Davis 1973) with a varimax rotation (Kaiser, 1958) on the
202 diversity of Silurian–Permian trilobites, consisting of the number of genera in each family or
203 subfamily per stage. The resulting factors are then used to define evolutionary faunas.
204 Selecting the correct number of factors (evolutionary faunas) to focus on is still rather
205 subjective; Sepkoski (1981) selected the factors located before the slope break of the
206 successive factor eigenvalues plotted logarithmically. Here, we selected the first factors
207 covering 95% of the total variance. We defined trilobite faunas following the factor analysis,
208 where each selected factor represents a single fauna (Sepkoski, 1981; Figueirido et al., 2012).

209 Next, the composition of each fauna is defined as the group of families or subfamilies
210 recording the highest scores in each factor. Because a family or subfamily could record high
211 scores in more than one single factor, we also performed a hierarchical cluster analysis (HCA)
212 with the UPGMA linkage method (Sokal and Michener, 1958) and the Morisita’s similarity
213 index (Morisita, 1959), which is insensitive to the sample size. It allows grouping families and
214 subfamilies with rather similar genus richness among time bins considered (stages). Finally,
215 as suggested by Alroy (2010c), we also studied the different faunas on their net diversification
216 changes, and not just on their taxonomic richness, by applying a (PCoA; with Euclidean
217 distance index) on the log-transformed values of taxonomic richness through time (Foote,
218 2000; Alroy, 2000). FA, HCA and PCoA were carried out using the software PAST version
219 3.14 (Hammer et al., 2001).

220

221 2.5. Environmental data

222

223 Because multiple abiotic factors can influence the diversification and distribution of
224 trilobites through space and time, we gathered several types of palaeoenvironmental data from
225 the PBDB related to the occurrence of studied taxa. For each abiotic factor, we evaluated the

226 relative trilobite genus diversity among **environmental** categories through time, as well as
227 within each evolutionary fauna. We thus estimated the latitudinal distribution of families and
228 subfamilies through time, and divided each hemisphere in three latitudinal bins: 0–30°, 30–
229 60°, and 60–90° (**Fig. SUPPL. A**). The bathymetrical distribution of studied taxa has been
230 synthesized in four categories along a depth gradient: shallow, inner shelf, outer shelf, and
231 slope/basin. The latter two are relatively deep environments, while shallow and inner shelf are
232 rather shallow. Finally, we evaluated the preferential depositional environment with three
233 categories: siliciclastic, carbonate and mixed environments.

234 In addition, we studied the relationship between trilobite total diversity (as well as diversity
235 of each evolutionary fauna) and different environmental proxies estimated for the Palaeozoic
236 from the literature. The considered proxies include (1) the volume of sedimentary material
237 deposited on the continental margins and ocean basins ([Hay et al., 2006](#)); (2) sea-level ([Haq
238 and Schutter, 2008](#)); (3) pCO₂ ([Foster et al., 2017](#)); (4) $\delta^{18}\text{O}_{\text{apatite}}$ ([Veizer and Prokoph, 2015](#))
239 as a proxy for temperature change; (5) $\delta^{13}\text{C}$ ([Saltzman and Thomas, 2012](#)) as a proxy for the
240 global carbon cycle variation linked to changes in primary production and climate variations;
241 (6) $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio ([McArthur et al., 2012](#)) as a proxy for seafloor spreading and/or
242 continental weathering ([Jones et al., 1994](#); [Capo et al., 1998](#)); (7) a fragmentation index
243 ([Zaffos et al., 2017](#)), which approximate the amount of continental coastal environments
244 available; and (8) the mean tropical sea-surface temperature ([Song et al., 2019](#); mean values
245 from [Scotese et al., 2021](#)). To evaluate the relationship between trilobite diversity and these
246 environmental proxies, we performed pairwise correlation tests on the detrended values of
247 these proxies and diversity ([McKinney, 1990](#); [Alroy, 2000](#)). Time series were detrended by
248 means of the generalized differencing approach and using the `gen.diff()` R function of [Lloyd
249 \(2008\)](#). Correlations were done for the entire dataset and for each evolutionary fauna
250 separately. Pairwise correlation tests were performed using Spearman's rank correlation

251 index. Because multiple comparisons were computed between diversity and the eight
252 environmental proxies, we adjusted the probability values by means of the false discovery rate
253 approach (Benjamini and Hochberg, 1995). Analyses were carried out in the R statistical
254 environment (v. 3.6.2; R Core Team 2019; <https://cran.r-project.org/>).

255

256 3. Results

257

258 3.1. Palaeobiodiversity

259

260 During the Silurian–Permian, both total and sample-standardized (SQS) diversities (Fig. 2)
261 show very similar trends. The Silurian was characterized by a relative high diversity with
262 important fluctuations and marked by a strong decline in the Pridoli. Trilobite genus richness
263 increased in the Llandovery and remained high in the Wenlock despite slight variation in
264 richness. A decrease of diversity occurred in the Ludlow-Pridoli before a diversification
265 during the entire Early Devonian to reach a maximum richness for the studied period with
266 more than 180 genera documented in the Emsian (Fig. 2). The Middle Devonian shows a
267 sharp decline of trilobite diversity to lower values than the Silurian and with the loss of about
268 80% of the genera. Then, the Late Devonian is characterized by a low diversity. A final small
269 peak in diversity was documented in the Tournaisian, before another decline from which
270 trilobite diversity never recovered and remained low until the end of the Permian despite a
271 very slight increase in the middle Permian (Fig. 2). Positive net diversity changes were
272 documented five times between the Silurian and Permian, namely the Early Silurian (2 peaks),
273 the Early Devonian, the Mississippian and the Cisuralian (Fig. 3). Four periods of extinction
274 dominance occurred: in the late Silurian, the Middle Devonian, the Viséan and at the end of
275 the Permian (Fig. 3). Peaks of both maximum positive and negative net changes occurred both

276 in the Devonian with a gain of 28 genera in the Pragian and a loss of 44 genera in the Eifelian
277 respectively (among respectively 124 and 134 genera in total).

278

279 3.2. Trilobite evolutionary faunas

280

281 A factor analysis of genus richness within families/subfamilies among Silurian–Permian
282 chronostratigraphic stages identifies four trilobite evolutionary faunas (Fig. 4). Indeed, four
283 factors are required to cover at least 95% of the total variance (Fig. SUPPL. B). The first
284 factor explains 52% of the total variance, the second 35% while factors 3 and 4 are less
285 important with respectively 7% and 3% of the explained variance. Interestingly, each fauna
286 dominated a single time interval and replaced each other (Fig. SUPPL. C). Therefore, we
287 named the four identified faunas according to their time distribution. The Silurian Fauna
288 lasted from the Rhuddanian to the Famennian but was dominant only until the Pridoli (Factor
289 3 of FA, Fig. SUPPL. C; Fig. 4). The Devonian Fauna was present during the same period but
290 became dominant only from the Lochkovian to the Givetian (Factor 2 of FA, Fig. SUPPL. C;
291 Fig. 4). The Kellwasser Fauna was present only for a very short period, from the Eifelian to
292 the Tournaisian, and was important only during the Late Devonian and particularly in the
293 Famennian (Factor 4 of FA, Fig. SUPPL. C; Fig. 4). Finally, a Late Palaeozoic Fauna
294 emerged in the Famennian, became dominant in the Tournaisian and lasted until the end of
295 the Permian (Factor 1 of FA, Fig. SUPPL. C; Fig. 4).

296 The families/subfamilies contributing importantly to each fauna are reported on Table 1.
297 The Silurian Fauna was dominated by cheirurids, encrinurids and odontopleurids, while the
298 main components of the Devonian Fauna were tropydocoriphids, acastids and phacopids.
299 Phacopids and cyrtosymbolines were the main members of the Kellwasser Fauna and finally
300 the Late Palaeozoic Fauna was dominated by phillipsiids. Some families contributed equally

301 to more than one factor. For example, scutelluids, pterygometopids, harpetids and
302 crassiproetines (not represented in the table 1) were minor components of the Silurian and
303 Devonian faunas. HCA helped to classify these questionable families and subfamilies into the
304 fauna with which they were most related (Fig. 5). Similarly, phacopids were distributed
305 between the Kellwasser and the Devonian faunas, and the HCA attached them to the Silurian
306 Fauna. Because they represented a higher proportion of the Kellwasser Fauna (Fig. SUPPL.
307 D), they are attributed to this fauna.

308 PCoA shows that families and subfamilies were relatively equally distributed based on
309 their diversity changes (Fig. 6). Cyrtosymbolinae, Mirabolinae, Brachymetopidae and
310 Phillipsiidae show the highest PCoA1 values, signifying a diversity peak in the Late-
311 Devonian-Early Carboniferous, while the last two stand out with higher PCoA2 values (Fig.
312 6). The families and subfamilies belonging to the Silurian and Devonian Faunas defined by
313 the factor analysis are close in the PCoA, meaning a rather similar diversity trajectories
314 compare to the other families. It confirms the factor analysis results which showed that some
315 families belonged to either fauna, such as Aulacopleuridae, Cheiruridae and
316 Eodrevermanniinae. However, there is a relatively good separation between most families in
317 the ordination belonging to the Silurian fauna, which scattered along positive PCoA1 and
318 negative PCoA2 values and most families from the Devonian Fauna, which have negative
319 PCoA1 and positive PCoA2 scores (Fig. 6). The only differences were that Drevermanniinae
320 were closer to the Silurian Fauna and Lichidae, Odontopleuridae and Cheiruridae closer to the
321 Devonian Fauna.

322 Based on the abundance and turnover analyses, we can associate each family or subfamily
323 with the fauna with which it has more affinity. The Silurian Fauna is composed of 11 families
324 and subfamilies, i.e., Calymenidae, Cheiruridae, Encrinuridae, Illaenidae, Lichidae,
325 Odontopleuridae, Pterygometopidae, Raphiophoridae, Rorringtoniidae, Scharyiidae, and

326 Warburgellinae (Fig. 7). This fauna reached its maximum diversity in the Silurian before a
327 long decline until the end Devonian. The Devonian Fauna is composed of eight families and
328 five subfamilies, i.e., Acastidae, Aulacopleuridae, Calmoniidae, Cornuproetinae,
329 Crassiproetinae, Dalmanitidae, Dechenellinae, Eodrevermanniinae, Harpetidae,
330 Homalonotidae, Proetinae, Scutelluidae and Tropydocoryphidae (Fig. 7). Most of these clades
331 already existed in the Silurian but the diversity peak of this fauna was in the Early Devonian.
332 The Kellwasser Fauna is composed of Cyrtosymbolinae, Drevermanniinae, Mirabolinae and
333 Phacopidae, with a combined diversity increasing from the Silurian to the Late Devonian
334 before a steep decline. The components of the Late Palaeozoic Fauna are Brachymetopidae
335 and Phillipsiidae, which diversified mainly in the Early Carboniferous and survived until the
336 end of the Permian (Fig. 7).

337 Different evolutionary faunas coexisted at the same time, but one was generally dominant,
338 except in the Pridoli and the Lochkovian when both Silurian and Kellwasser Faunas were
339 almost equally prevalent. The three major peaks of diversity during the Silurian–Permian
340 interval correspond each to the diversification of one evolutionary fauna (Fig. 4). However,
341 the Kellwasser Fauna, which dominated during a period of reduced diversity, did not develop
342 during a diversification event. Once an evolutionary fauna lost its dominance, it was
343 definitive. The pace of temporal decline of faunas was not similar. While the Silurian Fauna
344 progressively declined through more than 60 million years, the Devonian and Kellwasser
345 faunas disappeared abruptly in less than 20 million years. After a rapid and significant loss of
346 diversity in the Mississippian, the Late Palaeozoic Fauna survived for nearly 150 million
347 years before becoming extinct.

348

349 3.3. Palaeoenvironmental distribution of studied taxa

350

351 3.3.1. Latitude

352

353 Most trilobite genera lived at low latitudes from the Rhuddanian to the Givetian (Fig. 8A).
354 For the same period, the proportion of trilobites living/dwelling beyond 60° latitude (i.e. high
355 latitudes) increased until the end of the Silurian, although it remained largely minor. High
356 latitude habitats were progressively depopulated by trilobites before being abandoned in the
357 Frasnian. High latitude data from the Givetian to the Cisuralian should be taken with caution
358 because there are no data at all in the PBDB from these areas at this time. It could be a
359 sampling bias linked to the lack of research in these regions. The Frasnian is the only period
360 when diversity became more important in the middle latitudes (Fig. 8A). The trend has been
361 reversed since the Famennian with increasing numbers of trilobites dwelling at low latitudes
362 (Fig. 8A). It is difficult to analyse post Mississippian data because they are based on the
363 presence of only a few genera, leading to considerable uncertainty, but most trilobites
364 appeared to live at low latitudes. However, some trilobites seemed to invade the high latitudes
365 again in the Permian.

366 The latitudinal distribution of each fauna somewhat mirrors latitudinal trends for all
367 trilobites (Fig. 8B). Small differences are found in the Kellwasser Fauna, which records a
368 large proportion of genera at high latitudes during the Silurian (Fig. 8B). The Devonian Fauna
369 shows a greater proportion of diversity at high latitudes (above 60° latitude), probably related
370 to the diversification of calmoniids (Abe and Lieberman, 2009). Interestingly, genera
371 belonging to the Devonian Fauna that survived after the Late Devonian crisis were
372 constrained to low latitude habitats. The Late Palaeozoic Fauna developed initially at mid
373 latitudes, only later diversified in high and low latitude environments. Unfortunately, the low
374 abundance of this fauna prevents any definitive interpretation. In the Carboniferous and
375 Permian, only the Late Palaeozoic Fauna was present beyond 30° latitude (Fig. 8B).

376

377 3.3.2. Bathymetry

378

379 The bathymetrical distribution of trilobites changed over time (Fig. 9B). Trilobites living in
380 deep water (i.e., Outer Platform and Slope/Basin facies) were an important part of the Silurian
381 Period before losing their importance in the Devonian. During this Period, trilobites
382 diversified preferentially in shallower environments (i.e., Inner platform) but the Late
383 Devonian corresponded to an increase in trilobites living in basinal environments (Fig. 9B).
384 The importance of deep-water trilobites continued to increase in the Mississippian, but later
385 they became rarer, excepted in the Guadalupian (Fig. 9B).

386 Most faunas showed similar bathymetric trends from the Silurian to the Middle Devonian.
387 The Late Palaeozoic Fauna, however, seems to have diversified in inner and outer platform
388 environments during this interval (Fig. 9C). Interestingly, during the Late Devonian only the
389 Kellwasser Fauna was present in the deep-water facies (Fig. 9C). In the Carboniferous, the
390 Late Paleozoic Fauna invaded shallow and deep-water environments, therefore dominating
391 the whole bathymetric gradient.

392

393 3.3.4. Depositional environment

394

395 In the analysed dataset, most trilobites inhabited carbonate environments in all studied
396 intervals (Fig. 10A). Diversity was almost equivalent between uniquely carbonate and
397 siliciclastic plus mixed environments during the Silurian. Trilobites with a carbonate affinity
398 became particularly important from the Middle Devonian (Fig. 10A, Fig. SUPPL. E). Beyond
399 this trend, it appears that diversification and extinction events occurred in any type of

400 environment (Fig. 10A). After the Serpuhkovian crises (end-Mississippian), few trilobites
401 lived in siliciclastic environments (Fig. 10A).

402 The Silurian Fauna showed a preference for carbonate lithology throughout its history.
403 Neither both the Devonian and Kellwasser faunas did show evident preference during the
404 Silurian but they occurred more and more in carbonates in the Devonian. With the exception
405 of the Pennsylvanian, the Late Palaeozoic Fauna was preferentially recorded in carbonate
406 environments (Fig. 10A).

407

408 3.4. Correlation of global trilobite and evolutionary fauna diversities with environmental
409 proxies

410

411 Total trilobite diversity and the evolutionary faunas were not correlated to any proxy, because
412 all the rho values are below 0.5 (except for the Kellwasser Fauna) and the correlations are not
413 significant because the adjusted p values are over to 0.05 (Table 2). Changes of a single proxy
414 could not explain diversity dynamics. However, higher diversity levels in the Silurian and
415 Devonian correspond to higher fragmentation index, pCO₂ and temperature, greater
416 sedimentary material deposited in the oceans and lower sea-level. There are also some links
417 between faunas and abiotic factors, the Kellwasser Fauna proliferating when the temperature
418 was high and disappeared when the temperature decreased in the early Carboniferous. In
419 addition, peaks of δ¹³C coincided with peaks of the Silurian and the Late Palaeozoic Fauna
420 whereas the Devonian Fauna developed during a period of a lower δ¹³C.

421

422

423 **4. Evolutionary faunas**

424

425 4.1. Late Ordovician mass extinction and the early Silurian recovery

426

427 The Late Ordovician extinction event resulted in the disappearance of about 60% of genera
428 and 25% of families (Sepkoski, 1996). It was probably a consequence of an important
429 glaciation and a subsequent sea-level fall (Sheehan, 2001; Harper et al., 2014). Although
430 trilobites were highly diverse in the early Palaeozoic, this extinction strongly affected them,
431 particularly the Cambrian faunas (Owen et al., 1991; Sheehan, 2001). All the families that
432 successfully crossed the Ordovician/Silurian boundary without significant losses originated in
433 the Ordovician (Owen et al., 1991; Adrain et al., 1998; Sheehan, 2001). Calymenids,
434 cheirurids, encrinurids, illaenids, lichids, odontopleurids, pterygometopids, raphiophorids,
435 rorringtoniids, scharyiids and warburgellines survived Late Ordovician events (Sepkoski,
436 1996; Sheehan, 2001; Harper et al., 2014) and proliferated in many places starting in the
437 Llandovery (Figs. 4, 7). These families and subfamilies were components of the Silurian
438 Fauna, which is a subset of the Whiterock Fauna as Adrain et al. (1998) already
439 underscored (Adrain et al., 2000, 2004). The families and subfamilies of the Silurian Fauna
440 were not the only ones to live in Silurian waters. Some families and subfamilies of the
441 Devonian Fauna were already present, such as acastids, scutelluids, aulacopleurids and
442 proetines (Fig. 7). The recovery was quick because the diversity of Early Silurian trilobites
443 was similar to that of the Cambrian and Ordovician at local scale (i.e., alpha diversity),
444 despite a decrease in provincialism and β diversity (Adrain et al., 2000; Chatterton and
445 Ludvigsen, 2004).

446 Polar areas were devoid of trilobites in the Rhuddanian (Fig. 8A) because the Late
447 Ordovician extinction strongly affected high latitude trilobites (Adrain et al., 2004). The
448 latitudinal distribution of trilobites already played a major role in their survival in the
449 beginning of the Palaeozoic (Westrop and Ludvigsen, 1987). Consequently, the Early Silurian

450 radiation occurred preferentially at low latitudes (Adrain et al., 1998). Similarly, many
451 Silurian trilobites lived in shallow environments (Thomas and Narbonne, 1979; Siveter, 1995;
452 Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Stocker et al., 2019;
453 Wendruff et al., 2020; Yuan et al., 2020) because the Hirnantian extinction had a lesser
454 impact on shallow water communities than on deep-water ones (Adrain et al., 2000).

455

456 4.2. Silurian

457

458 No important trilobite diversity changes occurred in the Silurian likely due to the relative
459 climate stability (Tinn et al., 2020). Nonetheless, Silurian trilobites were subject to minor
460 taxonomic changes at low taxonomic ranks linked to environmental variations. The earliest
461 events happened locally in the early Llandovery of the North-western Canada (Chatterton et
462 al., 1990). This minor extinction also affected global diversity (Fig. 2).

463 The first important event occurred at the Llandovery-Wenlock boundary and is known as
464 the Ireviken event (Jeppsson, 1987; Munnecke et al., 2003). During this event, there was a
465 sea-level fall associated with a positive excursion of $\delta^{13}\text{C}$ linked to anoxia and dysoxia. These
466 environmental changes affected biotas such as conodonts, corals and ostracods (Aldridge et
467 al., 1993). Fifty percent of the trilobites of Gotland disappeared (Ramsköld, 1985). Although
468 the Ireviken event was mainly documented in Scandinavia, it occurred elsewhere in the world
469 (Calner, 2008; Molloy and Simpson, 2012; Noble et al., 2012). It corresponded to the most
470 important period of extinctions and migrations for Silurian trilobites of North-western Canada
471 (Chatterton et al., 1990) and central USA (Mikulic and Kluessendorf, 1999). The global
472 diversity was affected by this event (Fig. 2).

473 In the early Ludlow, another important facies shift associated with positive excursion of
474 $\delta^{13}\text{C}$ and sea-level drop occurred. It was the Mulde event, which led to a diversity decrease.

475 However, this event had a stronger impact on pelagic faunas such as graptolites than on the
476 benthic biota, which were mainly characterized by faunal turnover (Calner, 2008). Therefore,
477 trilobites were not strongly affected by this event and occur in the sediment recording this
478 event (Jarochowska et al., 2014; Spiridonov et al., 2017). In addition, trilobites took
479 advantage of the new conditions as odontopleurids arrived in Poland and in Scandinavia just
480 after this event (Porębska et al., 2004; Calner et al., 2006). No important environmental
481 affinity occurred during the Silurian, a relatively stable period. Since the Aeronian, trilobites
482 started to diversify beyond 60° latitude in Gondwana and Baltica, with several families
483 restricted to high latitudes (Adrain et al., 1998). During the whole Silurian, high latitudinal
484 trilobites were thus well-represented (Fig. 9). Latitudinal distribution partly explains the
485 important proportion of Silurian trilobites in both mixed and siliclastic environments. Indeed,
486 polar trilobites proliferated preferentially in siliclastic environment whereas faunas living in
487 carbonate deposits proliferated at low latitudes (Cocks and Fortey, 1990), where carbonate
488 factories mainly occur (Michel et al., 2019).

489 Moreover, the Silurian was a period of large deposits of sedimentary material with a high
490 $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (Fig. 11), indicating a time of important erosion and weathering (Capo et al.,
491 1998). Colder and more humid episodes occurring in the Silurian (e.g., P-episodes postulated
492 by Jeppsson, 1990), which increased weathering and erosion leading to more clastic deposits.
493 The Silurian was also the last period of important erosion and sedimentation due to limited
494 land plant cover (Hay et al., 2006), before the development of vascular plants in the Devonian
495 (Pawlik et al., 2020). Consequently, there were large terrigenous inputs to the continental
496 margins, which explains why many trilobites diversified in siliclastic environments.
497 Nevertheless, carbonate environments were still preferred by Silurian trilobites (Mikulic and
498 Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Hughes and Thomas, 2011; Wendruff
499 et al., 2020; Fig. 10).

500 Silurian trilobites were all benthic **unlike in** the Ordovician (Thomas and Lane, 1984), **and**
501 the substrate type had a strong effect on benthic communities (Henderson and Dann, 2010;
502 Hopkins, 2014). Substrate type has also shown to be important for macroevolutionary
503 dynamics of origination and extinction (Foote, 2006; Kiessling et al., 2010), and faunal
504 replacements (Tomašových, 2006; Miller and Connoly, 2001). In addition, Silurian trilobites
505 developed in relatively deep environments until the Ludlow (Fig. 9). Aulacopleurids were the
506 first groups to diversify in **deeper environments** (Fortey and Owens, 1975). They were
507 followed by many families and subsequently deep environments concentrate a relevant
508 proportion of the total diversity (Storey et al., 2016). Trilobite proliferation in deep
509 environments **s** coincided with the Silurian long-term transgression until the Wenlock (Haq and
510 Schutter, 2008). Differentiated **trilobite** biofacies **can** be recognized along the whole
511 bathymetric profile, proliferating in various facies (Thomas, 1979; Mikulic and Kluessendorf,
512 1999; Chatterton and Ludvigsen, 2004) both carbonate and clastic (Fig. 10).

513 A third relatively important event marked the Silurian: the Lau event in the Ludfordian.
514 This event had the most important impact on Silurian trilobites (Fig. 2) and corresponds **s** to the
515 beginning of the decline of the Silurian Fauna (Fig. 4). The Lau event **is** mostly recorded in
516 central and Northern Europe (Lehnert et al., 2003; Antoshkina, 2018) and **was** characterized
517 by a sea-level fall before a transgression and a perturbation in the carbon cycle as in the
518 Ireviken and Mulde events (Calner, 2008; Munnecke et al., 2010; Bowman et al., 2019).
519 Trilobites were affected by this event as were many other groups like acritarchs, chitinozoans,
520 polychaetes, tentaculids and ostracods in Scandinavia but also in Canada, Poland and in
521 Britain (Jeppsson and Aldridge, 2000 and references therein; Eriksson et al., 2009). At the
522 same time, a decrease **in** trilobite diversity occurred in North Africa even if the Lau event has
523 not yet been recorded in this region (Bault et al., 2021). The decrease of diversity also
524 concerned trilobites from Uzbekistan and Tajikistan between the Ludlow and Pridoli (Ivanova

525 *et al.*, 2009). In the Prague Basin, trilobite extinctions occurred in the Kozłowski zone, just
526 after the Lau event (Manda and Kříž, 2006). However, the impact of this event on trilobites
527 mainly **was in the form of** taxonomic changes and trilobites were part of the fauna
528 **contributing** to the recovery in the Prague Basin (Lehnert *et al.*, 2003; Manda and Frýda,
529 2014). Long-term sea-level drop began in the Ludlow (Haq and Schutter, 2008).
530 **E**nvironmental changes (i.e., sea-level fall and carbon isotope disruption) particularly affected
531 the shallow environments and the fauna at low latitudes (Calner, 2008). Thereby, Pridoli
532 trilobites were mainly found in deep environments at higher latitudes. Calner (2008)
533 **highlights** important changes in carbonate platforms after the Lau event, explaining **that**
534 trilobites living in carbonate environment were affected. Within the Silurian Fauna,
535 Raphiophoridae and Encrinuridae disappeared shortly after the Pridoli (Chlupáč, 1994). The
536 decline of the Silurian Fauna also **corresponds** to a reduction of continental margins, as
537 suggested by a decrease of the fragmentation index (**Fig. 11**), partly due to the closure of the
538 Iapetus Ocean and the collision of Baltica and Laurentia (Roberts, 2003; Scotese, 2021). As
539 many Silurian trilobites lived along the coasts of these two continents (Cocks and Fortey,
540 1990; Adrain *et al.*, 1998, 2000), these two palaeogeographical changes may have played a
541 role in the weakening of the Silurian Fauna. Moreover, although the Silurian began with an
542 icehouse climate with glaciations events (Calner, 2008; Munnecke *et al.*, 2010; Trotter *et al.*,
543 2016; Cuervo *et al.*, 2018), a progressive warming of the oscillating climate occurred (Azmy
544 *et al.*, 1999; Gambacorta *et al.*, 2019) **with** high temperatures **reached** in the Late Silurian and
545 Lochkovian (Joachimski *et al.*, 2009). Thus, the **decline** of the Silurian Fauna occurred when
546 the climate no longer resembled the one during its peak.

547 In parallel with the gradual decline of the Silurian Fauna, a gradual increase in the
548 Devonian Fauna occurred since the Ludfordian (**Fig. 4**). The passage from one fauna to the
549 other constituted a temporally diffuse turnover, the Devonian Fauna having a strong positive

550 diversification from the Ludlow while the Silurian Fauna did not rebound after the Pridoli
551 decline (Fig. 4). As for trilobites, a progressive faunal turnover occurred for another clade of
552 marine arthropods, the decapods, in response to sea-level fluctuations and explosive radiations
553 (Schweitzer and Feldmann, 2015). Schweitzer and Feldmann (2015) suggest a potential
554 competition between decapods to explain such faunal turnover. This competition hypothesis
555 could also explain the Silurian-Devonian faunal transition among trilobites.

556

557 4.3. Early Devonian

558

559 The Devonian Period was characterized by vast continental seas with many carbonate
560 environments (Tinn et al., 2020) and a climate that continued to warm (Torsvik and Cocks,
561 2013). The transition between the Silurian and the Devonian did not show important
562 taxonomical changes and only low extinction rates (Chlupáč, 1994). Many families
563 diversified in the Lochkovian such as acastids, which lived in shallow siliciclastic
564 environment (Morzadec, 1992; Chlupáč, 1994). Proetids, scutelluids and dalmanitids also
565 diversified in this stage (Chlupáč, 1994), although they already existed in the Silurian. These
566 families belonged to the Devonian Fauna, which become the dominant fauna. Diversity
567 increased in the Pragian (Fig. 2). The global regressive event at the Lochkovian-Pragian
568 boundary possibly led to this diversification (Chlupáč and Kukul, 1986; Chlupáč, 1994) with
569 the increase in speciation rates by vicariance (Abe and Liebermann, 2009). This
570 diversification was registered worldwide with an increase in diversity in the Pragian of North
571 Africa (Bault et al., 2021), Czech Republic (Chlupáč et al., 1985) and Falklands Islands
572 (Carvalho, 2006) for instance. Subsequently, trilobites diversified more in shallower
573 environments (Fig. 9) in a period of global lowstand of relative sea-level (Haq and Schutter,
574 2008), while the Silurian Fauna had little preference for these shallow environments.

575 Therefore, such changes accelerated the decline of the Silurian Fauna to the benefit of the
576 Devonian Fauna, confirming that bathymetry played a major role in replacement patterns
577 (Jablonski and Bottjer, 1991; Adrain et al., 2004). At the Pragian-Emsian transition, a
578 transgression known as the Basal Zlichov Event occurred (Johnson et al., 1985; House, 2002),
579 leading to a decrease of provincialism (Chlupáč, 1994). After this event, the early Emsian
580 coincided with a slightly less diverse period. The following Daleje event corresponded to a
581 worldwide sea-level rise and sedimentological changes (House, 1985, 2002; Chlupáč and
582 Kukul, 1986) influencing trilobites (Chlupáč, 1994). After the transgression, blind and
583 reduced-eye trilobites developed as well as offshore trilobites, and the fauna from shallower
584 environments remained highly diverse (Fig. 9). This led to a peak of low taxonomic rank
585 richness in the late Emsian (Fig. 2, Chlupáč, 1994; Bault et al., 2021). It was particularly the
586 time of the adaptive radiation of calmoniids (Eldredge and Branisa, 1980; Eldredge and
587 Cracraft, 1980) and Chlupáč (1994) also noticed the increasing diversity during the Early
588 Devonian of proetids, homanolotids, aulacopleurids, dalmanitids, scutelluids, acastids
589 (asteropygines) and harpetids. Taxa of the Devonian Fauna were thus the main taxa
590 responsible for the Early Devonian diversification. Phacopids, which are major taxa of the
591 Kellwasser Fauna, also participated in the diversification of the Devonian (Fig. 6) with a
592 maximum diversity in the Middle Devonian (Chlupáč, 1975; Crônier et al., 2011). The
593 Emsian also showed high diversity in different places like Ardennes (Crônier and Van
594 Viersen, 2007), Colombia (Morzadec et al., 2015) and Morocco (Crônier et al., 2018),
595 although it was not the case everywhere (Khaldi et al., 2016; Van Viersen and Taghon, 2020).
596 The high diversity reached in the Early Devonian was the maximum post-Ordovician
597 diversity (Adrain, 2008).

598 Carbonate and reef environments were widespread throughout the Devonian, favoured by
599 the greenhouse climate and the presence of large epicontinental seas (Copper and Scotese,

600 2003; Joachimski et al., 2009; Copper, 2011; Tinn et al., 2020). Consequently, trilobites
601 proliferated more in these carbonate environments (Chlupáč, 1994) relative to siliciclastic
602 environments since the Early Devonian (Fig. 10). This interval also records the highest
603 diversity in high latitude regions, with the flattest latitudinal diversity gradient. This pattern is
604 probably related to the greenhouse climate (Cocks, 2007; Joachimski et al., 2009), as it is
605 known that greenhouse intervals record rather flat latitudinal biodiversity gradients (Mannion
606 et al., 2014). The Devonian Fauna diversification also occurred at high latitudes, notably with
607 the development of calmoniids in the cold waters of the Malvinokaffric Realm (Carvalho and
608 Ponciano, 2015). A diversification occurring at different latitudes at the same time seems to
609 characterize the trilobites because the Whiterock Fauna also originated at different latitudes
610 during its Ordovician radiation (Adrain et al., 2004). Such a biogeographic macroevolutionary
611 pattern, however, is not the most common one, as highest origination rates occur frequently in
612 the tropics (Jablonski, 1993; Brown, 2013).

613 Simultaneous with the Early Devonian diversification of the Devonian Fauna, a slowdown
614 in the decline of the Silurian Fauna is observed between the Lochkovian and Eifelian (Fig. 4),
615 during a period of diversification (Chlupáč, 1994), but without an increase in total diversity.
616 Between the Lochkovian and Eifelian, cheirurids, lichids and odontopleurids proliferated
617 (Chlupáč, 1994).

618

619 4.4. Middle Devonian

620

621 No important changes in trilobite fauna characterized the transition to the Middle Devonian
622 (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) but the Middle Devonian events affected the
623 trilobite diversity negatively (Fig. 2). It was the onset of the decline of the Devonian Fauna
624 while the Silurian Fauna fall accelerated (Fig. 7). The basal Choteč event, corresponds to a

625 deepening associated with anoxia and dysoxia (House, 2002) and occurred in the early
626 Eifelian. These environmental changes affected the trilobites at the global scale with
627 migrations and extinctions despite a stable rate of diversification (Chlupáč, 1994; Lerosey-
628 Aubril and Feist, 2012). Trilobite families did not react in the same way because at the
629 opposite of the decline of many families, Lichidae, Acastidae and Proetidae showed important
630 innovations (Lerosey-Aubril and Feist, 2012). Transgression and anoxia could be more
631 important at the regional scale as in North Africa (Klug et al., 2000; Ouali Mehadji et al.,
632 2004), leading to a sharper decline of trilobites (Bault et al., 2021). Conversely, the sea-level
633 rise offered new shallow carbonate areas where trilobites proliferated (Fig. 10) and diversity
634 increased (Crônier and Van Viersen, 2007; Bignon et al., 2008). The following Eifelian Kačak
635 event and its oxygen-depleted conditions also influenced Devonian faunas (House, 1985,
636 2002; Walliser, 1996) including trilobites with extinctions and migrations (Feist, 1991;
637 Morzadec, 1992; Chlupáč, 1994). However, Eifelian events were not the most devastating
638 Middle Devonian events. The middle Givetian Taghanic event is associated with an important
639 sea-level rise that killed many taxa, particularly ammonoids (House, 1985, 2002; Walliser,
640 1996). Trilobites were severely affected by this event, particularly those living in shallow
641 environments. Lichids, cheirurids and calmoniids as well as some proetid and aulacopleurid
642 subfamilies went extinct (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), whereas deep-
643 water clades survived (Feist, 1991).

644 The decrease in diversity in deep-water environments (Fig. 9) and high latitude (Fig. 8)
645 was gradual in the Devonian, highlighting durable effects. Long-term transgression associated
646 to the succession of rapid sea-level fluctuations (Haq and Schutter, 2008) affected basinal
647 trilobites while the decline in high latitudes was possibly linked to the progressive climate
648 cooling in the Early and Middle Devonian (Joachimski et al., 2009; Scotese et al., 2021)
649 affecting cold-water taxa. A cooler climate is associated with a steeper latitudinal gradient,

650 possibly related to a decrease in high latitude diversity (Mannion et al., 2014). Furthermore,
651 northward migration of Gondwana (Scotese and McKerrow, 1990; Scotese, 2021) must also
652 have resulted in a decrease in high latitude coastlines. No lithological selectivity happened
653 with the Middle Devonian events because both carbonate and clastic environments were
654 involved in the decline (Fig. 10). Therefore, the disappearance of the Devonian Fauna
655 corresponded to the decline of the trilobites rather than a faunal replacement, as was the case
656 for the Silurian Fauna.

657

658 4.5. Late Devonian

659

660 After the Taghanic event, no important changes affected trilobites which reached the late
661 Frasnian without drastic changes (Fig. 2). Generic diversity remained low with few
662 originations (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Absent in the
663 Givetian, the Kellwasser Fauna replaced the Devonian Fauna in the Late Devonian (Fig. 4).
664 The Kellwasser Fauna, primarily phacopids and cyrtosymbolines, began to become highly
665 diverse in the Frasnian (Fig. 4) with the adaptive radiation of phacopids in shallow neritic to
666 outer shelf habitats (Feist, 1991). The only event occurring in this period was the Frasnian
667 event, which affected both pelagic and benthic organisms (Walliser, 1996). This event only
668 had a low impact on trilobites (Lerosey-Aubril and Feist, 2012). On the other hand, the Upper
669 Kellwasser event occurring at the end of the Frasnian was one of the five mass extinctions
670 (Raup and Sepkoski 1982; McGhee et al., 2013). This event was characterised by sea-level
671 changes with a transgression followed by a regression and an important episode of anoxia
672 (House, 2002; Bond and Wignall, 2008; Carmichael et al., 2019; Lu et al., 2021). The impact
673 on the biota was important and many clades were severely affected (Buggish, 1991). This
674 event had a strong effect on both low and high taxonomic levels of trilobites. Indeed, three of

675 the five orders still living in the Frasnian disappeared: Corynexochida, Harpetida and
676 Odontopleurida (Lerosey-Aubril and Feist, 2012). These orders were already impoverished in
677 genera after being severely affected by the Taghanic event and the disappearance of their last
678 genera at the end of the Frasnian led to their extinction (McNamara and Feist, 2006; Feist and
679 McNamara, 2007; McNamara et al., 2009). Subsequently, the Silurian Fauna disappeared
680 with the Frasnian-Famennian crisis and the extinction of Odontopleuridae (Feist, 1991; Feist
681 and McNamara, 2007).

682 Only two orders survived to the Kellwasser events, i.e., Phacopida and Proetida, but many
683 of their families and subfamilies vanished: Asteropyginae, Cornuproetinae and
684 Tropidocoryphinae (Chlupáč, 1994). After the Kellwasser biocrisis, the first trilobite to
685 recover worldwide was the phacopid *Pulvinocephalus* in the early *triangularis* zone (Feist,
686 2019). Then, drevermanniines and cyrtosymbolines appeared in the *crepida* zone of the early
687 Famennian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). However, trilobite diversity
688 remained low until the late-early Famennian when the recovery really happened, resulting in a
689 Famennian taxonomic richness similar to the Frasnian one (Fig. 2).

690 Phacopida and Proetida trilobites took advantage of Late Devonian environmental changes
691 and invaded shallow and deep environments globally (Brauckmann et al., 1993; Lerosey-
692 Aubril and Feist, 2005; Feist et al., 2003, 2009; Crônier et al., 2013). The Kellwasser Fauna
693 became the dominant fauna in the Famennian. It was the only fauna that diversified during a
694 time of global decrease in diversity but survived only a short time. This evolutionary fauna
695 could be characterized as an opportunistic (Levinton, 1970) or crisis fauna.

696 Although the Kellwasser event severely affected offshore communities, the recovery
697 largely occurred in deep environments (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012).
698 Temperature and bathymetry seem to be two key parameters in diversification of the
699 evolutionary fauna although the correlations are not strong (Table 1). The Silurian and the

700 Kellwasser faunas that succeeded each other are faunas with different bathymetric affinities.
701 In addition, they evolved in different global temperature contexts. Temperature started to
702 increase in the Frasnian (Fig. 11), to reach Lochkovian values, i.e., before the diversification
703 of the Devonian Fauna. The proliferation of the Kellwasser Fauna in warm waters conditions
704 seems to explain why the recovery occurred in a carbonate environment first and not in high
705 latitudes (Figs. 8, 10). The higher faunal diversity at middle latitudes is related to a lower
706 latitudinal gradient during greenhouse periods (Mannion et al., 2014). During its origins in the
707 Silurian, the Kellwasser Fauna was mainly composed of high latitude genera in contrast to the
708 low latitudes domination in the Late Devonian. A greater intensity of Middle and Late
709 Devonian events in the tropics could lead to the migration of extratropical genera toward low
710 latitudes. Indeed, reef communities representing complex ecosystems were strongly affected
711 by the Frasnian-Famennian extinction event, resulting in greater devastations at low and
712 middle latitudes (Buggish, 1991; McGhee, 1996; Walliser, 1996; Gong et al., 2002; Bond et
713 al., 2013; Barash, 2017, Huang et al., 2018). Another explanation for the displacement of the
714 Kellwasser Fauna towards lower latitudes could be related to the ecology of extratropical
715 Silurian phacopids. Some of them were adapted to relatively deep environments near the
716 storm wave base (Holloway, 1980; Sánchez et al., 1991; Rustán et al., 2011b; Fig. 9). Thus,
717 after the deepening linked to the Devonian events, they could invade other places deserted by
718 previous evolutionary faunas.

719 In addition to taxonomic changes, important morphological changes affected trilobites
720 around the Frasnian-Famennian boundary. Eye reduction and blindness occurred in different
721 taxa and in different parts of the globe (Feist, 1991, 2019; Crônier et al., 2004; McNamara
722 and Feist, 2008, 2016; Lerosey-Aubril and Feist, 2012; Schoenemann, 2018) and was related
723 to deepening or turbidity causing a decrease of light (Feist et al., 2009). This common
724 explanation does not apply to all cases and a propensity to an endobenthic behaviour was

725 suggested for reduced-eye and blind trilobites (Feist and Clarkson, 1989; Crônier and
726 Courville, 2003; Feist and McNamara, 2016). A size reduction could also affect trilobites
727 (McNamara and Feist, 2016). The first Famennian trilobites were the phacopids
728 *Pulvinocephalus* (*Cryphopsides*), followed by *Nephranops*, which appeared in the early
729 Famennian in the *triangularis* zone in deep offshore environment (Crônier, 2007; Feist,
730 2019). This reflected the post-Kellwasser trend of trilobites to move toward deeper habitats
731 (Chlupáč, 1994; Feist et al., 2009; Lerosey-Aubril and Feist, 2012; Bault et al., 2021; Fig. 8).
732 Nonetheless, many trilobites still occurred in shallow environment (Fig. 9; Crônier and
733 François, 2014; Crônier et al., 2020).

734 Subsequently, other anoxic/hypoxic events and sea-level changes happened, i.e., Condroz
735 and Annulata events (Walliser, 1996; House, 2002), with a low impact on trilobites. A second
736 diversification occurred in the late Famennian during the Dasberg event among both Proetida
737 and Phacopida (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), following a transgressive
738 event leading to a diversification in nektic fauna such as some clymeniids (House, 2002).
739 Near the Devonian/Carboniferous boundary, another important biotic turnover linked to
740 anoxia/dysoxia and sea-level fall occurred (Walliser, 1996; House, 2002; Kaiser et al., 2016;
741 Zhang et al., 2020). Trilobites were strongly affected by this event (Fig. 2), with the
742 disappearance of the order Phacopida as well as blind and reduced-eye Proetida trilobites
743 (Lerosey-Aubril and Feist, 2012). The Hangenberg event was lethal for both shallow and deep
744 water trilobites (Chlupáč, 1994), but this event had a stronger impact on deeper water
745 trilobites and consequently, survivors mostly lived in shallower areas (Feist and Petersen,
746 1995). Important faunal changes coincided with this event (Brauckmann et al., 1993). The
747 Kellwasser Fauna almost disappeared with the Hangenberg event at the end of the Devonian,
748 resulting in the extinction of phacopids (Lerosey-Aubril and Feist, 2012) and the decline of
749 cyrtosymbolines, so that this subfamily was considered extinct for a long time (Feist, 1991).

750 Climate cooling and glaciation at the Devonian-Carboniferous boundary (Isaacson et al.,
751 2008; Kaiser et al., 2016) affected more severely a fauna accustomed to warmer temperatures.

752

753 4.6. Carboniferous and Permian

754

755 The early Carboniferous recovery was achieved with the survival of two families,
756 Brachymetopidae and Phillipsiidae, which characterize the Late Palaeozoic Fauna (Figs. 4, 7).
757 While the brachymetopids already existed in the Devonian, the phillipsiids emerged and
758 diversified in the Tournaisian (Owens, 1990; Lerosey-Aubril and Feist, 2012; Vanderlaan and
759 Ebach, 2015), and were largely responsible for the peak in diversity of the last trilobite
760 evolutionary fauna. The diversification of this fauna was very rapid after the Late Devonian
761 extinction events and could be considered as a recovery fauna. Tournaisian diversity
762 recovered to the highest taxonomic richness values since the Eifelian (Fig. 2). This rise of
763 diversity was not homogeneous at the global scale and trilobite diversity remained low in
764 places such as China (Fan et al., 2020). This diversity peak was mainly due to the great
765 radiation of phillipsiids whereas the diversity of other families remained low (Owens, 1990).
766 With this diversification, trilobites and especially phillipsiids occupied various environments
767 from reefs to the outer platform (Fig. 9; Owens, 1990). There were no differential trends in
768 bathymetric repartition because no long-term sea-level changes affected the Famennian–
769 Tournaisian transition (Haq and Schutter, 2008). The Tournaisian diversification coincided
770 with a higher $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (Fig. 11), indicating a possible increase in continental sediment
771 supply due to erosion. As a result, trilobites invaded siliciclastic environments whereas they
772 previously preferred shelf carbonate environments (Owens, 1990; Lerosey-Aubril and Feist,
773 2012; Fig. 10). While the Late Palaeozoic Fauna was restricted to the mid-latitudes in the
774 Devonian, it invaded the low latitudes deserted by other trilobite evolutionary faunas in the

775 Carboniferous. As in the Middle Devonian, the high latitudes remained deserted in a context
776 of low temperatures (Scotese et al., 2021). In addition, the paleogeographic changes and
777 particularly the ascent of the Gondwana removed flooded continental areas in polar regions
778 (Scotese, 2021). The decrease of potential places where trilobites could develop in high
779 latitudes accelerated their decline beyond 60°.

780 Contrary to pelagic clades, trilobites survived anoxia and sea-level changes of the Mid-
781 Tournaisian event (Walliser, 1996). Subsequently, the decline of phillipsiids was responsible
782 for the decline of the Late Palaeozoic Fauna in the Visean and Serpukhovian (Fig. 2) in all
783 depositional environments and at all depths. The stronger decline of diversity occurred mainly
784 in the Serpukhovian (Lerosey-Aubril and Feist, 2012; Fig. 2 SQS diversity). Then, trilobite
785 diversity stagnated while other benthic faunas strongly diversified in the second part of the
786 Carboniferous (Shi et al., 2021). As this fauna never again reached a similar taxonomic
787 richness and remained essentially undiversified for the next tens of millions of years, it could
788 be considered as a 'dead clade walking' (Jablonski, 2002; Barnes et al., 2021). From the
789 Serpukhovian, the fauna developed preferentially in low latitudes due to the establishment of
790 a progressive icehouse climate (Cocks, 2007; Shi and Waterhouse, 2010; Fig. 8). After the
791 Mississippian, only a small proportion of trilobites were found in deep-water facies due to the
792 decline of phillipsiids in basinal environments (Fig. 9; Owens, 1990). The Mid-Carboniferous
793 events (Saunders and Ramsbottom, 1986; Walliser, 1996) led to the extinction of many
794 benthic and pelagic taxa. However, trilobite diversity was already low at this time and no
795 significant changes happened (Lerosey-Aubril and Feist, 2012). The beginning of the
796 Pennsylvanian was characterised by another period of origination and a rise of diversity, but
797 not at the same magnitude as the Tournaisian (Fig. 2). Trilobites followed a global trend
798 resulting in the diversification of numerous clades at this period, boosted by the closure of the
799 Rheic Ocean and advantageous environmental changes (Shi et al., 2021). A higher proportion

800 of trilobites lived in siliciclastic environments than in carbonate environments. This was a
801 consequence of the cooling of the Late Palaeozoic Ice Age, which had an impact on the
802 carbonate factory (Balseiro and Powell, 2020). With this cooling, tropical faunas slightly
803 declined (Fig. 9). Powell (2005) noticed that brachiopods from low latitudes were strongly
804 affected too, suggesting that tropical taxa disappeared because they had a narrower latitudinal
805 distribution. At the end of the Pennsylvanian, another diversity decrease occurred (Lerosey-
806 Aubril and Feist, 2012). Trilobites did not show important diversity changes at the end of the
807 Carboniferous and the beginning of the Permian (Lerosey-Aubril and Feist, 2012) during a
808 period characterized by an important glaciation and a low marine invertebrate diversity (Alroy
809 et al., 2008). Since the Asselian, the Late Palaeozoic Fauna developed again preferentially in
810 carbonate environments (Fig. 10). With the climate warming, the trilobite diversity slightly
811 rose in the Sakmarian-Artinskian (Lerosey-Aubril and Feist, 2012). The reappearance of the
812 high latitude fauna in this warmer phase during a period of glaciation is notable (Cocks, 2007;
813 Haig et al., 2014, 2017). Then, another decrease is linked to very low origination rates
814 because of unfavourable environment (Lerosey-Aubril and Feist, 2012). The Late Palaeozoic
815 Fauna disappeared at the Permian-Triassic boundary sealing the fate of the trilobites
816 (Lerosey-Aubril and Feist, 2012; Song et al., 2013).

817

818 **5. Ecological changes**

819

820 The Devonian was a key period in Palaeozoic history with important changes in both
821 marine and terrestrial ecosystems. On the continents, land plants (Cleal and Cascales-Miñana,
822 2014; Pawlik et al., 2020; Dahl and Arens, 2020) and are suspected to be a major driver of
823 environmental changes occurring from the Devonian to the Permian. In the Late Devonian,
824 vascular plants developed on land with the consequence of increased burial of organic carbon

825 in marine sediments and the enhancement of silicate weathering (Algeo and Scheckler, 1998,
826 2010; Pawlik et al., 2020; Dahl and Arens, 2020). These upheavals dropped the atmospheric
827 CO₂ levels and led to a positive $\delta^{13}\text{C}$ shift in marine carbonates (Fig. 11) leading to climate
828 cooling (Algeo and Scheckler, 1998; Algeo et al., 2001), although effect of land plants was
829 not the only mechanism evoked for weathering (Godd ris et al., 2017; Racki et al., 2018;
830 McDonald et al., 2019). However, recent studies argued that land plants hampered weathering
831 (D'Antonio et al., 2020) leaving the land plant effect an ongoing debate. Diversification of
832 vascular plants affected marine environments with the supply of nutrient fluxes and plant litter
833 in epicontinental seas leading to increase of primary productivity and thus, eutrophication and
834 anoxia (Algeo and Scheckler, 1998; Zhang et al., 2020; Lu et al., 2021). Trilobites and
835 particularly those of the Devonian Fauna were affected by anoxic events. In addition to these
836 changes, diversification of vascular land plants could lead to a late Famennian glaciation and
837 especially the Carboniferous-Permian glaciation (Algeo and Scheckler, 1998). Environmental
838 changes induced by continental plants affected trilobites in the same way as changes in
839 marine ecosystems did, particularly the Kellwasser Fauna, which appreciated warm climate.
840 Therefore, changes in ecosystems in the second part of the Palaeozoic challenged trilobites,
841 which never regain their former diversity despite the Tournaisian diversification.

842 In parallel to the plant terrestrialization, the Devonian Nekton Revolution (Klug et al.,
843 2010) occurred in the oceans with the diversification of many nektic animals, although the
844 nekton was diversified prior to the Devonian (Whalen and Briggs, 2018). Development of
845 such fauna could influence trilobite diversity in two different ways. Nektic organisms could
846 be new predators for trilobites or new competitors for food resource. Concerning predation,
847 the Palaeozoic trophic links remain largely unknown (Brett and Walker, 2002) but some
848 assumptions are made on the possible predators. Besides, the number of durophagous
849 predators sharply increased in the Devonian (Signor and Brett, 1984; Brett, 2003). In parallel,

850 trilobite ecdysis was different from modern arthropods because they needed more time to
851 reconstruct their exoskeleton (Brandt, 2002). It implied longer intermoult periods, enhancing
852 their vulnerability to predators (Brandt, 2002). Babcock (2003) envisaged different trilobite
853 predators appearing progressively in the Palaeozoic seas: phyllocarids, eurypterids,
854 malacostracans, jawless and jawed fishes, cephalopods, some echinoderms, and even other
855 trilobites. There was a rise in predator diversity from the Middle Devonian with the
856 diversification of nautiloids, placoderms, elasmobranchs and Sarcopterygii/Actinopterygii
857 (Klug et al., 2010) contemporary to the decrease of the Devonian Fauna. Ammonoids
858 appeared in the Emsian while nautiloids developed (Klug et al., 2010). Nautiloids were
859 suspected to hunt trilobites since the Early Palaeozoic (Brett and Walker, 2002; Brett, 2003;
860 Bicknell et al., 2019), their increasing diversity could mean increasing predation on trilobites.
861 Concerning ammonoids, their potential predation on trilobites remains uncertain, particularly
862 because there is no evidence that ammonoids had jaws and radula in the Palaeozoic (Nixon,
863 1996; Tanabe et al., 2015). Despite the lack of strong evidence of fish predation on
864 arthropods, jawed fishes were able to eat chitinous arthropods and shelly benthic organisms
865 (Mark-Kurik, 1995; Brett and Walker, 2002). Consequently, the frequency of healed bite
866 marks and the peeling on trilobite exoskeletons increased since the Devonian (Brett, 2003).
867 Crustaceans, asteroids and gastropods could also have predator/scavenging behaviour (Gale,
868 1987; Brett and Walker, 2002). Marine predators could also play a major role in the
869 Mississippian trilobite dynamic, particularly regarding the Viséan-Serpukhovian extinction in
870 the absence of important environmental events. Camerate crinoids showed the same diversity
871 trends as trilobites with a Tournaisian diversification followed by a strong decline in the
872 Viséan (Sallan et al., 2011). After the Late Devonian extinctions, the predators were scarce
873 and benthic prey including trilobites and crinoids could diversify. Subsequently, predators and
874 especially durophagous fishes proliferated, strongly affecting their prey diversity.

875 Consequently, camerate crinoids dropped (Sallan et al., 2011) and a similar pattern could
876 occur with trilobites, explaining the short Tournaisian recovery.

877 In response to increasing predation, trilobites adopted different strategies. In the Devonian,
878 many trilobites tended to develop spines, which were supposed to be helpful against
879 predators. Spines functioned as defensive structures to protect trilobites or as camouflage
880 (Kloc, 1992; Pates and Bicknell, 2019). However, spines were inefficient against predators
881 with large jaws, which developed from the Late Devonian and in the Mississippian (Brett,
882 2003; Sallan et al., 2011). Another way to escape from predation is size reduction, as it was
883 the case for crinoids (Waters and Maples, 1991; Brett, 2003). Indeed, it seems that the larger
884 trilobites were more attacked than the others (Bicknell et al., 2019). Conversely, predation is
885 avoided by achieving larger body size too. An enlargement could be done with the
886 development of spines (Johnsen et al., 2013) without a strong increase in biomass. Cryptic
887 behaviour as infaunal moulting could also be considered as defensive behaviour (Rustán et al.,
888 2011a; Rustán and Balseiro, 2016). Moreover, many Kellwasser Fauna genera were
889 characterized by eye reduction, which could be interpreted as endobenthic behaviour (Feist
890 and Clarkson, 1989; McNamara and Feist, 2016). Consequently, changes in predation affected
891 trilobite faunas, taxa with infaunal moulting and small size abilities were thus better equipped
892 to cope with increasing predation.

893 As noted above, from the Silurian to the Permian, the nektic fauna and benthic trilobites
894 were decoupled, as the nekton diversity was low in the Early Devonian, the Devonian Nekton
895 Revolution persisted throughout the Devonian environmental events and the Mississippian
896 showed opposite trends between nekton and benthos (Klug et al., 2010; Sallan et al., 2011;
897 Whalen and Briggs, 2018). This decoupling was not only due to predation but also to different
898 reaction facing Devonian environmental events as it was suggested for North Africa

899 ([Ebbighausen et al., 2011](#); [Bault et al., 2021](#)). Indeed, similar benthic fauna showed the same
900 variation as trilobites, like brachiopods ([Carlson, 2016](#)).

901 An increase in resource competition with the appearance of new clades could affect
902 trilobites, similarly as in other communities, by impeding diversification ([Bailey et al., 2013](#))
903 leading to extinctions ([Smith and DeSantis, 2020](#)), or the opposite, inducing adaptive
904 radiation ([Meyer and Kassen, 2007](#); [Bailey et al., 2013](#)). In trilobites, resource competition
905 could partly explain the Early Devonian diversification. Indeed, a strong resource competition
906 in a dense population or with new ecological opportunities could favoured inter- and
907 intraspecific diversification ([Rainey and Travisano, 1998](#); [Bailey et al., 2013](#); [Aristide and](#)
908 [Morlon, 2019](#)). Conversely, the arrival of new competitors with the same food niches could
909 lead to the decline or demise of a taxon ([Smith and DeSantis, 2020](#)). With the diversification
910 of predators ([Klug et al., 2010](#)), the predator/scavenger trilobites saw the arrival of new
911 competitors in the Devonian. The predator/scavenger behaviour concerned trilobites from the
912 four evolutionary faunas and especially Corynexochida, Lichida, Odontopleuridae,
913 Calymenoidea, Phacopina and secondarily conterminant Proetida ([Fortey and Owens, 1999](#)).
914 However, the trilobite clades that persisted in the late Palaeozoic were probably all predators
915 or scavengers ([Fortey and Owens, 1999](#)), so the competition was potentially enhanced for the
916 particle feeding (e.g., aulacopleurids) and the filter (e.g., harpetids, raphiophorids) trilobites.
917 Thus, the resource competition could explain the low diversity of trilobites from the Middle
918 Devonian and the inability of radiating afterwards, except for the moderate Tournaisian peak.
919 Phases of low resources accentuated the competition effects on the demise of taxa ([Vakulenko](#)
920 [et al., 2018](#)). Consequently, the extinction of potential prey because of the Devonian events,
921 which affected several taxa ([Buggish, 1991](#); [Walliser, 1996](#); [House, 2002](#)), and the decrease
922 of nutrient supply in the Middle and Late Devonian ([Large et al., 2015](#)) could participate in
923 the decline of trilobites in the late Palaeozoic.

924 It is complicated to know whether predation, resource competition or asymmetrical effect
925 of Devonian events had an influence, but faunal changes occurring in the Devonian-Permian
926 had an evident consequence on trilobite macroevolution.

927

928 **6. Conclusion**

929

930 Based on abundance and faunal turnover over time, we identify four evolutionary faunas
931 characterizing trilobites from the Silurian to the Permian:

932 1. The Silurian Fauna derived from the Ordovician fauna that survived the Hirnantian
933 extinction events and was dominant until the Pridoli. This evolutionary fauna was dominated
934 by Cheiruridae, Encrinuridae and Odontopleuridae but several other families and subfamilies
935 developed in this diverse fauna. The Silurian trilobites developed more at high latitudes and in
936 a siliciclastic environment than later faunas. This evolutionary fauna progressively lost its
937 dominance with the Devonian environmental changes, although it may have survived until the
938 Frasnian-Famennian boundary.

939 2. Another evolutionary fauna has progressively dominated the trilobite community since the
940 Pridoli, represented mainly by Acastidae and Tropydocoryphidae. This is the Devonian
941 Fauna, whose members already existed at the beginning of the Silurian. This evolutionary
942 fauna developed mainly in the Devonian with the environmental changes, i.e., a greenhouse
943 environment, an increasing carbonate environment and drowned epicontinental seas. The
944 development of this fauna led to an important diversification of trilobites to the highest post-
945 Ordovician taxonomic richness. However, the Devonian Fauna was challenged by
946 environmental and ecological changes. Several Middle Devonian events affected the
947 trilobites, leading to a sharp decline in diversity and the disappearance of the Devonian Fauna
948 at the end of the Frasnian.

949 3. The Kellwasser Fauna had the shortest life span, only in the Late Devonian and
950 Tournaisian. This is the only evolutionary fauna that is characterized by low diversity, as the
951 Middle Devonian environmental changes decimated the ancient evolutionary faunas.
952 Dominated by Phacopidae and Cyrtosymbolinae, this evolutionary fauna invaded both
953 shallow and deep environments. The taxa of this fauna are characterized by important
954 morphological changes such as the eye-reduction. At that time, trilobites inhabited warm,
955 carbonate environments. The gradual cooling that began in the Famennian and the
956 Hangenberg event at the Devonian-Carboniferous boundary led to the disappearance of this
957 evolutionary fauna.

958 4. Only the order Proetida developed in the Late Palaeozoic Fauna, dominated by
959 Phillipsiidae. Although trilobites were able to recover in the Tournaisian, a further decline in
960 the late Mississippian left them poorly diversified despite their survival until the Permian-
961 Triassic crisis.

962

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970

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977
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1616

1617 **Figures**

1618

1619 **Figure 1.** Schematic representation of the evolutionary history of the trilobite orders through
1620 time (modified after Gon, S.M., <https://www.trilobites.info>). The vertical axis (time)
1621 approximates a log scale to enable more detailed illustration of the Cambrian and Ordovician
1622 diversifications. Neither the horizontal axis nor the diagram imply phenetic variance and
1623 amplitude.

1624

1625 **Figure 2.** Palaeobiodiversity of trilobites from the Silurian to the Permian. Taxonomic
1626 richness from the PBDB estimated as total diversity and the sample-standardized (SQS with a
1627 quorum of 70) diversity. Other curves correspond to the diversity estimated by [Fan et al.](#)
1628 [\(2020\)](#), [Alroy et al. \(2010c\)](#), [Lerosey-Aubril and Feist \(2012\)](#), [Chlupáč \(1994\)](#) and [Bault et al.](#)
1629 [\(2021\)](#) at regional or global scale. Diversities were estimated for each stage at the generic
1630 rank except for [Fan et al. \(2020\)](#) who used the species rank. Timescale from [Cohen et al.](#)
1631 [\(2013, updated\)](#).

1632

1633 **Figure 3.** Net change of trilobites from the Silurian to the Permian. Net change per stage,
1634 which corresponds to the number of origination of genera minus the number of extinction of
1635 genera, enables emphasizing periods of origination or extinction. Timescale from [Cohen et](#)
1636 [al. \(2013, updated\)](#).

1637

1638 **Figure 4.** Diversity of each of the four trilobite evolutionary faunas from the Silurian to the
1639 Permian. Evolutionary faunas modelled by means of a factor analysis. Black line represents

1640 the total diversity and the white part corresponds to the part of the diversity not explained by
1641 the model. Timescale from [Cohen et al. \(2013, updated\)](#).

1642

1643 **Figure 5.** Two-way hierarchical cluster analysis (UPGMA linkage and Morisita's similarity
1644 index) of the post Ordovician trilobite families and subfamilies and their genus richness
1645 among time intervals. Clusters of families correspond to the Silurian Fauna (green), the
1646 Devonian Fauna (orange), the Kellwasser Fauna (yellow) and the Late Palaeozoic Fauna
1647 (blue).

1648

1649 **Figure 6.** Principal coordinate analysis (PCoA)(Euclidean distance) between trilobite families
1650 and subfamilies according to their net diversification change through time. Evolutionary
1651 faunas as defined by the factor analysis ([Fig. 4](#)).

1652

1653 **Figure 7.** Taxonomic composition and total diversity of each trilobite evolutionary fauna.
1654 Black lines correspond to the net change (logged) for each fauna. Timescale from [Cohen et al.](#)
1655 [\(2013, updated\)](#).

1656

1657 **Figure 8.** Distribution (in percentage of genera) through depth and latitude of trilobite
1658 diversity globally (A) and for each evolutionary faunas (B). Timescale from [Cohen et al.](#)
1659 [\(2013, updated\)](#).

1660

1661 **Figure 9.** Bathymetrical distribution (A) on the shelf environment; (B) for the total trilobite
1662 diversity through time and (C) for the four evolutionary faunas. Distribution is expressed in
1663 the percentage of genera. Small circles indicate the samples with 10 or less genera. Timescale
1664 from [Cohen et al. \(2013, updated\)](#).

1665

1666 **Figure 10.** Lithological repartition through time of trilobites (A) for the total diversity and (B)
1667 for the four evolutionary faunas. Diversity corresponds to the number of genera. Timescale
1668 from [Cohen et al. \(2013, updated\)](#).

1669 **Figure 11.** Comparison of trilobite total diversity with global environmental proxies. Existing
1670 (dark grey) and reconstructed (light grey) mass of continental and oceanic sediments from
1671 [Hay et al. \(2006\)](#). Sea-level from [Haq and Schutter \(2008\)](#); pCO₂ from [Foster et al. \(2017\)](#);
1672 δ¹⁸O apatite from [Veizer and Prokoph \(2015\)](#); δ¹³C from [Saltzman and Thomas \(2012\)](#);
1673 ⁸⁷Sr/⁸⁶Sr ratio from [McArthur et al. \(2012\)](#); Fragmentation index from [Zaffos et al. \(2017\)](#) and
1674 mean tropical sea-surface temperatures ([Song et al., 2019, mean values from Scotese et al.,](#)
1675 [2021](#)). Timescale from [Cohen et al. \(2013, updated\)](#).

1676

1677 **Table 1.** Factor scores of the four first four factors. Only the family and subfamilies with a
1678 score higher than 0.5 are here reported and distributed into classes (>0.5, >1 and >2).

1679

1680 **Table 2.** Results of the pairwise correlation tests of detrended values of environmental
1681 proxies with detrended global total diversity and for each evolutionary fauna. rho =
1682 Spearman's rank correlation coefficient; p* = adjusted *p* values.

1683

1684 **Figure SUPPL. A.** Table of the attribution of each PBDB category to latitudinal,
1685 environmental and bathymetrical categories used in this article.

1686

1687 **Figure SUPPL. B.** Eigenvalues for the first ten eigenvectors given by the factor analysis of
1688 trilobite family and subfamily diversity from the Silurian to the Permian.

1689

1690 **Figure SUPPL. C.** Factor loadings of the first four factors generated by the factor analysis.

1691 Timescale from [Cohen et al. \(2013, updated\)](#).

1692

1693 **Figure SUPPL. D.** Percentage of phacopids from the Silurian to the Carboniferous.

1694 Timescale from [Cohen et al. \(2013, updated\)](#).

1695

1696 **Figure SUPPL. E.** Number of collection recorded in the PBDB for each environmental

1697 category.

1698

1699 **Supplementary material.** Dataset from the Paleobiology Database with (1) number of

1700 occurrences of each genus per stage; and the simplified raw data of (2) bathymetry; (3)

1701 lithology and (4) palaeolatitude.