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1 **The influence of palaeogeography and tectonic events on trilobite distributions in**
2 **Morocco and north-western Algeria**

3

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14

15 **ABSTRACT**

16 The effects of sea-level changes and anoxia on Devonian trilobites have been studied for a
17 long time but the importance of palaeogeographic and tectonic events in this key-period is
18 still not well understood. In the Devonian, trilobites invaded many different marine
19 environments and areas in North Africa where important palaeogeographic changes occurred.
20 Distribution patterns of trilobites through time and space have been analysed using a
21 hierarchical cluster analysis and diversity indices. Our examination of the literature suggests
22 that trilobites were scarce during the Lochkovian before an important diversification in the
23 Pragian. Trilobites flourished in many North African regions without there being important
24 taxonomic differences between basins, because of free migration in relatively flat palaeo-
25 topography and homogeneous environments. During the Middle Devonian, early Variscan

26 tectonic movements transformed the Eastern Anti-Atlas area into a basin with a platform
27 topography. Geographical barriers such as deep basins prevented trilobite migrations. At the
28 beginning of the Eifelian, the reduction of migration between the different regions of this area
29 coincided with a decrease in diversity. Consequently, tectonic events played an important role
30 in the decline of trilobites during the Middle Devonian, especially when these were combined
31 with sea-level changes and anoxic/hypoxic events. A recovery occurred in the Famennian
32 involving only new genera. As at the global scale, cyrtosymbolines developed in shallow seas
33 whereas phacopids evolved in deeper environments. The basin and platform system still
34 hampered migrations although sea-level variations led to episodic exchanges. The late
35 Famennian regression reduced trilobite diversity dramatically in the study area.

36

37 **Keywords:**

38 Arthropods,

39 Anti-Atlas,

40 associations,

41 diversity,

42 faunal succession,

43 tectonic

44 palaeobiogeography

45

46

47 **1. Introduction**

48 During the Devonian, trilobite communities were strongly influenced by spatial and
49 temporal ecological changes at the global scale as well as regionally (Crônier & Van Viersen,
50 2007; Abe & Lieberman, 2012; Crônier & François, 2014; Bignon & Crônier, 2015). The

51 development of hospitable shallow platforms during the Early Devonian led to a trilobite
52 diversification (Chlupáč, 1994) but the sea-level changes and anoxic/hypoxic events during
53 the Middle Devonian caused a sharp decrease of their diversity (Feist, 1991; Lerosey-Aubril
54 & Feist, 2012). These kinds of spatial and temporal palaeoenvironmental changes were
55 observed in the trilobite communities from North Africa (Bault et al., 2021). This area was
56 located on the continental shelf of north-western Gondwana (McKellar & Chatterton, 2009)
57 and was flooded during the Silurian transgression (Bultynck & Walliser, 2000) leading to a
58 Devonian epicontinental sea (Kauffman, 1998). Thus, an abundant and diverse trilobite fauna
59 proliferated during the Early Devonian before a long decline due to events that occurred
60 during the Middle and Late Devonian.

61 To understand the trilobite response to palaeoenvironmental changes and their biodiversity
62 dynamics at a regional scale, our study is focused on the Devonian North African
63 communities from two well-known areas, i.e., the Moroccan Anti-Atlas and the Algerian
64 Ougarta Range. These two areas are famous for their detailed stratigraphy, their numerous
65 faunal studies and their recognised environmental changes (Wendt et al., 1984; Wendt, 1985,
66 1993, 2021a, 2021b; Wendt & Belka, 1991; Benhamou et al., 2004; Ouali Mehadji et al.,
67 2011; Abbache et al., 2019; Frey et al., 2019). The trilobite fauna from this North African
68 area was first studied by Le Maître (1952) followed by numerous publications by G. Alberti
69 (e.g. 1964, 1966a, 1966b, 1967a, 1967b, 1969, 1970, 1981a, 1981b, 1982, 1983) and H.
70 Alberti (e.g. 1972, 1973, 1974, 1975a, 1975b, 1976a, 1976b). This area is still studied
71 nowadays as is reflected in more recent publications by Becker et al. (2018), Crônier et al.
72 (2018a-b), Feist & Belka (2018), Feist & Weyer (2018), Zaplaski & Klug (2018), Van
73 Viersen & Lerouge (2019) and Chatterton et al. (2020). There were many taxonomic changes
74 in the study area throughout the Devonian including periods of great taxonomic diversity
75 among the trilobites, following trends identified on a global scale (Chlupáč, 1994; Bault et al.,

76 2021). The Anti-Atlas Range and Ougarta Range also provided a high diversity of
77 environments exhibiting temporal and geographical changes because of sea-level fluctuations.
78 The Variscan tectonic events led to different palaeotopographies (Hollard, 1967, 1981;
79 Wendt, 1985; Bultynck & Walliser, 2000).

80 The present work concentrates on trilobite occurrences to analyse the dynamic of trilobite
81 faunas confronted with environmental changes in time and space and to thus understand how
82 the diversity of trilobites may be influenced by the diversity and nature of environments.
83 Trilobite associations were determined by performing multivariate analyses before their
84 diversity and ecology were assessed.

85

86 2. Geological settings

87 The Moroccan study area, i.e., the Anti-Atlas Range, extends from the Dra region in the
88 south-west toward the north-east, to the Tafilalt in Morocco and ends below the Bechar Basin
89 in Algeria (Hollard, 1967). The Algerian study area, i.e., the Ougarta Range (Saoura Valley,
90 North-western Algerian Sahara), extends towards the north-west, in the Anti-Atlas (Fig. 1A).
91 During the Devonian, the study area included numerous marine basins, which were part of the
92 Sahara platform, a passive continental margin of Gondwana (Wendt et al., 1984). From the
93 south-west toward the north-east, these basins are the Fom Zguid area, the Maïder Basin and
94 Tafilalt Basin in the eastern Anti-Atlas in Morocco, the Ougarta Basin and to the North the
95 Bechar Basin (i.e., Ben Zireg area) in Algeria (Fig. 1B).

96

Fig. 1 near here

97 The current correlation based on conodonts between the Tafilalt and the Maïder formations
98 (Bultynck & Walliser, 2000) is associated here with their main environmental characteristics
99 (Fig. 2). The succession of formations of Ougarta was described by Boumendjel et al. (1997).
100 Although the connection between the Devonian strata of the Ougarta Range and those of the

101 Anti-Atlas region are covered by the Cretaceous ‘Kem-Kem Group’ (Benhamou et al., 2004),
102 the similar basinal facies found in these areas suggests a connection during the Devonian
103 (Hollard, 1967; Wendt et al., 1984). The northern and western parts of the Maïder region were
104 continental during the main part of the Devonian and were only flooded during the Famennian
105 when the sea level rose (Kaufmann, 1998). Figure 2 summarises the formations studied along
106 with their dominant lithologies (Fig. 2).

107 Fig. 2 near here

108

109 **Early Devonian**

110 In the Lower Devonian, the eastern Moroccan Anti-Atlas was characterised by rather
111 uniform facies (i.e., Maïder and Tafilalt; Fig. 2) varying mostly in thickness due to a
112 homoclinal carbonate ramp topography (Lubeseder et al., 2010). However, palaeocurrents
113 indicate the presence of a shallow pelagic platform in the Tafilalt with two distinct slope
114 directions - one to the south-west and the other to the north-east (Wendt, 1995). The dominant
115 sedimentology consists of shales interbedded with cephalopod limestones (Kaufmann, 1998).
116 In Algeria, the Ougarta corresponded to a platform (Ouali Mehadji et al., 2011).

117 The Lochkovian deposits of the eastern Anti-Atlas are mainly composed of shales and
118 black graptolite limestones (Fig. 2). These deposits reflect relatively deep environments,
119 which are not favourable for benthic faunas (Morzadec, 2001; Klug et al., 2013; Frey et al.,
120 2014). In the Tafilalt, the particular Hamar Lagdad area is characterised by volcanic tuff
121 deposits (Hollard, 1967; Klug et al., 2018). At the end of Lochkovian and the beginning of
122 Pragian, a regressive phase enabled benthic faunas to develop (Hollard, 1967; Morzadec,
123 2001). Nevertheless, Bultynck and Walliser (2000) reported a dominance of shales and
124 hemipelagic limestones in the eastern part of the Anti-Atlas whereas the western part was
125 composed of neritic deposits. At the same time, in the Hamar Laghdad area, a reef system

126 settled on volcanic shoals (Hollard, 1981; Brachert et al., 1992). In the Ougarta Basin, the late
127 Lochkovian-Pragian regressive phase led to a mud-dominated platform environment
128 subjected to storm and fair-weather waves while to the north the Bechar Basin corresponded
129 to a carbonate platform (Ouali Mehadji et al., 2011).

130 During the early Emsian (Fig. 2), limestones and argillaceous limestones still covered the
131 Anti-Atlas without important environmental changes (Hollard, 1967) and are very
132 fossiliferous (Kaufmann, 1998; Klug et al., 2008; De Baets et al., 2010). Conversely, in the
133 Fom Zguid area shallow environmental conditions above storm-wave base led to sandstone
134 deposits despite transgressive sequences (Jansen et al., 2004; Ouanaimi & Lazreq 2008). In
135 Algeria, the Ougarta Basin deepened from the late Pragian due to a subsidence phase and was
136 covered by shales and marls while the Bechar Basin became more siliciclastic (Ouali Mehadji
137 et al., 2011).

138 The transition between the early and late Emsian was marked by a global transgression: in
139 the Anti-Atlas the Daleje event (House, 1985) led to green shale deposits in a basinal
140 environment (Kaufmann, 1998). Hollard (1967) noted a difference of faunas and facies
141 between the Maïder and the Tafilalt with the Tafilalt becoming more argillaceous with a less
142 diverse benthic fauna than the Maïder (Fig. 2). The northern Tafilalt was a pelagic platform
143 with thinner deposits (Kaufmann, 1998). In Algeria, the Ougarta Basin remained deep and
144 dominated by shales and marls (Ouali Mehadji et al., 2011) whereas the Bechar Basin was
145 covered by shales and siltstones (Massa, 1965). At the end of the Emsian, limestone deposits
146 formed in the Anti-Atlas (Fig. 2) because of a fall in the sea level. Conversely, the Fom
147 Zguid area was characterised by shales and nodular limestones corresponding to more open
148 water and hemipelagic conditions (Jansen et al., 2004). Based on trilobites, Chatterton et al.
149 (2006) confirmed the establishment of a relatively deep environment, which was below the
150 storm wave base but within the photic zone while the north of the Dra Valley was deepening.

151 This area was influenced by the tectonic subsidence triggered by the Variscan extent phase
152 ([Ouanaimi & Lazreq, 2008](#)). In Ougarta, the regression led to a shoreface or a foreshore
153 environment with sandstone deposits ([Ouali Mehadji et al., 2011](#)).

154

155 **Middle Devonian**

156 During the Middle Devonian, the collision of Gondwana and Laurussia resulted in the
157 Variscan orogeny. In the Anti-Atlas, this episode is marked by the development of a neritic
158 shelf followed by a platform and basin system, accompanied by palaeoenvironmental changes
159 ([Wendt et al., 1984](#); [Kaufmann, 1998](#); [Baiddet et al., 2008](#); [Wendt, 2021a](#)). The first phase of
160 this tectonic movement occurred at the Emsian/Eifelian boundary ([Lubeseder et al., 2010](#)).

161 The Maïder Basin separated the Tafilalt Platform in the north-east from the Maïder Platform
162 in the south-west ([Fig. 3](#)). While the Maïder Platform was emerging, the Tafilalt Platform
163 remained a pelagic platform with the north-eastern Dra Valley and the Ougarta Basin
164 deepening to a distal ramp ([Limam et al., 2021](#)).

165 The Foug Zguid area continued its transition toward a hemipelagic platform from the
166 Emsian onwards ([Jansen et al., 2004](#)). During the Eifelian, marlstones and shales became
167 increasingly important. To the north-east, the environment was less uniform. [Kaufmann](#)
168 ([1998](#)) explained that three different facies occurred in the Maïder and the Tafilalt. A neritic
169 facies characterised by argillaceous wackestones and numerous fossils was present in the
170 northern and western parts of the Maïder near the emerged Maïder Platform. A neritic fauna
171 including trilobites developed in the limestones of the western side of the Maïder Platform at
172 Jbel Ou Driss ([Bultynck, 1985](#); [Feist & Orth, 2000](#)). Condensed pelagic deposits, i.e.,
173 condensed nodular limestones and marls with abundant fossils, accumulated in the pelagic
174 Tafilalt Platform. These two platforms corresponded to shallow water environments ([Wendt](#)
175 [et al., 1984](#)). Finally, a basinal facies existed in the centre of the Maïder Basin and to the east

176 of the Tafilalt Platform in the Tafilalt Basin. It mainly corresponded to marlstones and shales
177 with scattered faunas. [Wendt et al. \(1984\)](#) specified that the Maïder Basin was deeper than the
178 Tafilalt Basin. In Algeria, the Ougarta Basin became deeper during the Eifelian, from a
179 foreshore environment at the end of the Emsian to a distal platform ([Maillet et al., 2013](#);
180 [Crônier et al., 2018a](#)). Henceforth, hemipelagic deposits were found as marlstones
181 interbedded with thin-bedded limestones.

182 The global transgression events of the Middle Devonian were well pronounced in the Anti-
183 Atlas ([Kaufmann, 1998](#)). The successive Choteč and Kačák events corresponded to hypoxies,
184 which was probably due to a sea level rise during the Eifelian leading to black shale deposits
185 ([Kaufmann, 1998](#); [Döring, 2002](#)).

186 The differentiation between platforms and basins in the eastern Anti-Atlas continued to
187 intensify in the Givetian. On the edge of the Maïder Platform, coral-stromatoporoid
188 limestones developed and extended to the early Givetian ([Kaufmann, 1998](#)). A second
189 tectonic phase of early Variscan movements occurred during the middle Givetian ([Lubeseder
190 et al., 2010](#)). It implied the subsidence of the Maïder Basin, which induced the extension of
191 the basinal facies ([Kaufmann, 1998](#)). The mid-Givetian Taghanic event was identified in
192 Morocco and Algeria with shale deposits and condensed layers ([Kaufmann, 1998](#)). The distal
193 platform of the Ougarta region continued to subside during the Givetian with shale deposits
194 interbedded with limestones ([Maillet et al., 2013](#)). To the north, the Bechar Basin showed
195 similar facies to the Tafilalt Platform with the appearance of pseudonodular limestones in the
196 Givetian ([Massa, 1965](#)).

197 Fig. 3 near here

198

199 **Late Devonian**

200 During the Late Devonian, the Anti-Atlas Range and Ougarta Range were influenced by

201 the same regional events (Benhamou et al., 2004). Variscan tectonics intensified in the eastern
202 Anti-Atlas, which is reflected in differences of facies and thickness (Hollard, 1974; Wendt,
203 1985, 1988; Wendt & Belka, 1991; Belka et al., 1999; Frey et al., 2019) resulting in the
204 differentiation of basins and platforms (Wendt et al., 1984, 2021a, 2021b; Michard et al.,
205 2008). The active extensional dislocation of the former platform caused by early Variscan
206 tectonic movements and differential subsidence (Wendt et al., 1984) led to the differentiation
207 of two sub-basins; i.e., the Tafilalt Basin, a slowly subsiding shallow basin in the east and the
208 Maïder Basin, a rapidly subsiding basin in the west (Fig. 3). These two sub-basins were
209 connected *via* the narrow N-S Cephalopod Ridge, i.e., the Tafilalt Platform with shallower
210 water (Wendt, 1985, 1995; Wendt et al., 2006; Toto et al., 2008; Lubeseder et al., 2010). At
211 the beginning of the Frasnian, the Tafilalt Platform emerged before being flooded again
212 (Michard et al., 2008) and the Maïder Platform partly emerged (Wendt et al., 1985). On the
213 north-western margin of the Algerian Sahara, a tectono-eustatic control is reflected in
214 differences in lateral facies and thickness in sediments accumulated on a distal platform and
215 in basins (Abbache et al., 2019). The Late Devonian marked the most important phase of
216 epirogenic movements in the Saoura leading to an important subsidence (Benhamou et al.,
217 2004). The Upper Devonian is characterised by alternate deposits of clay-sand and limestone,
218 especially including "griottes" nodular limestones with benthic and pelagic faunas, which
219 indicates an opening to marine environments (Crônier et al., 2018a; Abbache et al., 2019).

220 In North Africa, a transgression occurred during the Late Devonian. In Morocco, the
221 highest sea-level occurred in the late Famennian (Wendt & Belka, 1991; Becker et al., 2004).
222 In the Ougarta, the high stand occurred at the end of the Frasnian but the sea-level stayed high
223 with high stand deposits until the late Famennian (Ouali Mehadji et al., 2012) when a
224 regression led to shallower environments in Morocco and Algeria.

225 During the Frasnian, in the Anti-Atlas a clay sedimentation with sideritic and nodular

226 levels (Frey et al., 2019) developed in the Tafilalt Basin and the Maïder Basin and even
227 occasionally on the Tafilalt Platform, reflecting rising sea levels (Wendt, 1988; Lubeseder et
228 al., 2010; Frey et al., 2019). At the same time, sandy limestones, thick-bedded crinoid or
229 cephalopod limestones rich in nektonic and planktonic faunas associated with black
230 bituminous shales were deposited on the Tafilalt Platform (Wendt, 1985; Michard et al., 2008;
231 Frey et al., 2019). A condensed sedimentation took place in the south-western Maïder Basin
232 and on the northern Tafilalt Platform (Wendt, 1988; Wendt & Belka, 1991; Hüneke, 2006),
233 probably reflecting a differentiation in both water depth and oxygen availability (Frey et al.,
234 2019). In the late Frasnian, shallow subtidal to supratidal deposits developed in the Tafilalt
235 Platform that are characterised by strongly reduced thicknesses and the Maïder Platform
236 emerged (Wendt et al., 1984; Wendt & Belka, 1991). In the south-eastern part of the Maïder
237 Basin, the Kellwasser levels are represented by dark and massive cephalopod limestones
238 (Wendt & Belka, 1991; Frey et al., 2019). The Ougarta Basin is the continuation of these
239 Tafilalt and Maïder basins to the south-east in the Algerian Sahara (Wendt et al., 1984;
240 Wendt, 1985; Abbache et al., 2019). In this area, the top of the Cheffar el Ahmar Formation is
241 a distal ramp sedimentation with green shales interbedded with nodular limestones followed
242 by “griotte” limestones interbedded with red shales. The fauna consists of ammonoids,
243 ostracods and chitinozoans (Abbache et al., 2019).

244 During the Famennian, a marly and nodular calcareous sedimentation developed in the
245 Tafilalt Basin, in shallow environments. At the same time basinal facies dominated by shaly
246 and calcareous sedimentation with intercalations of siliciclastic turbidites were laid down in
247 the Maïder Basin, in deeper environments (Wendt et al., 1984; Döring, 2002) with diverse
248 cephalopods (Korn & Bockwinkel, 2017). In the Tafilalt Platform, deposits of quartz-rich
249 brachiopod coquinas, crinoidal limestones, thick-bedded cephalopod limestones and nodular
250 limestones formed during the early Famennian. Similar facies were found in the eastern

251 Maïder Platform (Wendt, 1985). A deeper environment like a slope or basin with shale
252 deposits characterised the Ougarta region. Pyritised ammonoids and brachiopods were found
253 in nodular limestones interbedded with shales (Abbache et al., 2019). The deepening of the
254 Ougarta trough was probably due to subsidence and not to transgression (Ouali Mehadji et al.,
255 2012). The deepening continued during the middle and late Famennian in the Tafilalt
256 Platform where marls and nodular limestones were deposited in slightly deeper environments
257 and debris flows and slumps on the margins during the late Famennian (Wendt et al., 1984).
258 Locally, limestones varied greatly in thickness and fossil content (cephalopods, crinoids,
259 brachiopods). Sedimentology documented phases of moderate to good aeration in more or
260 less shallow water conditions (Wendt et al., 1984; Wendt, 1988). The continuous deepening
261 during the late Famennian led to the decrease of diversity of benthic faunas (Wendt et al.,
262 1984) while the centre of Maïder Platform was henceforth flooded and pelagic cephalopod
263 limestone accumulated (Wendt, 1985). The Ougarta region remained deep during the middle
264 and the late Famennian and became a basin with a restricted water circulation (Benhamou et
265 al., 2004; Abbache et al., 2019). In this environment, red “griottes” limestones were deposited
266 with shaly beds and turbidites (Ouali Mehadji et al., 2012; Abbache et al., 2019).
267 Ammonoids, brachiopods and trilobites were found within the nodular limestones (Benhamou
268 et al., 2004; Crônier et al., 2013; Mottequin et al., 2015, Allaire et al., 2020). Although this
269 facies is not an indicator of palaeobathymetry (Benhamou et al., 2004), Abbache et al. (2019)
270 concluded that these sediments were deposited in a basinal environment. The *Nereites*
271 ichnofacies confirms this kind of deep environment (Bendella et al., 2014). Ouali Mehadji et
272 al. (2012) identified a narrow basin during the middle Famennian leading to a more
273 homogeneous elongated basin in the late Famennian.

274 At the end of the Famennian, a fine-grained clastic sedimentation, the Hangenberg Black
275 Shale, was sedimented in most parts of north-western Africa (Kaiser et al., 2011; Klug et al.,

276 2016). Sandy marls and cross-bedded sandstones covered the southern part of the Tafilalt
277 Platform (Wendt et al., 1984). In Ougarta, sandstone beds occurred that were devoid of fossils
278 and sometimes included channels (Abbache et al., 2019). Within sandstones assigned to the
279 “Grès de Ouarrourout” Formation, Ouali Mehadji et al. (2012) identified the maximal
280 regression surface.

281 At the beginning of the Tournaisian, the Tafilalt and southern Maïder Platforms
282 corresponded to a deltaic environment (Wendt et al., 1984). The Ougarta region corresponded
283 to a siliciclastic platform (Abbache et al., 2019) with temporary emersions leading to deltaic
284 environments or lagoons (Ouali Mehadji et al., 2012).

285 In the southern Ougarta region, in the Erg Djermel area, no trilobites were found within the
286 Upper Devonian deposits, i.e., in black shale deposits corresponding to deep environments
287 from the Frasnian to the late Famennian (Abbache et al., 2019). In the north of Ougarta, in the
288 Ben-Zireg area, trilobites have not yet to be recorded within “griottes” calcareous deposits
289 associated with rare shaly layers corresponding to a middle to distal platform (Abbache et al.,
290 2019). In Morocco, the Foum Zguid area and the Dra Valley deepened from the Eifelian to
291 the late Famennian due to global transgression (Becker et al., 2004). These deep environments
292 are not favourable to the development of trilobite communities and thus fossils are rare apart
293 from ammonoids and crinoids (Hollard, 1963; Becker et al., 2004).

294

295 3. Material and methods

296 3.1. Material

297 In order to analyse the trilobite records and their shifts, we completed an existing dataset
298 (Bault et al., 2021) based on the occurrence of trilobites from Morocco and Algeria (Fig. 1).
299 77 studies from the literature were considered because of their updated taxonomy and/or good
300 temporal resolution (Appendix A). The dataset contains 2892 specimens (Appendix B) from

301 the Lochkovian to the Famennian distributed within 69 localities from five basins (Fig. 1).
302 Sections separated by a few hundred metres were combined within the same locality. To
303 avoid possible duplicates the specimen count was restricted to only the highest number of
304 complete exoskeletons plus the disarticulated cephalia or pygidia per occurrence. Other parts
305 of trilobites such as free cheeks or hypostomes were not included. For each relevant
306 occurrence, the dataset contains the following information: taxonomic information,
307 abundance, location, stratigraphic position (substages) and lithological information
308 (formations). Throughout our data compilation work, only genera were considered to
309 maximise potential correlations between the distinct assemblages, as many species are only
310 described locally. Species level is often inadequate for biodiversity purposes (Cecca, 2002).
311 As the Late Devonian *Phacops* Emmrich 1839 differs from the Early and the Middle
312 Devonian representatives of the genus, they were counted as a distinct genus called *Phacops*
313 sensu lato (Crônier et al., 2011). We used a preliminary revision of asteropygines in open
314 nomenclature while waiting for the revision of the whole subfamily. As a result, previous
315 *Metacanthina* species *M. issoumourensis* Morzadec, 2001, and *M. maderensis* Morzadec,
316 2001 are joined with *Minicryphaeus giganteus* Bignon et al., 2014 in the Genus 1, whereas
317 *Asteropyge wallacei* Termier and Termier, 1950 is included in the Genus 2. Overall, the
318 dataset comprises 135 genera (Appendix B) used for biodiversity indices (see section 4.3).
319 However, we excluded genera found in only one sample because they did not provide any
320 linkage with others samples for the clustering, which led to a selection of 67 genera spread
321 over 123 samples (or assemblages) used for a cluster analysis.

322

323 3.2. Clustering

324 An analysis of associations was carried out using 123 samples at a given substage and
325 formation to help us understand the temporal and spatial relationships between trilobite faunas

326 and their environments. The term association is used here for recurrent assemblages of
327 trilobites with a similar taxonomic composition (Brenchley & Harper, 1998; Crônier & Van
328 Viersen, 2007; Crônier & François, 2014; Bignon & Crônier, 2015). To reduce sampling bias
329 the relative abundances of 67 genera were quantified in seven classes, i.e., the percentage of
330 the abundance of each genus in a sample (Harnik, 2009). Indeed, the number of specimens is
331 influenced by the sampling effort (Thompson, 2004), which cannot be estimated as our data
332 were obtained from various bibliographic references.

333 Data were analysed using a hierarchical cluster analysis (HCA). This agglomerating
334 technique groups recurring samples according to their level of taxonomic similarity (Davis,
335 1986; Harper, 1999; Hammer & Harper, 2008). It produces dendrograms highlighting the
336 relationships in two modes - an R-mode clustering, grouping the taxa according to their
337 probability of co-occurrence and a Q-mode clustering, grouping the samples, i.e., of similar
338 generic composition. HCA was carried out using the average linkage algorithm and the
339 Pearson correlation similarity index (Hammer & Harper, 2008).

340 To identify environmental gradients, a Detrended Correspondence Analysis (DCA) was
341 carried out. Correspondence Analysis (CA) is suitable for grouping samples from taxonomic
342 abundance (Greenacre, 1984; Jongman & Jongman, 1995; Legendre & Legendre, 1998) but
343 DCA is more reliable (Hammer & Harper, 2008; Holland et al., 2001; Bonelli & Patzkowsky
344 2008) for reducing the Pinocchio (Fig. SUPPL. A1) and arch effects (Fig. SUPPL. A2). This
345 ordination method maximises the correspondences between taxa and samples. It also provides
346 ordination scores for both taxa and samples according to the relative abundance of taxa by
347 involving a compression of the total information along the first axis, which often reflects
348 paleoenvironmental gradients (Hammer & Harper, 2008). Unfortunately, several taxa need
349 modern revision to clarify their generic determination. Moreover, microfacies analyses would

350 be suitable for a better characterization of the environments. In their absence, an additional
351 DCA would improve our determination of the relationships between some samples.

352 Finally, an analysis of similarities (ANOSIM) was carried out to statistically test the
353 differences in the generic composition of groups of taxa. This non-parametric test is based on
354 Bray-Curtis dissimilarity values as it only uses the rank order of dissimilarity values between
355 groups and within groups (Clarke, 1993; Hammer & Harper, 2008). P-values were obtained
356 through 5000 random permutations.

357

358 3.3. Diversity indices

359 To complete the multivariate analysis information and help understand the impact of
360 migrations and environmental changes on the diversity, α and β diversities (Whittaker, 1960)
361 were estimated. The total taxa diversity is determined by the mean taxa diversity at the habitat
362 level (α) and the differentiation among habitats (β). The Shannon index H' of α diversity was
363 used to take into account the number of taxa within a sample (taxa richness) and the
364 individual distribution within these taxa (taxa equitability). It considers the relative abundance
365 of each taxon and gives weight to rare species. This index varies from 0 for a sample with
366 only one single taxon to high values for samples with many taxa. $H' = -\sum_{i=1}^S p_i \log_2 p_i$,
367 with S the number of taxa and $p_i = \frac{n_i}{N}$, with n_i the number of individuals of the taxon i and N
368 the number of individuals for all taxa. The Shannon index H' of α diversity was estimated
369 through time according to substages or formations and through environment according to
370 associations. Diversity for associations is calculated as the mean taxonomic richness of
371 samples of each association while the diversity for substages or formations is calculated as the
372 total taxonomic richness in these stratigraphic units.

373 Several measures related to compositional heterogeneity of β diversity were used to
374 quantify differentiation (Baselga, 2010; Balsega & Orme, 2012). The first measure is an index

375 of taxa replacement (i.e., turnover) emphasizing the role of rare taxa as the difference in taxa
376 composition between localities measured as Simpson dissimilarity (i.e., turnover component
377 of Sørensen dissimilarity). This measure enables the identification of the environmental
378 impact or spatial and temporal constraints on the number of taxa that are replaced between
379 localities (Qian et al., 2005). The second measure is an index of nestedness, which occurs
380 when taxa-poor assemblages are a subset of more diverse assemblages (Wright & Reeves,
381 1992; Ulrich & Gotelli, 2007) measured as nestedness-resultant component of Sørensen
382 dissimilarity (Baselga, 2010). This measure indicates non-random species loss as common
383 species are less likely to disappear (Gaston et al., 2000). The last measure is an index of the
384 Overall β diversity measured as Sørensen dissimilarity (Sørensen, 1948) corresponding to the
385 global taxonomic difference between samples. Components of β diversity were estimated
386 through time between substages and through environment between associations.

387 HCA, ANOSIM, DCA and Shannon index H' were achieved by using the software PAST
388 v3.24 (Hammer et al., 2001). β diversity was computed by using the 'Betapart' package
389 (Baselga & Orme, 2012) in the R statistical environment (version 3.6.3; R Core Team 2020).

390

391 **4. Results**

392 4.1. Delineated associations and faunal gradients

393 The 67 trilobite genera distributed within the 123 assemblages are grouped into 16
394 associations or occurrences, in four main clusters by HCA (Fig. 4; details in fig. Suppl. B).

395 Details of each trilobite association are given in table.

396

Table near here

397 Cluster I groups five associations (i.e., *Morzadecops* Association Ia, *Ganetops* Association
398 Ib, *Montanproetus* Association Ic, *Sculptoproetus* Association Id and *Piriproetus* Association
399 Ie), covering the entire Early Devonian and the early Eifelian; Cluster II groups six

400 associations (i.e., *Hollandops* Association *Ia*, *Morocops* Association *Ib*, *Gerastos*
401 Association *Ic*, *Chotecops* Association *IId*, *Paralejurus* Association *Ile* and *Psychopyge*
402 Association *IIf*), from the Pragian to the Givetian; Cluster III groups only one association
403 (*Lepidoproetus* Association *IIIa*) mainly found in the Maïder during the Pragian. Finally,
404 Cluster IV groups all four associations (*Cyrtosymbolina* association *IVa*, *Osmolskabole*
405 Association *IVb*, *Trimeroccephalus* Association *IVc* and *Phacops s.l.* Association *IVd*)
406 restricted to the Late Devonian (Famennian) of the Tafilalt and Ougarta. The ANOSIM results
407 show a significant difference between the 16 associations (R coefficient = 0.59, p value =
408 0.0002).

409 Fig. 4 near here

410 DCA enabled us to offset HCA limits and better understand the spatio-temporal
411 distribution of the assemblages according to their taxonomic record. The Famennian samples
412 did not share trilobites with the Early and Middle Devonian (Fig. 4) so they were removed
413 from DCA to avoid a Pinocchio effect and were analysed in an additional DCA (Fig. 5).
414 Similarly, the early Famennian samples BJ-Fa26 and Be-Fa26 were removed.

415 Fig. 5 near here

416 For the Early and Middle Devonian, DCA shows a time trend (Fig. 5A). The Early
417 Devonian (Lochkovian, Pragian and early Emsian) associations show the highest values on
418 both DC1 and DC2 axes, whereas the Middle Devonian associations show the lowest values
419 on both DC1 and DC2 axes (Fig. 5A). The Early Devonian associations group mostly the
420 Order Phacopida, whereas the Middle Devonian associations group mostly the Order Proetida
421 (Fig. 5A).

422 However, a look at the results in detail shows five associations are not overlapped by
423 others along one axis of DCA or another. The *Chotecops*, *Morzadecops*, *Ganetops* and
424 *Sculptoproetus* associations are clearly independent along the DC1 axis and the *Paralejurus*

425 and *Lepidoproetus* associations alone appear along the DC2 axis in the higher values (Fig.
426 5A). These associations belong to either the Lochkovian, or Pragian, or early Emsian or
427 Givetian. In contrast, late Emsian and Eifelian associations were strongly overlaid on both
428 axes.

429 For the Famennian, DCA shows a geographic gradient along DC1 axis, from Ougarta with
430 the lowest values to the Tafilalt having the highest ones (Fig. 5B).

431

432 4.2. Temporal and spatial distribution of clusters

433 4.2.1. Early Devonian

434 Details of temporal and spatial distributions are given in supplementary figures (Figs.
435 SUPPL. C to H). During the Lochkovian, trilobites seemed restricted to the Ougarta Basin.
436 They were few and dominated by the *Ganetops* genus (within Ass. *Iib*), which was the sole
437 genus in the southern part of the Ougarta region (Fig. 6). To the North, *Ganetops* was
438 associated with the *Morzadecops* genus at Zerhamra - the only genus capable of persisting in
439 the Pragian, which thus occurs in another association (i.e., *Morzadecops* Association *Ia*).

440 At the beginning of the Pragian, trilobites flourished in the Anti-Atlas area but are
441 unknown from the Ougarta Basin. Four associations covered this period but two were more
442 dominant, widespread over all the Anti-Atlas and intersected (Fig. 4), the *Lepidoproetus* (*IIIa*)
443 and *Paralejurus* (*Iie*) associations. The *Paralejurus* Association occurred in the Ben Zireg
444 area and developed in the Tafilalt and the Maïder areas too, whereas the *Lepidoproetus*
445 Association occurred predominantly in the Maïder area although it occurred also in the south-
446 western part of the Tafilalt area (Fig. 6). These two widespread associations were strongly
447 affected during the Emsian: the *Paralejurus* Association (*Iie*) disappeared and the
448 *Lepidoproetus* Association (*IIIa*) occurred only in the Dra Valley (at Lansser locality) for the
449 last time in the late Emsian. The *Sculptoproetus* Association (*Id*) and *Morocops* Association

450 (*Iib*) appeared in the Maïder area (respectively at Timarzite and Maharch localities) during
451 the Pragian but were rarer. They developed considerably during the Emsian where they
452 occurred in almost all basins (Fig. 6). The Emsian is represented by nine associations (Fig. 4).
453 In addition to the three associations, which had already occurred in the Pragian, five new ones
454 appeared in the early Emsian and an additional association in the late Emsian. The
455 *Morzadecops* Association (*Ia*) proliferated everywhere in the early Emsian but disappeared
456 immediately afterwards. The *Psychopyge* (*IIf*) and *Hollardops* (*Ila*) associations originated in
457 the early Emsian of Ougarta and then colonised the Anti-Atlas area during the late Emsian
458 (Fig. 6). The *Montanproetus* (*Ic*) Association lasted until the late Emsian and extended from
459 the Anti-Atlas toward the west (Ben Zireg). The two latter associations were rare during the
460 Emsian: The *Piriproetus* Association (*Ile*) is present only in two north-western Tafilalt
461 localities (Gara Mdouard-Jbel Issoumour) and the *Gerastos* Association (*Ilc*) only during the
462 late Emsian of the Maïder area (Jbel Issoumour SW).

463 Fig. 6 near here

464

465 4.2.2. Middle Devonian

466 Five Early Devonian associations are still found in the Eifelian but the *Hollardops* and
467 *Sculptoproetus* associations disappeared after the early Eifelian. These associations were
468 already rare and restricted to one basin: the *Hollardops* Association was restricted to the
469 western part of the study area (i.e., Maïder and Foug Zguid areas) and the *Sculptoproetus*
470 Association stayed confined in the Tafilalt area (Jbel Amlane, Fig. 7). In contrast, the
471 *Morocops* Association continued to be widespread in different basins during the early Eifelian
472 but also disappeared in the late Eifelian in many places despite a last occurrence (i.e.,
473 presence of *Koneprusia*) during the late Givetian in the north-western Tafilalt (Ras el Kebbar
474 locality). Similarly, the *Piriproetus* Association (*Ie*), which appeared in the northern Tafilalt

475 during the Emsian, proliferated during the early Eifelian but has not been recorded in strata
476 laid down later. They developed everywhere in the northern Tafilalt area but never occurred
477 elsewhere. Conversely, the *Gerastos* Association (*IIC*) occupied exclusively the Maïder area
478 where it appeared during the late Emsian although some *Gerastos* were also found
479 outnumbered in one Tafilalt locality and one Dra Valley locality. During the Givetian, the
480 *Gerastos* Association (*IIIh*) was still limited to the Maïder area but also developed in the
481 western part of the platform at Jbel Ou Driss (Fig. 7). Finally, the *Chotecops* Association (*IIId*)
482 was first identified in the Ougarta area (Ouarourout) during the early Eifelian before invading
483 the Tafilalt area during late Eifelian (Fig. 7). The *Chotecops* Association (*IIj*) was still found
484 in the western and the southern Tafilalt area during the Givetian but was apparently no longer
485 present in Algeria. All these associations disappeared at the end of the Givetian.

486 Fig. 7 near here

487

488 4.2.3. Late Devonian

489 Only one genus occurred in the study area during the Frasnian, at Marhouma in the
490 Ougarta region. *Chlupacops* is not found in another stage or in another locality and has not
491 been attributed to a particular association.

492 During the early Famennian, the Tafilalt area was only occupied in its northern part (at Bin
493 Jbilit-Bordj Est locality) by the genus *Cyrtosymbolina* (from Ass. *IVa*, Fig. 8). At the same
494 time, in the western Ougarta (Marhouma), the biodiversity was greater with three identified
495 genera, which are equally abundant within the *Trimerocephalus* Association (*IVc*). When the
496 *Cyrtosymbolina* association disappeared during the middle Famennian, the *Trimerocephalus*
497 Association invaded the Ougarta region but also the western edge of the Tafilalt area. In the
498 extreme south-east of this area (Tamtert Zereg locality), the new *Phacops s.l.* Association
499 (*IVd*) appeared. This genus is also associated with *Trimerocephalus* in the Tafilalt area

500 ('KeA-Fb34' sample) (Fig. 4). The *Phacops s.l.* Association replaced the *Trimerocephalus*
501 Association in many late Famennian localities although *Trimerocephalus* remained only at
502 Bechir locality (Ougarta). However, none of these two associations have been found in the
503 uppermost Famennian. In the Tafilalt area, the *Osmolskabole* Association (*IVb*) replaced the
504 *Cyrtosymbolina* Association (*IVa*) in many places from the middle Famennian and persisted
505 until the latest Famennian where they occurred only in the extreme north-western part (at
506 'Bordj Est' locality, Fig. 8). *Osmolskabole* was found with *Trimerocephalus* and *Phacops s.l.*
507 only at Korb-el-Atil (Morocco) during the middle Famennian.

508 Fig. 8 near here

509

510 4.3. Evolution of biodiversity indices through time

511 α and β diversity were low in the late Lochkovian with Shannon index H' of 1.06 and
512 overall β diversity of 0.2 (Fig. 9A). Then, the diversity indices increased during the Pragian
513 reaching a plateau of high diversity until the early Eifelian with Shannon index $H' > 2$ and
514 overall β diversity > 0.9 . The diversity indices decreased progressively during the late Eifelian
515 to the early Givetian, before a sharp decrease from the middle Givetian to the end of the
516 Frasnian with null or almost null values. In the early Famennian, both α and β diversity
517 indices increased again. However, when the α diversity index stayed low compared to that of
518 the Early and the Middle Devonian with a Shannon index H' of 0.84, overall β diversity
519 reached values similar to the Early Devonian. In the late Famennian, α diversity increased to
520 1.89 before decreasing in the latest Famennian. During this period, overall β diversity evolved
521 differently with a slight decrease in the middle Famennian followed by an increase in the late
522 Famennian, the time of the highest disparity of the Late Devonian (Fig. 9A). Components
523 related to compositional heterogeneity of β diversity show different trends. The β turnover
524 component follows the overall β diversity trends whereas the β nestedness component always

525 shows lower values (Fig. 9A) indicating that most of the β diversity corresponds to the
526 replacement of genera by others in different localities (Balsega, 2010). Moreover, β
527 nestedness component changed exactly oppositely to the overall β diversity in the Early and
528 the Middle Devonian (Fig. 9A). Consequently, during periods of low diversity, the localities
529 with smaller numbers of species were subsets of biotas found in localities with greater
530 trilobite diversity.

531 Fig. 9 near here

532 Trilobite association of the Tafilalt remained diverse during nearly all the Devonian
533 contrary to the Maïder and Ougarta where the associations contained in the formations were
534 unevenly diverse (Fig. 9B). Although the presence of trilobites at Ben Zireg and Foum Zguid
535 areas were not continuous through time, Shannon index H' was relatively high as in the other
536 basins (Fig. 9B). The formations from the late Emsian and the Eifelian contained the most
537 diverse trilobite faunas in all basins (Fig. 9B).

538

539 **5. Palaeoenvironments of trilobite associations**

540 It is widely known that trilobite associations vary between regions but the ecological
541 drivers are largely unknown. HCA performed on the Devonian trilobite taxa of Morocco and
542 Algeria enabled us to delineate twelve Early and/or Middle Devonian associations and four
543 Late Devonian associations. The associations reflect distinctive taxonomic affinities and
544 palaeoenvironmental preferences. Similar analyses on Devonian trilobites from the Ardenne
545 Massif showed that trilobite associations were dependent on palaeobathymetric domains and
546 sea-level variations (Crônier & Van Viersen, 2007). Subsequently, these associations (most
547 particularly during the Givetian) were highlighted as equilibrated communities were able to
548 maintain their organisation during rather strong and short environmental perturbations. These

549 associations were able to flourish again during similar favourable environmental conditions.
550 Only global events influenced the trilobite association (Bignon & Crônier, 2015).

551 During the Lochkovian, trilobites were rare in the study area. Only *Ganetops*,
552 *Protacanthina* and to a lesser extent, *Morzadecops*, proliferated during the late Lochkovian in
553 the Ougarta region (Ass. *Ila*). These asteropygines preferred the shallow siliciclastic
554 environment of the Saoura Valley (Fig. 6; Morzadec, 1997) and similar environmental
555 settings, also developing in the Iberian and Cantabric ranges and in the Armorican Massif
556 (Morzadec, 1992). Subsequently, an increasing number of trilobites began to populate the
557 region. Their remains are frequently found in the strata, whose carbonate content is also
558 increasing. This suggests a lower sea-level and concerns distinct invertebrate faunas (Frey et
559 al., 2014). In such environments, the *Lepidoproetus* Association (*IIla*) flourished; proetids
560 like *Lepidoproetus*, *Dalejproetus* and *Podoliproetus* preferred these rather shallow
561 environments with open marine conditions (Johnson & Fortey, 2012). The *Lepidoproetus*
562 Association survived during the late Emsian of the Dra Valley in deeper water environments.
563 Trilobites of this association are usually found in calcareous shales deposited above the photic
564 zone but probably below the storm weather wave base (Chatterton et al., 2006). However,
565 only *Hollandiella* was encountered in these deeper environments and in layers above the
566 transgressive Daleje event (House, 1985).

567 During the Pragian, the *Paralejurus* Association (*IIId*) also established itself (Fig. 6).
568 *Paralejurus* and *Reedops* were predominant in limestones at intermediate depth but also in
569 shallower environments such as the bioherms of Hamar Laghdad (McKellar & Chatterton,
570 2009). *Reedops* was probably semi-infaunal or infaunal (McKellar & Chatterton, 2009)
571 whereas Schraut & Feist (2004) excluded a semi-endobenthic life habit for *Paralejurus*.
572 Consequently, these two genera were rarely found together notwithstanding some exceptions -
573 *Paralejurus* co-occurred with *Reedops cephalotes hamlagdadianus* Alberti 1983 but the latter

574 species appears to have been ecologically more flexible with respect to the type of substrate
575 (Chlupáč, 1977). During this period, the *Sculptoproetus* Association (*Ile*) developed and is
576 often found in the nodular marly limestones from the north-eastern part of Jbel Issoumour
577 (Alberti, 1967b, 1969), indicating a slightly deeper environment than those preferred Pragian
578 associations. The *Sculptoproetus* Association evolved during the Emsian; *Sculptoproetus*
579 abounds in marly limestones indicating an intermediate water depth environment (Fig. 6).

580 During the Emsian, *Morzadecops* first associated with other asteropygines during the
581 Lochkovian, flourished and dominated the *Morzadecops* Association (*Ia*). *Morzadecops*
582 occurs in marls and limestones interbedded with clay in moderately shallow water depth
583 environments (Klug et al., 2008). The *Montanproetus* Association (*Ic*) also developed during
584 the Emsian but it was mainly found in calcareous deposits in shallow carbonate environments
585 (Fig. 6). The associated *Kayserops* preferred a more shallow environment (Morzadec, 2001).
586 *Psychopyge* is widely distributed in several marine basins during the Emsian. It was rarely
587 associated to other genera (Fig. 4) and dominated the *Psychopyge* Association (*IIf*). The
588 *Psychopyge* are present in marls or limestones interbedded in thick marl deposits from
589 relatively distal environments dominated by pelagic faunas (Morzadec, 1988).

590 Although the *Morocops* Association (*IIfb*) was first encountered during the Pragian at the
591 Maharch locality with the presence of *Cyphaspis* (Van Viersen & Holland, 2016), it
592 proliferated in the late Emsian and the early Eifelian. This association was dominated by
593 *Morocops*, which co-occurred with *Cyphaspis* and *Austerops*. The presence of *Austerops*
594 could indicate a pioneer community (Khaldi et al., 2016). The *Morocops* Association also
595 developed in the moderately deep-water environment of the Dra Valley (Chatterton et al.,
596 2006) and the platform environment of Ougarta after the late Emsian transgression (Khaldi et
597 al., 2016). It was also able to live in the epicontinental basin between fair weather and storm
598 wave base of Hamar Laghdad (Brachert et al., 1992). Hence, the *Morocops* Association

599 abounded in a water environment below the fair-weather wave base. At the same time, the
600 *Piriproetus* Association (Ia) was encountered at the edge of the pelagic Tafilalt Platform in
601 moderate depth below the fair-weather wave base (Figs. 6,7); Kaufmann, 1998; Chatterton et
602 al., 2020). *Piriproetus* occurred in a facies dominated by marly limestones but they
603 disappeared from this environment after the early Eifelian.

604 During the late Emsian, the *Hollardops* Association (IIa) also flourished and was
605 dominated by *Hollardops*, *Timsaloproetus* and *Erbenochile*. These taxa proliferated in marls
606 or limestones interbedded within marls. They were mostly present in Ougarta, an area
607 considered relatively deep and dominated by shales (Ouali Mehadji et al., 2011) (Fig. 6). A
608 similar environment developed in the western Dra Valley where *Timsaloproetus* was found
609 (Chatterton et al., 2006). *Hollardops* enjoyed in intermediate water depth below fair-weather
610 wave base like in the Maïder and the Ougarta region (Chatterton & Gibb, 2010) but they
611 disappeared with a more open marine environment (Morzadec, 2001). Finally, *Erbenochile*
612 proliferated in relatively deep marine environments (Chatterton et al., 2006), which
613 corroborates the moderately deep marine conditions such as an offshore transition for the
614 *Hollardops* Association. The *Gerastos* Association (IIc) also flourished during the Emsian at
615 Jbel Issoumour South-west (Fig. 6). In this balanced community (Fig. 4), *Morocops* or
616 *Cyphaspis* did not prevail over *Gerastos* contrary to many late Emsian assemblages affiliated
617 with the *Morocops* Association. Conversely, the *Gerastos* associations from the Middle
618 Devonian were dominated by *Gerastos*, which was the only genus in many localities (Fig. 4).
619 *Gerastos* is found in limestones from the Maïder where they found detritus for food in the
620 shallow shelf marine environment (Gibb & Chatterton, 2010).

621 The *Chotecops* Association (IId) was the only association to appear and expand during the
622 Middle Devonian and was dominated by *Chotecops* associated with *Helmutia* and
623 *Struveaspis*. The *Chotecops* Association was encountered in Ougarta and Tafilalt (Fig. 7) in

624 marls or in thin limestone layers in marl deposits from the quiet environments of a distal
625 platform or basin (Feist & Orth, 2000; Crônier et al., 2018a).

626 All the associations that appeared during the Early or Middle Devonian disappeared in the
627 late Givetian. Only *Chlupacops*, a genus with reduced-eyed taxa was found in the limestones
628 of deep marine environments in the Ougarta Basin (Feist et al., 2016).

629 After the Kellwasser event, trilobites were rare in the study area. The first trilobite after the
630 crisis was *Cyrtosymbolina* in the early Famennian. The increasing depth of water during the
631 Famennian (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) led to trilobites
632 flourishing again, which meant we could use them to examine the relationships between
633 different basins over time. During the early Famennian, only cyrtosymbolines proliferated in
634 the shallow pelagic Tafilalt Platform in the *Cyrtosymbolina* Association (IVa). They became
635 common in the photic offshore environments of North Africa and many other places
636 (Lerosey-Aubril & Feist, 2012). Members of the *Cyrtosymbolina* Association occur mainly in
637 limestones but also in marlstones and argillaceous limestones, such as shallow carbonate
638 marine environments (Fig. 8).

639 In the Ougarta Basin, blind trilobites such as *Trimerocephalus*, *Trifoliops* and *Enygmapyge*
640 occurred since the early Famennian. The *Trimerocephalus* Association (IVc) established in
641 many localities of the Ougarta Basin (Fig. 8) in deep marine environments of the slopes and
642 basins. They were collected from rare often nodular limestones indicating a weak water
643 circulation (Benhamou et al., 2004; Crônier et al., 2013). *Trimerocephalus* also occurred at
644 Korb-el-Atil in the Tafilalt Basin associated with *Osmolskaboie* and *Phacops sensu lato* (Fig.
645 8) within a marine environment dominated by shales (Wendt & Belka, 1991). During the late
646 Famennian, the *Trimerocephalus* Association is only found at Béchir, again in a deep marine
647 environment, before its demise at the end of the Famennian.

648 The *Osmolskabole* Association (*IVb*) appeared during the middle Famennian in the
649 limestones of the Tafilalt Platform (Fig. 8) because they appreciated the photic offshore
650 environment. Consequently, this pelagic platform became convenient for the members of this
651 association because of the sea-level rise (Wendt & Belka 1991). The *Osmolskabole*
652 Association also flourished in the deeper marine environments of the slowly subsiding Tafilalt
653 Basin (at Korb-el-Atil and Ouidane Chebbi localities), in argillaceous limestones.
654 Nonetheless, this association did not occur in the Maïder Basin because this area was deeper
655 than the Tafilalt Basin (Wendt et al., 1984).

656 During the late Famennian, Cyrtosymbolines were still abundant in the Tafilalt Platform.
657 However, the *Osmolskabole* Association was no longer present in the Tafilalt Basin, probably
658 due to a transgression (Wendt & Belka, 1991; Becker et al., 2004). At the end of the
659 Famennian, the *Osmolskabole* Association is still found in the limestones of the north Tafilalt
660 Platform whereas the south became a deltaic area (Wendt et al., 1984). Indeed, trilobites did
661 not appreciate brackish water although some attempts to colonize these environments
662 happened in the clade history (Mángano et al., 2021). The *Osmolskabole* Association and
663 cyrtosymbolines in general were restricted to moderate water depth environments from
664 platform to slope, which are represented today by limestone deposits.

665 Finally, the *Phacops s.l.* Association (*IVd*) flourished in the Ougarta region (at Tamtert
666 Zereg locality) during the Famennian, to the east of the location of the *Trimerocephalus*
667 Association (Fig. 8) in nodular ‘griotte’ limestones corresponding to a basinal environment
668 (Benhamou et al., 2004). The *Phacops s.l.* Association extended into the late Famennian with
669 the continuous deepening of this area (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et
670 al., 2019) and replaced the *Trimerocephalus* Association (at Marhouma locality). The
671 *Phacops s.l.* Association still abounds in nodular limestones alternating with claystones, or in
672 marlstones, in moderate to deep marine environments such as basins. Samples with *Phacops*

673 *s.l.* are generally slightly younger than those of *Trimerocephalus* even if these two genera
674 may co-occur (Crônier et al., 2013). Therefore, a progressive replacement occurred in the
675 Ougarta Basin in the deeper offshore environment and already recognised at the global scale
676 (Crônier & François, 2014). At the end of the Famennian, a sea-level drop occurred and all
677 the deep water trilobites disappeared from the studied area.

678

679 **6. Connection between basins and their history through time**

680 6.1. Lochkovian

681 Trilobite diversity was low in the study area in the Lochkovian (Fig. 9A). They only
682 occurred in the Saoura Valley where trilobites populated the sediment surface in the late
683 Lochkovian after a regional regression (Ouali Mehadji et al., 2011). Only asteropygines lived
684 in these shallow siliciclastic environments (Morzadec, 1997). To the west, the eastern Anti-
685 Atlas became too deep to allow benthic faunas to settle during the Lochkovian (Hollard,
686 1967) and thus, this environment was neither favourable for asteropygines (Morzadec, 1992),
687 nor for other trilobites as they were completely absent from this area.

688

689 6.2. Pragian

690 The Pragian regression led to a higher carbonate content with more sand in the Saoura
691 Valley where asteropygines no longer proliferated (Morzadec, 1997; Ouali Mehadji et al.,
692 2011). Indeed, the composition of trilobite associations was linked to the sediment
693 accumulation rate and the type of shelf (Bignon & Crônier, 2015) and no other trilobites
694 replaced them. The eastern Anti-Atlas became more carbonate too (Hollard, 1963; Kaufmann,
695 1998). New trilobite communities were established (Hollard, 1967; Morzadec, 2001) in these
696 favourable environments leading to a strong increase of their diversity in North Africa (Fig.
697 9A) simultaneously to the global Pragian diversification (Chlupáč, 1994, Bault et al., 2021).

698 However, despite this high diversity three genera dominated the shallow water environments
699 of the Anti-Atlas region: *Paralejurus*, *Reedops* and *Lepidoproetus*. These genera and some
700 other genera, constituted two associations: the *Paralejurus* Associations was dominant in the
701 Maïder and the *Lepidoproetus* Association was dominant in the Tafilalt (Fig. 6). Nevertheless,
702 the *Paralejurus* Association developed to the west in the Tafilalt and in the north of the
703 Ougarta region at Ben Zireg and to the east near Fom Zguid. Thus, there was a strong
704 connection between these different basins during the Pragian. This is due to a relatively
705 homogeneous environment in the Anti-Atlas region at this time, considered as a homoclinal
706 ramp (Kaufmann, 1998; Lubeseder et al., 2010). Exchanges also occurred with the
707 neighbouring Bechar area, which was facilitated by the same carbonate platform environment
708 (Ouali Mehadji et al., 2011) and with the south-west Fom Zguid area where *Reedops* and
709 *Cyphaspis* were reported. All the Pragian trilobites populated in a relatively shallow
710 environment of various carbonate platforms. However, *Paralejurus* and its associated
711 trilobites preferred slightly deeper environments than *Lepidoproetus*, which is why they rarely
712 co-occurred. The shoal of Hamar Laghdad (Hollard, 1981, Brachert et al., 1992; Klug et al.,
713 2018) showed a high diversity of trilobites.

714

715 6.3. Emsian

716 In the early Emsian, diversity decreased (Fig. 9A). While the Pragian dominant species
717 almost disappeared from the studied area, other genera proliferated despite no important
718 environmental changes in the Anti-Atlas (Kaufmann, 1998). *Morzadecops* spread over the
719 entire eastern Anti-Atlas and *Sculptoproetus* lived in the Tafilalt. In the Ougarta region, a
720 local transgression (Ouali Mehadji et al., 2011) led to a comeback of trilobites with the
721 moderately deep water genus *Psychopyge* but no connection existed with the Anti-Atlas;
722 Ougarta region remained isolated from other basins to the west and to the north. The Bechar

723 basin was also excluded from the trilobite dispersal with *Prodrevermannia* the only genus
724 occurring in that region (Alberti, 1983). *Morzadecops*, which preferred a shallow environment
725 (Morzadec, 2001), could not proliferate in the Ougarta region. However, although
726 *Sculptoproetus* lived in moderately deep-water (Chatterton et al., 2006), it was not found in
727 the Ougarta region. Hence, the deep waters of the Tafilalt Basin between Ougarta and Anti-
728 Atlas prevented the dispersal of shallow and moderately deep-water trilobites from one of
729 these regions to the other.

730 In Morocco, the Maïder and Tafilalt platforms were still connected and the *Morzadecops*
731 Association (*Ia*) flourished in both areas. However, the *Sculptoproetus* Association (*Id*) was
732 restricted to the Tafilalt area while it appeared in the Maïder area during the Pragian. The
733 Tafilalt area being typically shallower than the Maïder area (Wendt, 1995), trilobites migrated
734 to shallower places but no transgression occurred at this time (Kaufmann, 1998). There were
735 no more dispersal to the south-west as the Foug Zguid area became shallower (Jansen et al.,
736 2004) where trilobites did not develop.

737 During the late Emsian Daleje transgression (Johnson et al., 1985; Kaufmann, 1998;
738 House, 2002), the studied area became deeper (Kaufmann, 1998, Belka et al., 1999).
739 Trilobites developed in this new environment leading to the highest α diversity and a high β
740 diversity (Fig. 9A) simultaneously with the global diversity peak (Chlupáč, 1994; Adrain,
741 2008). Late Emsian trilobites constituted a stable equilibrium community. Some of the
742 common trilobites of the Pragian persisted into the early Emsian, such as *Paralejurus*,
743 *Reedops* and *Sculptoproetus*. However, no Pragian or early Emsian trilobite genus became
744 common in the late Emsian; they were all declining and restricted to few areas. The only
745 exception was *Psychopyge*, which invaded the Anti-Atlas. Thus, during this period of
746 diversification, the genera quickly renewed themselves by showing innovations and novelties
747 (Chlupáč, 1994). Numerous genera appeared in the late Emsian and among them with the

748 phacopids *Morocops* and *Hollardops* respectively dominating the Anti-Atlas (Crônier et al.,
749 2018b) and the Ougarta region. Connections between the different basins were strong,
750 favoured by the relatively homogeneous environments in North Africa, moderately deep
751 water, with an important proportion of muddy regions (now shales) covering the platforms
752 (Hollard, 1967; Kaufmann, 1998; Jansen et al., 2004; Chatterton et al., 2006; Ouali Mehadji et
753 al., 2011). Exchanges between Anti-Atlas and the deeper Ougarta region became possible:
754 *Hollardops* and *Erbenochile* occurred in Ougarta, Maïder and Dra Valley (Morzadec, 2001;
755 Chatterton et al., 2006; Chatterton & Gibb, 2010; Khaldi et al., 2016). *Psychopyge* were also
756 found in both the eastern Anti-Atlas and the Ougarta region (Fig. 6). Although the Tafilalt and
757 Maïder areas became different during the late Emsian in terms of both facies and fauna
758 (Hollard, 1967), a strong connection was present between these two areas. *Sculptoproetus*
759 proliferated in the Maïder area suggesting an invasion from the Tafilalt area. At the same
760 time, *Morocops*, as well as *Cyphaspis*, flourished in the Tafilalt, Maïder and near Foug Zguid
761 areas. Ben Zireg was also involved in the exchanges with *Montanproetus* existing in the
762 Bechar Basin and the Maïder area. Nevertheless, it remains difficult to demonstrate the supply
763 of trilobites from one basin to another without a finer temporal resolution. Although trilobite
764 exchanges were numerous, some trilobites remained restricted to a basin such as *Gerastos* and
765 *Piriproetus* in the Maïder Basin. Significant taxonomic turnovers occurred between the late
766 Emsian localities as is highlighted by the high β diversity (Fig. 9). More important local
767 environment variability in the eastern Anti-Atlas (Hollard, 1967) is a potential explanation for
768 this high taxonomic turnover.

769

770 6.4. Eifelian

771 The transition between the Early and Middle Devonian was marked by the onset of
772 tectonic events leading to a platform and basin topography (Wendt et al., 1984; Kaufmann,

1998; Lubeseder et al., 2010). This event is due to the Variscan orogeny, which disrupted the eastern Anti-Atlas. A deep basin (i.e., Maïder Basin) separated two platforms (i.e., Maïder and Tafilalt platforms). As most trilobites lived in shallow environments, they did not cross the basin to invade other localities. More specifically, the deep Maïder Basin acted as a natural barrier, which led to the development of distinct trilobite communities in the Middle Devonian. This barrier also effectively prevented the dispersion of these communities by pelagic or planktonic larvae, which had been identified in several Devonian trilobites (Speyer & Chatterton, 1989; Chatterton et al., 1990; Chatterton & Speyer, 1997). Indeed, these protaspides could not cross this deep basin because of unfavourable paleocurrents, paleoenvironmental conditions, or/and a too wide distance for their life duration. Consequently, in contrast to the Lower Devonian, trilobite distributions of the Eifelian show almost no connections between the Tafilalt and Maïder areas. To the west of the Maïder Basin, *Gerastos* and *Cyphaspis* evolved whereas *Piriproetus* then *Chotecops* developed in the Tafilalt (Fig. 7). The trilobites from the west of the Maïder Basin evolved in a relatively shallow environment (Gibb & Chatterton, 2010) and did not cross the deep Maïder Basin (Wendt et al., 1984). On the other hand, *Cyphaspis* occurred to the south-west at Foum Zguid (Van Viersen & Holland, 2016) showing a connection between the Maïder and the western Anti-Atlas areas. *Gerastos* that appeared in the late Emsian, proliferated in the Maïder during the Eifelian and covered the edges of the Maïder Platform including the western part at the Jbel Ou Driss locality (Fig. 7). *Gerastos* replaced *Morocops* during the Middle Devonian in the shallow neritic environments, while the distribution of this genus decreased from late Emsian to be restricted in some Maïder localities. To the eastern side of the Maïder Basin, a community of trilobites dominated by the genus *Piriproetus* (*Ass. Id*) expanded in the pelagic Tafilalt Platform. The trilobites from this association living in a moderately deep environment were unable to cross the Maïder Basin. While no connection existed to the west of Tafilalt,

798 trilobite exchanges still occurred to the east. Indeed, *Chotecops*, present in deep environments
799 (Feist & Orth, 2000; Crônier et al., 2018a) occurred in both Tafilalt and Ougarta areas.
800 Variscan orogeny created a basin between the Tafilalt and the Ougarta areas but this basin
801 seems shallower than the Maïder Basin (Kaufmann, 1998) thus enabling *Chotecops* to cross
802 this basin to invade new localities but not *Piriproetus*. *Chotecops* probably never settled in the
803 Maïder because this basin was too deep. Moreover, they did not flourish in the shallow
804 environments of the Maïder Platform margins. *Austerops*, present in Ougarta, Maïder and Dra
805 Valley, was the only genus living on both sides of the Maïder Basin (Chatterton et al., 2006;
806 McKellar & Chatterton, 2009; Crônier et al., 2018a). Its presence in these areas was recorded
807 since the late Emsian (Fig. 6).

808 In both Tafilalt and Maïder, the Eifelian faunas replaced those of the Emsian and the
809 trilobite associations were influenced by the palaeobathymetry (Crônier & Van Viersen,
810 2007). The origination rate and trilobite changes were not particularly high at the
811 Emsian/Eifelian boundary on an overall scale (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012).
812 Thus, North-African faunal changes rather seemed attributed to topographic changes where
813 some trilobite genera took advantage of this new heterogeneous environment.

814

815 6.5. Givetian

816 The overall Middle Devonian Choteč, Kačak and Taghanic events (House, 2002; Becker et
817 al., 2016) had an impact on trilobites and their diversity at the overall scale (Lerosey-Aubril &
818 Feist, 2012) and from North Africa (Fig. 9A). Most of them disappeared during the Givetian
819 and only three associations have been reported in the studied area: the *Gerastos* Association
820 with *Gerastos* sometimes associated with *Cornuproetus* or *Cyphaspis* in the Maïder area; the
821 *Chotecops* Association dominated by *Chotecops* and *Helmutia* in the Tafilalt area and the
822 *Morocops* Association at Ras el Kebbar locality (Maïder). The same distinction between areas

823 was identified during the Eifelian. However, the presence of *Gerastos* at the Jbel Ziata
824 locality in the Tafilalt (Feist & Orth, 2000) associated with *Chotecops* showed that trilobite
825 exchanges were rare but remained possible. The weak regressive regime during the early
826 Givetian enabled such migrations from the Maïder to the Tafilalt areas (Lubeseder et al.,
827 2003) as well as the proximity of the Maïder Platform with the Tafilalt Platform to the north
828 of the Maïder Basin (Kaufmann, 1998). All the trilobites occurred in the eastern Anti-Atlas,
829 whereas the Foum Zguid area and the Ougarta Basin seem relatively depopulated. Unlike in
830 the Ardenne Massif (North of France), the Kačak event did not lead to a replacement of
831 faunas in North Africa (Bignon & Crônier, 2015) but instead to an extinction of existing
832 faunas. However, like in the North of France, the environmental changes favoured *Dechenella*
833 in the Tafilalt (Feist & Orth, 2000).

834

835 6.6. Frasnian

836 Overall, the Frasnian trilobite record is scarce (Feist, 1991; Lerosey-Aubril & Feist, 2012).
837 In the studied North African area, the reduced-eyes *Chlupacops* was the only genus
838 encountered in the Ougarta Basin in deep environments (Feist et al., 2016). This basin seems
839 to have been disconnected from the others. The low trilobite diversity recorded during the
840 Frasnian could be explained by unfavourably shallow environmental conditions in the eastern
841 Anti-Atlas (Wendt et al., 1984, Wendt & Belka, 1991) whereas Feist (2002) described
842 trilobites from an outer platform environment in the neighbouring Meseta Central in
843 Morocco.

844

845 6.7. Famennian

846 After the Kellwasser crisis, some trilobites developed worldwide. While, cyrtosymbolines
847 proliferated in the shallow outer platform (Lerosey-Aubril & Feist, 2012), in deeper

848 environments such as basins, reduced-eyed and blind phacopids and proetids developed
849 (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012). A similar process occurred in North Africa
850 where cyrtosymbolines appeared during the early Famennian in the shallow Tafilalt Platform
851 and constituted a pioneer community. At the same time, in the deeper Ougarta Basin, the
852 number of blind phacopids increased. No trilobites have been found in the Maïder for this
853 period. No dispersal routes seem to have existed between the different basins at that time: the
854 *Trimerocephalus* Association was encountered in the Ougarta Basin, while the
855 *Cyrtosymbolina* Association was encountered in the Tafilalt area. Cyrtosymbolines could not
856 cross the deep Maïder and Tafilalt basins as the Tafilalt Platform acts as a natural barrier to
857 stop deep water trilobites coming from Ougarta. This trend remained through the Late
858 Devonian. In contrast, the distal platform of Ben Zireg (Abbache et al., 2019) seems to have
859 been a favourable environment to host trilobites but none have been found yet in the nodular
860 limestones and shales. Trilobite studies based upon localities at Ben Zireg since Alberti
861 (1983) remain scarce and this could explain the absence of trilobites in addition to the
862 sedimentary gaps (Abbache et al., 2019). Trilobites were absent throughout the Famennian in
863 the Maïder Basin, probably deposited in deeper water than that of the Tafilalt Basin (Wendt et
864 al., 1984; Kaufmann, 1998). Crônier & François (2014) suggested a depth superior to 60 m
865 for blind genera (i.e., *Trimerocephalus*) and Feist et al. (2016) indicated an offshore
866 environment near or beyond the limit of the photic zone. However, with its depth of 200 to
867 400 metres, the Maïder Basin had much deeper steep slopes according to stratigraphic studies
868 (Wendt et al., 1984). The Tafilalt Platform also acted as a barrier to trilobite dispersal.

869 The sea-level rise of the middle Famennian (Wendt et al., 1984; Wendt & Belka, 1991;
870 Abbache et al., 2019) allowed the proliferation of deep-sea phacopids. They were present at
871 that time, in many Ougarta localities and a connection appeared between the Tafilalt and
872 Ougarta areas. Exchanges were possible because the Tafilalt Basin and the Ougarta Basin

873 were probably interconnected during the Late Devonian (Wendt et al., 1984; Wendt, 1985;
874 Abbache et al., 2019). However, dispersal apparently only occurred from the Ougarta Basin to
875 the Tafilalt area, i.e., from deeper to shallower environments. Indeed, this unidirectional
876 supply of biodiversity suggests that only the deep-living taxa of Ougarta were able to cross
877 the deep basin between the Ougarta and the Tafilalt. The moderately deep-water taxa *Phacops*
878 *s.l.* and *Trimerocephalus* present in the Ougarta region were able to colonise the margins of
879 the quite deep Tafilalt Basin. Shallower areas also enabled the development of other trilobite
880 communities with new cyrtosymbolines appearing in the Tafilalt Platform dominated by the
881 *Osmolskaboie* genus (Alberti, 1973, 1974, 1975a, 1976a, 1976b; Lerosey-Aubril & Feist,
882 2005; Lerosey-Aubril & Feist, 2006). Because of the deepening of this area, they were
883 adapted to intermediate water depths and could have settled in the margins of this relatively
884 shallow Tafilalt Basin (Wendt et al., 1984) although they were still unable to cross a deep
885 basin to establish themselves in the Ougarta region. Moreover, in the intermediate
886 water/depth, other taxa developed during the middle Famennian. These were the large eyed
887 *Phacops s.l.*, which proliferated in the deeper part of the shallow Tafilalt Platform, associated
888 with *Trimerocephalus* or *Osmolskaboie*. On the other hand, *Phacops s.l.* only occurred in the
889 shallower part of Ougarta region to the south-east.

890 During the late Famennian, this connection was disrupted and the Tafilalt and Ougarta
891 areas are represented by two separate communities (Fig. 8). Despite the deepening of the
892 Tafilalt basin at this time, no trace of deep-water phacopids has been found there although
893 they were still present in the Ougarta Basin. Two explanations are possible - first, that they
894 were present but still not sampled and secondly, that a natural barrier, which has still not been
895 identified between the two basins prevented any trilobite exchange. This kind of natural
896 barrier could have resulted from the deepening between Ougarta and Tafilalt areas, preventing
897 any crossing of trilobites, or, alternatively, from a very shallow barrier, formed in the context

898 of Variscan orogeny, which was not favourable to Famennian trilobites (Hollard, 1974,
899 Wendt et al., 1984). Unfortunately, this area was covered by Cretaceous deposits (Benhamou
900 et al., 2004) thus preventing any information on the evolution of this basin. Cyrtosymbolines
901 were restricted to the shallowest part of Tafilalt, to the North. During this period of highstand
902 sea-level (Wendt & Belka, 1991), the rest of the Tafilalt was probably too deep to host them.
903 In contrast, *Trimerocephalus* has been recorded in the Ougarta region for this time in just one
904 locality, while *Phacops s.l.* dominated the rest of this area. These phacopids tended to replace
905 *Trimerocephalus* in the late Famennian (Crônier & François, 2014).

906 Finally, at the end of the Famennian, a regression occurred leading to a deltaic
907 environment with sandstone deposits in the eastern Anti-Atlas and Ougarta region (Wendt et
908 al., 1984; Kaiser et al., 2011; Abbache et al., 2019). This environment was unfavourable for
909 many benthic organisms and all deep-sea trilobites disappeared from these areas. Only two
910 cyrtosymbolines (i.e., *Pusillabole* and *Pseudowaribole*) remained in the shallow water
911 environment of the northern Tafilalt and were apparently unable to migrate to the Ougarta
912 Basin, which was probably too deep (Fig. 8). It is difficult to understand the facies
913 distribution of the Tafilalt because of the scarce outcrops and the potential reworking due to
914 debris flows (Wendt et al., 1984).

915 Originations and migrations always occurred from the shallower part of Tafilalt and
916 Ougarta region. In the Tafilalt, trilobites appeared in the shallowest part of the Tafilalt
917 Platform, located to the north (Wendt & Belka, 1991) before becoming a deeper basin in the
918 south. Trilobite migrations seemed to have started in its south-eastern part of the Ougarta
919 Basin. The *Trimerocephalus* Association from the early Famennian and the *Phacops s.l.*
920 Association from the middle Famennian appeared respectively at the Marhouma and Tamtert
921 Zereg localities (Fig. 8). These localities corresponded to an epicontinental platform
922 (Benhamou et al., 2004) and represented the shallowest part of the Ougarta Basin. Then,

923 following their occurrences, each genus invaded the deepest north-western part and
924 dominated the basin (Fig. 8). However, an influence from the south-west was unlikely
925 because the environment in the Gourara area was deep with basinal deposits (Benhamou et
926 al., 2004; Abbache et al., 2019).

927

928 6.8. Tectonical impact on trilobite faunas

929 During the Early Devonian, the Anti-Atlas area had a rather homogeneous environment
930 (Lubeseder et al., 2010). In this context, faunal changes were linked to global environmental
931 changes with first, the Pragian regression, which led to environmental changes driving faunal
932 changes (Chlupáč, 1994; Morzadec, 1997, 2001). Similar changes occurred in Bohemia with
933 the development of *Reedops* and *Odontochile* (Chlupáč et al., 1985). Then, the Daleje
934 transgression (Kaufmann, 1998; House, 2002) affected the North African trilobites with the
935 development of new faunas dominated among others by *Morocops* and *Hollardops*, adapted
936 to slightly deeper environments (Fig. 6). The same trend occurred worldwide, with
937 diversifications and innovations, particularly in offshore facies (Chlupáč, 1994). From the
938 Middle Devonian, the Variscan orogeny started to influence the regional topography (Wendt
939 et al., 1984; Kaufmann, 1998) and global events (sea-level changes and continental drift) were
940 no longer the only cause of biodiversity changes. Obviously, the Middle Devonian events
941 influenced the trilobite faunas, both quantitatively (Bault et al. 2021) and qualitatively (Fig.
942 7). Similarly, an important turnover occurred with the Kellwasser events (Lerosey-Aubril &
943 Feist, 2012) and consequently, the Famennian trilobites had nothing in common with their
944 predecessors in North Africa (Fig. 4). However, from the Eifelian, there were faunal
945 differences between nearby areas (Fig. 7). These differences were well marked in Morocco
946 and Algeria with strong differences between Maïder and Tafilalt whereas in other places such
947 as the Ardenne Massif, the faunas were still subject only to global changes (Bignon &

948 [Crônier, 2015](#)). The basin and platform topography affected the trilobites because of their
949 bathymetrical preferences ([Morzadec, 2001](#); [Chatterton et al., 2006](#)). Rapid changes and
950 instability made unpredictable regional **conditions** indicating that North African trilobite
951 communities conform to Gleasonian models where 'species-individualistic' responses to
952 environmental changes became prevalent in community ecology ([Gleason, 1927](#)). Regular
953 local and/or global changes hampered the ecological stasis spotted in other communities
954 ([Brett et al., 1996](#)).

955 Unlike topography, the type of sedimentation had a low impact on North African trilobites,
956 except for those due to global changes at the Lochkovian-Pragian boundary. Moreover, the
957 associations seemed less dependant on the sedimentation type laterally. For instance,
958 *Gerastos* has been found both in thick-layered limestones and in calcareous mudstones
959 interbedded with shales ([Gibb & Chatterton, 2010](#)). This kind of equilibrium community has
960 been already noted in the Middle Devonian trilobites of the Ardenne Massif ([Bignon &](#)
961 [Crônier, 2015](#)). Indeed, the *Dechenella* association raised and flourished when **carbonate**
962 platform environments appeared at the end of the Eifelian. This community was able to
963 maintain its organization during several dismantling episodes of the platform **during** the
964 Givetian, corresponding to a mixed **carbonate**-siliciclastic ramp. Only the global Taghanic
965 event of the late Givetian ([House, 1985](#)) broke the stability of this community. A similar
966 signal has currently been highlighted in Morocco regarding the stability of trilobite
967 organization despite environmental variations restricted in local and temporal terms ([Hollard,](#)
968 [1963, 1967](#); [Bultynck & Walliser, 2000](#); [Lubeseder et al., 2010](#)).

969

970 **7. Conclusions**

971 During the Devonian, the Anti-Atlas Range and its Algerian extensions were located on
972 the Saharan Platform, a passive continental margin of Gondwana. This area underwent several

973 ecological changes due to regional and global events with many sea-level changes,
974 anoxic/hypoxic events and tectonic events occurring throughout the Devonian. All these
975 changes affected the composition of trilobite communities and their diversity.

976 Trilobites were not well dispersed between the different areas of Northern Africa because
977 of spatial and temporal environmental changes. Devonian trilobites can be assigned to 16
978 associations with 12 of these associations existing during the Early and Middle Devonian and
979 four exclusively during the Famennian. Each of these trilobite associations flourished in a
980 specific environment, which was favourable for some genera but less so for others. In
981 siliciclastic environments, asteropygines prospered in the Ougarta region during the
982 Lochkovian, while the Pragian regression allowed the diversification of many trilobites in
983 shallow water environments. Both trilobite diversity and the number of associations further
984 increased during the Emsian. During this period, the different basins were well
985 interconnected. Faunal exchanges were facilitated by the absence of strong ecological or
986 topographical barriers and further favoured by a relatively homogeneous environment. The
987 Variscan orogeny modified the palaeogeographic setting during the Middle Devonian towards
988 a platform and basin topology. Geographical barriers formed and trilobite associations
989 became restricted to smaller areas with poor connections between them. This regional tectonic
990 context coupled with more widespread Middle Devonian events affected trilobites, which
991 were almost eradicated from this area in the Frasnian. After the Kellwasser events, trilobites
992 once again flourished regionally and globally although not to the diversity levels of the
993 Emsian or Eifelian. During the same period, cyrtosymboline associations proliferated in
994 shallow platform environments, while phacopid associations proliferated in deeper water
995 environments. Finally, new sea-level and sedimentological changes in the latest Famennian
996 led to the disappearance of numerous trilobites in the Northern African area under study.

997

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1006

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1383 **Figures**

1384

1385 **Fig. 1.** (A) Simplified geological map of Morocco and Algeria (modified from [Crônier et al.](#)
1386 [2018b](#)) and location of the five study areas in North Africa within the Anti-Atlas and Ougarta
1387 Ranges. (B) Geographical location of the 69 studied localities from the Maïder/Tafilalt area in
1388 Morocco and from the Ougarta area in Algeria.

1389

1390 **Fig. 2.** Main lithology for each formation present in the five Moroccan Anti-Atlas and
1391 western Algeria basins for the Devonian. Formation names in black, ID of samples in red.
1392 Ages from [Cohen et al. \(2013, updated\)](#).

1393

1394 **Fig. 3.** Geographical map of the eastern Anti-Atlas in Morocco with the limits of the Maïder
1395 Platform and Basin and the Tafilalt Platform and Basin in the Middle and Late Devonian
1396 (Modified from [Wendt & Belka, 1991](#) and [Frey et al., 2019](#)).

1397

1398 **Fig. 4.** Simplified dendrogram with R and Q modes from hierarchical cluster analysis (HCA)
1399 using the average linkage method as correlation setting and the Pearson correlation index as
1400 similarity index ([Hammer & Harper, 2008](#)). 67 taxa (genera) are clustered according to 123
1401 analysed samples (localities) from the Devonian of North Africa. Four clusters (I to IV) and
1402 16 associations are identified. Sample names and proportions of each occurrence are given in
1403 Fig. SUPPL. B).

1404

1405 **Fig. 5.** Scatter plot of North African samples according to DCA for (A) the Early and Middle
1406 Devonian, and (B) the Famennian; DC1 and DC2 axes reflecting potential environment
1407 gradient. Eigenvalues for DC1 and DC2 axes are respectively 0.96 and 0.91 for the Early and

1408 Middle Devonian with 105 samples, 0.95 and 0.09 for the Famennian with 16 samples.

1409 Associations defined by clustering have been reported: 12 associations for the Early and

1410 Middle Devonian, and 4 associations for the Famennian.

1411

1412 **Fig. 6.** Simplified diagrams exhibiting the different facies within five studied areas and their
1413 spatio-temporal evolution during the Early Devonian. Associations defined by clustering have
1414 been reported.

1415

1416 **Fig. 7.** Simplified diagrams exhibiting the different facies within five studied areas and their
1417 spatio-temporal evolution during the Middle Devonian and Frasnian. Associations defined by
1418 clustering have been reported.

1419

1420 **Fig. 8.** Simplified diagrams exhibiting the different facies within five studied areas and their
1421 spatio-temporal evolution during the Famennian. Associations defined by clustering have
1422 been reported.

1423

1424 **Fig. 9.** Diversity indices. (A) Diversity through time: α diversity estimated with Shannon
1425 Index H' , Overall β Diversity and its components, i.e., β Turnover component and β
1426 Nestedness component determined with Sorensen dissimilarity. (B) α Diversity per formation
1427 from five areas. (C) α Diversity and Overall β Diversity per association. Ages from Cohen et
1428 al. (2013, updated).

1429

1430 **Table. 1.** Trilobite associations and their environmental, faunal and temporal features. The
1431 remark column includes data on: diversity (Fig. 9) and occurrences (Appendix A and B).

1432 Reattributions of samples were made using DCA data (Fig. 5). **Bold font indicates the main**
1433 **characteristic for the associations.**

1434

1435 **Supplemental figures**

1436

1437 **Fig. A.** Scatter plot of North African samples according to Correspondence Analysis (CA) for
1438 the Early and Middle Devonian. (1) CA1 and CA2 showing a Pinocchio effect, and (2) CA2
1439 and CA3 showing an arch effect.

1440

1441 **Fig. B.** Dendrogram with R and Q modes from hierarchical cluster analysis (HCA) using the
1442 average linkage method as correlation setting and the Pearson correlation index as similarity
1443 index ([Hammer & Harper, 2008](#)). 67 taxa (genera) are clustered according to 123 analysed
1444 samples (localities) from the Devonian of North Africa. Four clusters (I to IV) and 16
1445 associations are identified. Occurrences of genera in samples are given in proportion of the
1446 total number of genera in the sample.

1447

1448 **Fig. C.** Geographical localisation of associations defined by clustering in the five studied
1449 Moroccan and Algerian areas for the Lochkovian.

1450

1451 **Fig. D.** Geographical localisation of associations defined by clustering in the five studied
1452 Moroccan and Algerian areas for the Pragian.

1453

1454 **Fig. E.** Geographical localisation of associations defined by clustering in the five studied
1455 Moroccan and Algerian areas for the Emsian.

1456

1457 **Fig. F.** Geographical localisation of associations defined by clustering in the five studied
1458 Moroccan and Algerian areas for the Eifelian.

1459

1460 **Fig. G.** Geographical localisation of associations defined by clustering in the five studied
1461 Moroccan and Algerian areas for the Givetian.

1462

1463 **Fig. H.** Geographical localisation of associations defined by clustering in the five studied
1464 Moroccan and Algerian areas for the Fammenian.

1465 **Appendix. Supplementary data**

1466

1467 **Appendix A.** Dataset constructed with 77 publications (**Appendix B**).

1468

1469 **Appendix B.** Compilation of 77 selected publications with sufficient chronostratigraphic

1470 information to calibrate occurrences at the stage and substage levels and taxonomic

1471 information to up-to-date taxonomy; set of references constituting a relatively complete fossil

1472 record of the Devonian in the Moroccan Anti-Atlas and western Algerian basins.

1473

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