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1 **MORPHOLOGICAL DISPARITY TRENDS OF DEVONIAN**

2 **TRILOBITES FROM NORTH AFRICA**

3

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19 **Abstract:** The Devonian was a time of drastic environmental changes that shaped the  
20 morphology of trilobites. This study aims to investigate their morphological evolution and to  
21 show the influence of some abiotic and biotic factors (bathymetry, feeding habits and visual  
22 abilities) on their shape. A dataset was compiled to investigate the shape of three structures  
23 (cephalon as a whole, the central part of the cephalon and pygidium) of Devonian trilobites  
24 from North Africa, using a geometric morphometric approach. Based on empirical  
25 morphospaces, the morphological changes were quantified through the Devonian stages. The  
26 results reveal important variations in the morphological disparity of the glabella shape, the  
27 facial suture location, the pygidial length and the presence of spines. In the Lochkovian, the  
28 morphological disparity was low, subsequently increased in the Pragian with numerous  
29 innovations, and reached a maximum in the Emsian. If the morphospace occupancy remained  
30 until the Eifelian, a severe loss of disparity occurred in the Givetian, a time known for  
31 important environmental changes. Disparity then remained low in the Late Devonian. The  
32 shapes inherited from the Silurian persisted throughout the Devonian whereas Pragian  
33 novelties were most affected by losses. These persistent shapes were more versatile for  
34 environmental adaptation, helping those trilobites to survive to environmental events.  
35 Similarly, the trilobite orders that survived Devonian events had a wide morphological  
36 spectrum and were better adapted to withstand environmental change.

37

38 **Key words:** Trilobites, North Africa, Devonian, Morphological disparity, Morphometrics,  
39 Evolution, environmental changes

40

41 Appearing as early as the Cambrian Explosion, trilobites diversified quickly to reach their  
42 maximum diversity at the end of the Cambrian (Westrop & Aldrain 1998) and then undergone  
43 an irregular decline until the end of the Permian (Sepkoski & Sheehan 1983; Foote 1993; Fan

44 *et al.* 2020). Especially, the Devonian marked an important step of this decline. Despite an  
45 important diversity increase in the Early Devonian, a protracted decrease at all taxonomic  
46 ranks (family, genus, species) occurred during the Middle Devonian up to the disappearance  
47 of three of the five orders (i.e., Odontopleurida, Harpetida and Corynexochida using [Adrain](#)  
48 [\(2011\)](#) classification updated by [Lamsdell & Selden \(2015\)](#) concerning the superfamily  
49 Aulacopleuroidea) in the Late Devonian during the Kellwasser events ([Feist 1991](#); [Chlupáč](#)  
50 [1994](#); [Crônier & vanViersen 2007](#); [Lerosey-Aubril & Feist 2012](#); [Bault et al. 2021](#)). In  
51 addition to these diversity losses, the visual abilities and the life environments have been  
52 modified in trilobites, and especially after the Frasnian/Famennian boundary ([Chlupáč 1994](#);  
53 [Lerosey-Aubril & Feist 2012](#)). Therefore, the Devonian is a critical period in the evolutionary  
54 history of trilobites. This interval of time is also well known to record major biotic and abiotic  
55 changes, such as the Devonian Nekton Revolution ([Klug et al. 2010](#)), the development of  
56 vascular land plants ([Pawlik et al. 2020](#)), exceptional sea-level highstands, widespread  
57 epicontinental shallow seas, greenhouse climates ([Tinn et al. 2020](#)) and several  
58 anoxic/hypoxic events and rapid sea level fluctuations ([House 2002](#); [Becker et al. 2016](#)).

59 Another important morphological indicator of evolutionary success or failure is the  
60 disparity, as measured by the occupancy of a morphospace ([Foote 1997](#); [Wills 2001](#); [Erwin](#)  
61 [2007](#), [Minelli 2016](#), [Guillerme et al. 2020b](#)). Success in diversity does not necessarily go  
62 together with success in disparity. Many taxa show high diversity with low disparity, while  
63 others are highly diverse but also exhibit high disparity ([Minelli 2016](#)). Taxonomic richness  
64 and morphological disparity are two complementary metrics, which can be decoupled ([Foote](#)  
65 [1991a, 1991b, 1993](#)). Such decoupled changes in taxonomic diversity and morphological  
66 disparity can suggest different proxies for understanding the ecological impact of the  
67 extinction event for example ([Wan et al. 2021](#)). Morphological disparity of trilobites has been  
68 extensively documented in the Cambrian and the Ordovician ([Foote 1991a](#); [Smith &](#)

69 [Lieberman 1999](#); [Webster 2007](#); [Hopkins 2013](#); [Jacobs & Carlucci 2019](#)). Contrariwise,  
70 Devonian studies are rare and often dedicated to developmental and ontogenetic topics  
71 exploring the intrinsic factors of morphological changes (e.g. [Crônier \*et al.\* 1998](#); [Crônier](#)  
72 [2013](#); [Oudot \*et al.\* 2019](#)). However, if biotic and abiotic factors are known to contribute to  
73 diversification, they also contributed to the morphological disparity ([Crônier \*et al.\* 2004](#);  
74 [Hopkins & Gerber 2017](#)). Some relationships have been noticed or demonstrated between  
75 trilobite shapes and ecological affinities such as bathymetric conditions ([Hopkins 2014](#)),  
76 feeding habits ([Fortey & Owens 1999](#)) or life habits ([Fortey 2014](#)). Although the  
77 environmental influence on the morphological disparity was rarely evaluated, [Hopkins \(2014\)](#)  
78 emphasized the effect of bathymetry, substrate and latitude on the trilobite shape for the entire  
79 Palaeozoic. As the result of these environmental effects, the morphological disparity can be  
80 dependant of the geographical location of populations through time ([Hopkins & Webster](#)  
81 [2009](#); [Abe & Liebermann 2012](#); [Esteve \*et al.\* 2017](#)). These recent studies have been done at  
82 the global scale or focusing on only one family. Nevertheless, for Devonian trilobites, no  
83 studies have been performed on the total richness available throughout a span time for a  
84 relatively well-constrained area.

85 During the Devonian time, the environmental and ecological changes were particularly  
86 well exhibited in North Africa wherein trilobites were especially well represented and diverse  
87 ([Lebrun 2018](#); [Bault \*et al.\* 2021](#)). This area is one of the richest in terms of Devonian trilobites  
88 with five orders and 15 families ([Bault \*et al.\* 2021](#)), corresponding to all known worldwide  
89 Devonian orders and the majority of families ([Crônier & van Viersen 2007](#)). In addition to its  
90 fossil record, this area is also particularly well known for its stratigraphy and its  
91 palaeoenvironmental context ([Massa 1965](#); [Hollard 1967](#); [Wendt & Belka 1991](#); [Becker \*et al.\*](#)  
92 [2004](#); [Abbache \*et al.\* 2019](#); among others). It allows establishing the relationship between the

93 trilobites characterized by their shape and their habits and their palaeoenvironmental  
94 affinities. Moreover, the Devonian events were all spotted in this area (Kaufmann 1998).

95 In the context of a period of diversity changes (Bault *et al.* 2021), analysing the  
96 morphological changes through time for a relatively well-constrained area, helps to better  
97 understand the impact of the Devonian biological events on benthic faunas. We focused our  
98 investigations on the Devonian trilobites gathered from North African area. To understand the  
99 fluctuations in time and space, the disparity patterns are assessed through morphological  
100 spaces in a stratigraphic and palaeoenvironmental framework. First, we investigated the  
101 evolution of the trilobite morphospace to identify the different morphotypes and to explore the  
102 presence of evolutionary key innovations in lineages for each stage. Then, we investigated  
103 how the morphological shape may be linked to different palaeoenvironmental and/or  
104 palaeoecological factors (such as bathymetry, feeding habits and visual ability) and detecting  
105 which factors contribute most to the observed patterns.

106

## 107 MATERIAL AND METHODS

108 Fig. 1 near here

### 109 *Trilobite data and frameworks*

110 We compiled a dataset to investigate the morphology of Silurian and Devonian trilobites from  
111 Morocco and Algeria (Fig. 1). This area was situated on the continental margin of the  
112 Gondwana at a latitude between 30° and 45°S (Scotese & Golonka 1992; Golonka 2002). It  
113 was a favourable place for the settlement of benthic communities such as trilobites (Morzadec  
114 2001; McKellar & Chatterton 2009). All figures of specimens illustrated over the last 80 years  
115 with a sufficient quality have been directly exploited for shape analyses (Appendix S1).  
116 Morphology of trilobites is here quantified by focusing on their most important structures, i.e.,  
117 cephala, glabella and pygidia (Fig. 2). The glabella is a subset of the cephalon and it is here

118 analysed with the occipital ring and prelabellar field as “central cephalon”. The cephalon is  
119 studied as a whole, including the central cephalon landmarks for morphological analyses. A  
120 first dataset contains 328 complete cephala, 959 complete central cephala and 605 complete  
121 pygidia; each structure being studied independently. This dataset includes all well-preserved  
122 and illustrated specimens during the last 80 years from 65 publications (Appendix S2). Only  
123 dorsal views were used and the right-side from each structure was selected except if the left-  
124 side was more completed; mirror images were used to correspond to the right side. A second  
125 dataset contains 30 complete specimens of 30 different species for which both the cephalon  
126 and the pygidium were simultaneously preserved.

127 Fig. 2 near here

128 For each specimen, taxonomy, age (stage) as well as ecological characteristics were also  
129 included in the dataset. Firstly, genera were classified by environmental affinities, i.e., by  
130 water depth conditions (Fortey 1975; Turvey 2005; Crônier & vanViersen 2007).  
131 Bathymetrical affinity for each genus was determine as the environment where it mainly  
132 occurred. Because these data were not available for each occurrence, we interpolated it with  
133 the data from other papers with the same stratigraphic context or from genera with the same  
134 affinity. Four categories are identified along the bathymetric profile: (1) the shoreface  
135 environment characterized by shallow and proximal conditions; (2) the upper offshore or  
136 inner shelf environment characterized by relatively shallow waters; (3) the median offshore or  
137 middle shelf environment characterized by relatively deep deposits; and (4) the lower offshore  
138 or outer shelf environment located below effective storm wave base. It is important to note  
139 that depth categories were based on sedimentological evidences and not from trilobite shapes  
140 to avoid analysis biases.

141 Secondly, genera were classified by their diet. We referred to Fortey and Owens (1999) to  
142 determine the feeding habits of genera based on hypostome features. Three diet categories are

143 recognized in our database: ‘Predator/Scavenger’, which ingested small preys, ‘Particle  
144 feeding’, which fed on nutrients and ‘Filter chamber’, which brought sedimentary material  
145 into suspension before selecting out edible particles (Fortey & Owens 1999). It should be  
146 noted that the estimates of feeding habits are only assumptions and the evidence in the fossil  
147 record is rare. For instance, only two examples confirmed as particle feeders are known (Zhu  
148 *et al.* 2014; Gutiérrez-Marco *et al.* 2017). Feeding habits are still an ongoing debate and  
149 advances in biomechanics (Bicknell *et al.* 2018, 2021) will help refine the trilobite diets.

150 Third, genera were classified by their eyes, preserved as calcite lenses on a visual surface  
151 (Clarkson *et al.* 2006). Each taxon has been assigned to one of the three categories: blind,  
152 reduced-eye, or well-developed-eye. The diagnostic features related to the eye size or to the  
153 number of lenses were considered to establish these categories. In trilobites, the visual ability  
154 has often been linked to environment or life habits (Clarkson 1967; Feist 1991). For this last  
155 analysis, blind cephalae were not considered because of the lack of three landmarks (i.e.,  
156 landmarks 8, 9 and 14; Fig. 2).

157

#### 158 *Landmark data*

159 The 2D shape of studied trilobites is here quantified by a geometric morphometric approach,  
160 which is now a standard set of techniques for quantifying shape independently of size by  
161 using homologous points (landmarks) on the surface of a series of objects (Bookstein 1991;  
162 Rohlf & Marcus 1993; Rohlf 1999; Adams *et al.* 2004, 2013; Mitteroecker & Gunz 2009;  
163 Zelditch *et al.* 2012). This method preserves the geometry of the landmark configurations  
164 throughout the analysis and thus permits representation of analytical results as actual shapes  
165 or forms. It is routinely used in biological and palaeontological studies.

166 The shape of cephalae is here described by a set of 15 landmarks and one curve of 24  
167 equally spaced semilandmarks between landmark 2 and landmark 7 (Fig. 2, Table 1). For



168 **central cephalon**, seven landmarks plus the semi-landmark curve have been digitized (Fig. 2,  
169 Table 1). Similarly, seven landmarks were digitized for pygidia (Fig. 2, Table 1). Landmarks  
170 were positioned in key locations to summarize the complexity of morphologies. The semi-  
171 landmarks were processed directly and not slided. Specimens with missing landmarks were  
172 excluded. The *x*- and *y*- coordinates of 2D landmarks and semi-landmarks were digitized (Fig.  
173 2) with TPSdig 2.32 (Rohlf 2010, 2015). The landmark 2D coordinates were then exported in  
174 the standard TPS file format (Rohlf 2012).

175 Table 1 near here.

176 Because we analysed specimens from different lineages, shapes can be different with  
177 extreme landmark locations and thus, geometric morphometric methods could not be applied  
178 (Zelditch *et al.* 2012). In our case this issue concerns only the cephalia where landmarks 10, 11  
179 and 12 can exhibit topological changes compare to relative position to other landmarks (Fig.  
180 2, Table 1). Pinocchio effect (Chapman 1990; Thulman 2019) can also affect landmarks 13  
181 and 16 (Fig. 2, Table 1). In order to assess the impact of these issues, we removed them to see  
182 if the morphospace is affected by these *biases* or not. To assess the possible impact of each  
183 landmark, we calculated the Pearson's correlation coefficient between each landmark  
184 dimension and the major ordination axes and their statistical significance by means of the  
185 'envfit' function of the 'vegan' R-package (Oksanen *et al.* 2020). The graphical output of  
186 these correlations as arrows proportional to these correlations on the PCA-based morphospace  
187 leads to a so-called correlation circle. In our case, this analysis shows that none of the  
188 previously mentioned "suspicious" landmarks (11, 12, 13, and 16) have an influence larger  
189 than the other landmarks (Fig. S1). Thus, our morphospaces are not determining by  
190 topological issues or a Pinocchio effect.

191

192 *Shape analyses*

193 Standardization of the landmark data (superimposition) to remove variability due to  
194 differences of size, placement, and orientation was performed by means of a generalized  
195 Procrustes analysis (GPA), which minimize the sum of square distances between equivalent  
196 landmarks (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O’Higgins 2000; Zelditch *et*  
197 *al.* 2012). We slid the semi-landmark curve optimizing the minimum Procrustes distance  
198 (Perez *et al.* 2006; Gunz & Mitteroecker 2013). The superimposed landmarks are projected to  
199 a linear tangent space at the full Procrustes mean (Rohlf 1999; Kendall 1984).

200 For each of the three studied structures (i.e., cephalon, central cephalon and pygidia), we  
201 performed a principal components analysis (PCA; Ringnér 2008; Abdi & Williams 2010) to  
202 reduce the high-dimensionality of the superimposed landmarks to fewer variables  
203 (eigenvectors), along which the shape variation is maximal. Each specimen can be  
204 represented by relatively few variables and can be plotted in a PCA-space (morphospace)  
205 defined by principal component axes (PCs), which are ordered by decreasing percentage of  
206 the total shape variance. The morphospace is centred on the average shape (consensus) and  
207 where each point represents a specimen shape and its position reflects the relative shape  
208 similarities and differences between specimens. Finally, among the studied specimens, series  
209 of virtual shapes were reconstructed by doing a back transformation from the PC scores for  
210 PC1 and PC2 to illustrate the largest shape changes over the morphospace. Shape analyses  
211 have been computed with the R scientific environment (v. 3.6.2; R Core Team 2019;  
212 <https://cran.r-project.org/>) and the packages ‘geomorph’ (v. 3.2.1; Adams & Otárola-Castillo  
213 2013) and ‘epaleo’ (v. 0.8.41; Monnet, unpub.), as well as the software PAST (version 3.24;  
214 Hammer *et al.* 2001). Figures from R outputs.

215 To identify some morphological clusters or morphotypes (Fig. S2), we performed a  
216 Hierarchical Cluster Analysis (HCA) with the package ‘epaleo’ on the Principal Component

217 scores by using the Euclidean distance measure and Ward's linkage algorithm. See [Everitt et](#)  
218 [al. \(2011\)](#) or [Murtagh & Contreras \(2012\)](#) for more details on methods.

219

### 220 *Morphospace analyses*

221 Morphospaces were established for the complete data set of all specimens independently for  
222 cephala, **central cephala** and pygidia. They were explored to evaluate the morphospace  
223 occupation first by the previously defined morphotypes, and then by the orders (using [Adrain](#)  
224 [\(2011\)](#) classification updated by [Lamsdell & Selden \(2015\)](#) concerning Proetida). Moreover,  
225 to investigate trilobite shape changes through time, individuals for each structures were  
226 categorized by stages on their respective morphospace. This allows visualizing how the  
227 different groups are distributed in the morphospace, to identify which morphotypes or orders  
228 are impacted by morphological changes and how, and to identify key morphologies among  
229 trilobites for a given stage for a successful diversification or disappearance.

230 **Morphospace occupation changes through time are reinforced by the estimation of one**  
231 **morphological disparity index ([Wills 2001](#); [Guillerme et al. 2020a](#)). We selected the sum of**  
232 **variances (SoV), which is an index measuring the average morphological dissimilarity**  
233 **estimated as the sum of univariate variance of all dimensions in the morphospace ([Foote](#)**  
234 **[1991b, 1993](#)). SoV is reconstructed for the three studied trilobite structures.**

235 Additionally, the morphospace was explored according to the inference of the potential  
236 influence on morphospace variation of three different factors related to life modes known to  
237 be changing with Devonian events: bathymetry, feeding habits and visual ability ([Chlupáč](#)  
238 [1994](#); [Lerosey-Aubril & Feist 2012](#)). Effect of eye reduction was investigated for all the  
239 structures, including those without eyes (i.e., **central cephalon** and pygidium). Eye reduction  
240 may affect other parts of trilobites by imposing a rearrangement of structures, such as the  
241 suture line position (and so fixigena) in Phacopida or Proetida. This analyse was done by

242 mapping each factor of each individual onto the morphospace. We computed a one-side  
243 nonparametric, permutational ANOVA on the PC axes to test statistically if a shape difference  
244 exists according to these three palaeoenvironmental and palaeoecological different factors  
245 (i.e., bathymetry, feeding habits and visual ability). Procrustes ANOVA with permutation  
246 procedures are performed using the Wilks' lambda test to quantify the amount of shape  
247 variation allocated to factors in a linear model and to estimate the probability of this variation  
248 for a null model (Collyer & Adams 2018). Statistical analyses based on PCA axes are  
249 advocated instead of original Procrustes coordinates because the scores of each axis are  
250 uncorrelated and the number of dimensions corresponds to the degree of freedom (Rohlf  
251 1993; Polly 2017). Then, to assess how the shape is distributed according to these factors, we  
252 highlighted the different categories of our factors on PCA. Morphospace analyses have been  
253 also computed with R 3.6.2 and PAST 3.24.

254

## 255 **RESULTS**

### 256 *Global morphological space*

257 For cephalata, the PCA yields 77 principal components (PCs), five of which explained 83.4% of  
258 the variance in shape of the studied trilobites: PC1, 47.1%; PC2, 15.6%; PC3, 11.9%; PC4,  
259 4.7%; and PC5, 4.1%. The remaining components accounted for less than 4% each. The  
260 morphological interpretation of the shape changes associated to PC1 and PC2 is depicted by  
261 overlying reconstructed shapes at various locations of the morphospace (Fig. 3A). PC1  
262 depicts the presence or not of genal spines and sagittal spine, the shape change of the glabella  
263 and the postero-lateral position (i.e., opistoparian, proparian or gonatoparian; Fig. 2) of the  
264 facial suture. Positive scores of PC1 show the presence of long genal or sagittal spines, a wide  
265 transversal (tr.) glabella at its base and an opistoparian facial suture with its terminal end to  
266 the posterior border (Fig. 3A). At the opposite, negative scores of PC1 show cephalata without

267 spines, a wide (tr.) glabella at the frontal lobe and a proparian facial suture with its terminal  
268 end to the lateral border. PC2 depicts the presence or absence of spines and the postero-lateral  
269 position of the facial suture too (Fig. 3A). However, the main shape change seems to be  
270 depicted by the shape of the occipital ring. **Low** scores of PC2 show a wide (tr.) occipital ring,  
271 while **high** scores of PC2 show a narrow (tr.) occipital ring. PC3 contrasts two different  
272 morphologies with spines (Fig. S3A). **Positive** scores of PC3 show a long sagittal spine  
273 without genal spine, while **negative** scores of PC3 show genal spines without sagittal spine.  
274 Finally, **negative** scores of PC4 indicate narrow (tr.) librigena, while **positive** scores show  
275 wide (tr.) librigena.

276 The set of individuals are grouped into five morphotypes, along the first two principal  
277 component axes, with only few individuals between them (Fig. S2A, Fig. 3A). HCA shows  
278 five main morphologies corresponding to five main morphotypes (Fig. S2). The most  
279 common shapes are depicted by **negative** PC1 and null PC2 scores (Fig. 3A). These shapes  
280 assigned to Morphotype 1 (MCp1) correspond to cephalo without sagittal and genal spines,  
281 with a wide frontal lobe (tr.) and a proparian facial suture (Fig. 3A). MCp1 spread to similar  
282 glabellar shape and facial suture position but with presence of genal spines, i.e., MCp3, and of  
283 sagittal spine, i.e., MCp2, depicted by **positive** PC1 and PC2 scores. Other morphologies are  
284 depicted by slightly **negative** PC1 and PC2 scores (i.e., MCp5) to **positive** PC1 and **negative**  
285 PC2 scores (i.e., MCp4). These two morphotypes 4 and 5 correspond to cephalo with a  
286 proparian or opistoparian facial suture, with a frontal lobe narrower (tr.) than in the other  
287 morphotypes, such as the basal part of the glabella is wider (tr.). The main difference between  
288 MCp4 and MCp5 is the presence of genal spines in MCp4. For all types of glabella (i.e., wide  
289 or narrow frontal lobe (tr.), MCp1 and MCp5), cephalo can exhibit spines but it requires  
290 narrower (tr.) glabellar furrows without an inflated frontal lobe (Morphotypes 2, 3 and 4).

291

Fig. 3 near here

292 For **central cephalata**, the PCA yields 62 PCs, two of which explained **82.3%** of the variance  
293 in shape of the studied trilobites: **PC1, 72.9%; PC2, 9.4%**. The remaining components  
294 accounted for less than **5%** each. PC1 depicts the variation of the glabellar shape. **Negative**  
295 PC1 scores depict individuals with a wide (tr.) frontal lobe compare to the glabellar base and  
296 without preglabellar field anteriorly (Fig. 3B). While **positive** PC1 scores depict individuals  
297 with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B). Rare  
298 intermediate shapes show a frontal lobe just slightly wider (tr.) than the glabellar base. Shapes  
299 with very narrow (tr.) or very wide (tr.) occipital and preoccipital rings do not exist. PC2  
300 depicts the presence or not of a preglabellar field and the width (tr.) of glabellar lobes.

301 The set of individuals are grouped into two morphotypes (MCn1 and MCn2; Fig. S2B),  
302 mainly along the first principal component axis PC1 (Fig. 3B). **Negative** PC1 and null PC2  
303 scores depict a common shape (Fig. 3B). This shape assigned to MCn1 corresponds to **central**  
304 **cephalata** with a wide (tr.) frontal lobe compare to the glabellar base and without preglabellar  
305 field anteriorly (Fig. 3B). **Positive** PC1 and null PC2 scores depict another common shape  
306 (Fig. 3B). This shape assigned to MCn2 corresponds to **central cephalata** with wide (tr.)  
307 preoccipital and occipital rings and with a preglabellar field (Fig. 3B).

308 For pygidia, the PCA yields 14 PCs, four of which explained 89.9% of the variance in  
309 shape of the studied trilobites: PC1, 42.5%; PC2, 22.2%; PC3, 14.2%, and PC4, 11.0%. The  
310 remaining components accounted for less than 5% each. PC1 (Fig. 3C) shows that the main  
311 shape change contrasts narrow (tr.) pygidia (negative scores) to wide (tr.) pygidia (positive  
312 scores). PC2 depicts the sagittal (sag.) length of the pygidial axis, PC3 depicts the presence of  
313 lateral and sagittal spines and PC4 depicts the curve of the pygidial border (Fig. S3B). Along  
314 PC3 and PC4, most of the shapes show individuals with no spines. Only few individuals  
315 located in the negative PC3 scores have small pygidial spines. These pygidial spines are  
316 generally short and never longer (sag.) than the pygidium itself. Positive scores on PC4

317 indicate a maximal (tr.) length below the anterior most point of sagittal pygidial length and  
318 conversely negative scores indicate a maximal (tr.) length above the anterior most point of  
319 sagittal pygidial length (Fig. S3B). No pygidia are present in the area of the morphospace that  
320 depicts pygidia with a very narrow (tr.) and a long (sag.) pygidial axis (i.e., negative PC1 and  
321 PC2 scores).

322 The set of individuals are grouped into three morphotypes (Fig. S2C). The most common  
323 shapes assigned to MPg1 and MPg2 are depicted by rather null scores of PC1 (Fig. 3C).  
324 These shapes correspond to pygidia with a medium size and with either a long (i.e., MPg1) or  
325 a medium length of pygidial axis (i.e., MPg2). MPg3 is depicted by negative PC1 and positive  
326 PC2 scores (Fig. 3C). The shapes associated to this cluster correspond to pygidia with a  
327 narrow (tr.) and a short (sag.) pygidial axis (i.e., MPg3).

328

329 Fig. 4 near here

### 330 *Morphospace occupation by time*

331 The changes in occupancy/filling of the morphospaces (i.e., the morphological disparity)  
332 through time are illustrated in figure 4 for the three structures. For cephalata, the morphological  
333 space was characterized by a reduced occupation from the Ludlow to the Lochkovian,  
334 followed by widespread occupation in the second part of the Early Devonian. During the  
335 Ludlow, the filling of morphological space was narrow (Fig. 4A) and was restricted to MCp1  
336 and MCp5. The location of morphotypes through time is given in figure S4A. **At this time, the**  
337 **morphological dissimilarity among specimens (i.e., SoV) was low.** Then, the morphological  
338 disparity remained reduced in the Lochkovian and restricted to only one cephalon assigned to  
339 a new morphotype (i.e., MCp4) in the early Lochkovian and three cephalata to MCp1 in the late  
340 Lochkovian (Fig. 4A). After this low disparity period, the disparity in the Pragian covered  
341 almost all the morphospace, with the only exception of some cephalata with sagittal spines i.e.,

342 MCp2 (Fig. 4A, Fig. S4A). This morphology appeared during Emsian when the morphospace  
343 reached its maximal coverage and SoV was the highest.

344 The transition to the Middle Devonian (Fig. 4A, Fig. S4A ) did not coincide with an  
345 important loss of morphological disparity for the central cephalon and the pygidium but the  
346 cephalon was more affected with the disappearance of MCp2. This morphology loss is  
347 confirmed by the strong decrease of SoV. Only cephalia characterized by low PC2 scores  
348 disappeared. These cephalia exhibit sagittal spines. However, the morphotypes 2, 3 and 4  
349 disappeared from North Africa in the late Eifelian (Fig. 4A, Fig. S4A ). These morphotypes  
350 correspond to cephalia with spines. If MCp1 and MCp5 persisted in the early Givetian, MCp1  
351 disappeared in the middle Givetian and MCp5 in the late Givetian. In the Late Devonian, only  
352 MCp1 reappeared.

353 As for cephalia, the morphospace occupation for central cephalia was not widespread from  
354 the Ludlow to the Lochkovian, but largely extended during the Pragian toward shapes with  
355 wide sagittal (sag.) preglabellar field and wide (tr.) occipital ring. However, SoV did not  
356 increased strongly throughout the Early Devonian. The morphospace occupation remained  
357 constant during the Emsian and the Eifelian but collapsed during the Givetian (Fig. 4B, Fig.  
358 S4B). This collapse concerned both density and expansion, with the disappearance of shapes  
359 with wide (tr.) frontal lobe in both morphotypes. This disappearance led to a morphospace  
360 occupation comparable to the Lochkovian one. During the Frasnian, SoV increased and  
361 corresponded to the morphological expansion that increased to specimens with a wide (sag.)  
362 preglabellar field and a wide (tr.) occipital ring despite the decrease of specimen density.  
363 Finally, the morphospace collapsed again during the Famennian to achieve a similar  
364 morphospace occupation as the Lochkovian or the Givetian (Fig. 4B, Fig. S4B).

365 As for cephalia and central cephalia, the morphological space for pygidia was characterized  
366 by a widespread occupation of shapes during the late Early Devonian (Fig. 4C, Fig. S4C).



367 From the Ludlow to the Lochkovian, the morphological space slightly increased by the  
368 apparition of MPg1 which is characterized by a long (sag.) pygidial axis (Fig. 4C, Fig. S4C).  
369 After this low disparity period, the morphological space reached a maximal occupation by  
370 continuing the previous morphologies but also by developing new one, i.e., MPg3 (negative  
371 PC1 scores) with narrow (tr.) pygidia from the Pragian to the Emsian (Fig. 4C, Fig. S4C). In  
372 this morphological space, MPg1 with long (sag.) pygidial axis developed but without co-  
373 occurring with pygidia with a long (sag.) axis and a narrow (tr.) outline. Morphologies with  
374 spines and curved pygidial border were also developed (negatives PC3 and PC4 scores).  
375 Narrowest (tr.) pygidia occurred only in the Pragian, never again. **The pygidium had the most**  
376 **important SoV increase of all the tagmata, but it started to decrease since the Emsian.**

377 The transition to the Middle Devonian did not coincide with a loss of morphological  
378 disparity; the three main morphotypes remain present (Fig. 4C, Fig. S4C). The reduction of  
379 the morphological space occurred during the late Eifelian. All the extreme shapes  
380 disappeared: narrow (MPg3) and wide (tr.) pygidia disappeared as well as long (MPg1) and  
381 short (sag.) pygidial axis and pygidia with curved pygidial border (Fig. 4C, Fig. S4C). If the  
382 pygidia with spines persisted in the Eifelian, they disappeared in the Givetian with the  
383 collapse of the morphospace **as underlined by the SoV decrease**; only one pygidium  
384 morphotype is represented, the MPg2. A slight expansion of the morphological space  
385 occurred during the Frasnian but remained relatively restricted compare to the Early  
386 Devonian. Only wide (tr.) pygidium were present. During the Famennian, the morphological  
387 space was a little bit more widespread and not so scarce but remained in the same occupation  
388 ranges until the latest Famennian where a reduction of the morphological space occurred. **In**  
389 **contrast, SoV slightly declined in the Famennian.** Only MPg2 persisted in the Late Devonian  
390 (Fig. 4C, Fig. S4C).

391

392

Fig. 5 near here

393 *Morphospace occupation by taxonomic orders*

394 For cephalata, the morphospace shows a reduced overlap between Phacopida and Proetida, two  
395 orders that occupied respectively a vast area (Fig. 5A). Lichida appeared somewhat an  
396 intermediate Order (Fig. 5A). Corynexochida is the only Order with a restricted area (Fig.  
397 5A). The main cephalic shape differences between these lineages are related to the position of  
398 the facial suture and the relative width (tr.) of the frontal lobe. Proetida were distinguished by  
399 an opistoparian facial suture and a wide (tr.) glabellar lobe equal to the frontal lobe (MCp4  
400 and MCp5). Proetida have no sagittal spines and no or short genal spines (according to PC3  
401 scores close to zero, Fig. S3A). At the opposite, Phacopida are distinguished by a wide (tr.)  
402 frontal lobe (according to **positive** scores of PC2) and mainly without spines (**morphotype 1**,  
403 according to **negative** scores of PC1). All of the Phacopida specimens have a proparian facial  
404 suture, no genal spines but some of them are characterized by the presence of sagittal spines.  
405 Corynexochida are distinguished by a prominent frontal lobe and no long (sag.) spines  
406 (MCp1). Finally, Lichida are characterized by a wide (tr.) frontal lobe as Phacopida and an  
407 opistoparian facial suture as Proetida. As Proetida and Corynexochida, Lichida have no  
408 sagittal spines and no or short (sag.) genal spines (according to PC3 scores close to zero).

409 For **central cephalata**, six orders are documented (Fig. 5B). The morphospace shows  
410 important overlap between Trinucleida, Phacopida, Proetida, Corynexochida, and Lichida  
411 (Fig. 5B). Phacopida and Proetida remain two orders that occupied respectively a vast area  
412 sharing a moderate overlap (Fig. 5B). Proetida are characterized mainly by MCn2 with a wide  
413 (tr.) preoccipital and occipital rings, while Phacopida are characterized mainly by MCn1.  
414 Corynexochida are characterized only by MCn1 with a wide (tr.) frontal lobe and no  
415 preglabellar field. Trinucleida are characterized by an intermediate morphology between wide  
416 (tr.) frontal lobe (i.e., MCn1) and wide (tr.) preoccipital and occipital rings (i.e., MCn2).

417 Lichida is another order with a vast area but sharing an important overlap with Phacopida  
418 (Fig. 5B). As for cephala, Lichida are characterized by various morphologies corresponding to  
419 both MCn1 and Mcn2 excluding the morphologies with a prelabellar field. Harpetida is the  
420 only Order with an isolated area with no overlap. They are characterized by narrow (tr.)  
421 **central cephala** with a broad prelabellar field.

422 For pygidia, the morphospace shows a large overlap of most orders. However, Phacopida  
423 and Corynexochida are quite separate (Fig. 5C). The main pygidial shape differences between  
424 lineages are related to the width (tr.) of pygidia and the length of the pygidial axis. Proetida  
425 are distinguished by a wide (tr.) pygidium with a medium-size pygidial axis (MPg2). As for  
426 Proetida, Phacopida can have a wide (tr.) pygidium with a medium-size pygidial axis (MPg1).  
427 However, most of them have a wide (tr.) pygidium with a long (sag.) pygidial axis (MPg1).  
428 Corynexochida is the only order with a narrow (tr.) pygidia (MPg3) with a small pygidial  
429 axis. Lichida order is characterized by a relatively important shape variation despite its weak  
430 number of specimens where the pygidial axis length or the pygidium (tr.) width seem to be  
431 not discriminant (MPg1, MPg2 and MPg3).

432

433 Fig. 6 near here

434 *Morphospace occupation by bathymetry*

435 For cephala, **central cephala** and pygidia, all habitat groups related to the depth/bathymetry  
436 show a very large overlap (Fig. 6A-C). Nevertheless, the results of the ANOVA (Table 2)  
437 show significant p-values ( $p < 0.05$ ) suggesting a shape difference between all habitat groups  
438 according to bathymetry with some exceptions. These exceptions mainly concerned cephala  
439 from deep environments or with important difference in water depth affinities (i.e., shallow  
440 vs. middle shelf). These datasets (i.e., cephala, **central cephala**, pygidia) reveal a  
441 differentiation between bathymetry-related groups. For cephala, MCp1 and MCp4 were

442 present at every bathymetric level, unlike other morphotypes (Fig. 6A). MCp2 gathers mainly  
443 trilobites, which lived in the middle shelf. Some trilobites from shallow environments have  
444 also this morphotype but they are rare and this trend never concerns the extreme shapes with  
445 long (sag.) spines (according to the **highest** PC2 scores). Almost all the trilobites, which lived  
446 in the inner shelf, correspond to MCp5. Two specimens from the middle shelf correspond also  
447 MCp5. MCp4 is dominated by trilobites from the middle shelf but trilobites with other  
448 bathymetrical affinities could also have this morphology. Finally, trilobites from shallow to  
449 middle shelf environments could have cephalata attributed to MCp3, but never encountered in  
450 the deep environment. All **central cephalon** morphologies were present at different depth  
451 except **central cephalata** with large (sag.) preglabellar field (Fig. 6B). For pygidia,  
452 morphological differences related to bathymetry affinities affect only the MPg3 which was  
453 absent from shallow and deep environments. MPg1 and MPg2 encountered at every  
454 bathymetric depth were present in the deep environment (Fig. 6C).

## 455 Table 2

456

### 457 *Morphospace occupation by vision*

458 For cephalata, **central cephalata** and pygidia (Fig. 6D-F), the morphospace shows a widespread  
459 area for large-eyed trilobites, while reduced-eye trilobites show a more restricted area. Blind  
460 trilobites show a restricted area (Fig. 6E-F). Nevertheless, the results of the ANOVA (Table  
461 2) show significant p-values ( $p < 0.05$ ) suggesting a shape difference between all vision groups  
462 according to visual abilities except between two compared groups of pygidia represented by  
463 reduced-eyed and blind taxa. These datasets (i.e., cephalata, **central cephalata**, pygidia) reveal a  
464 differentiation between visual abilities. For cephalata, reduced-eyes trilobites are not  
465 represented in MCp2, MCp4 and MCp5 and they are characterized by shape without spines or  
466 with very small spines. For **central cephalata**, both blind and reduced-eye trilobites are

467 represented by both MCn1 and MCn2. However, for MCn2, reduced-eye trilobites did not  
468 constitute a subset of the large-eyed trilobites but had their own unique morphology with wide  
469 (sag.) prelabellar field contrary to MCn1 for which they showed no new morphology (Fig.  
470 6E).

471 For pygidia, only MPg2 corresponds to blind or reduced-eyes trilobites, while all other  
472 morphotypes show large eyes trilobites.

473

#### 474 *Morphospace occupation by feeding habits*

475 For cephalia as for **central cephalia** and pygidia (Fig. 6G-I), the morphospace shows a  
476 widespread area for one group, i.e., predator/scavenger habits, while particle feeding and filter  
477 chamber habits show a restricted area. The results of the ANOVA (Table 2) show significant  
478 p-values ( $p < 0.001$ ) suggesting a shape difference between all diet groups according to  
479 feeding habits; only two compared groups of pygidia represented by particle feeding and  
480 predator/scavenger taxa show a p-value  $p < 0.05$ . For cephalia, particle-feeding trilobites were  
481 mainly restricted to MCp4 characterized by no genal spines except one specimen within  
482 MCp3 (Fig. 6G). In terms of morphology, predators and/or scavengers were distinguished  
483 from particle feeding trilobites, although these differences could be minor as for MCp4 where  
484 the facial suture was slightly different between both diet trilobites. For **central cephalia**,  
485 particle-feeding trilobites were also characterized by narrow (tr.) frontal lobes occurring  
486 mainly in MCn2 (Fig. 6H). At the opposite, Predator/Scavenger trilobites occupied all the  
487 morphospace. The greatest number of **central cephalia** allows having the repartition of filter  
488 chambers, which had very large prelabellar field and narrow (tr.) frontal lobes. For pygidia,  
489 particle-feeding trilobites show only MPg2 (Fig. 6I). They also have no spines occupying only  
490 the centre of the PC3-PC4 morphospace.

491

492 **DISCUSSION**

493 *Relationships between morphological spaces and proxies*

494 The maximum morphological disparity in trilobites with many different morphologies for  
495 both cephalia and pygidia was documented in the Ordovician but remained important in the  
496 Devonian (Foote 1993; Webster 2007). During this Devonian time interval, and according to  
497 our results, the overall dispersion of taxa in the morphospace shows (1) cephalia with spines or  
498 not, visual surfaces or not, proparian or opistoparian facial sutures, glabella with wide or  
499 narrow (tr.) anterior frontal lobes, and (2) pygidia with spines, wide or narrow (tr.) outlines  
500 and different lengths (sag.) of pygidial axis. The type of sutures was already an important  
501 criterion to segregate the trilobite morphologies in the Early Palaeozoic (Foote 1991a)  
502 although their ecological or life-history-strategy significance is uncertain (Hopkins 2014). The  
503 position of facial sutures corresponded to a trade-off between burrowing and moulting and  
504 could be an advantage to develop an infaunal lifestyle (Esteve *et al.* 2021). The presence of  
505 spines is identified as contributor to overall morphological variation for pygidia too, for which  
506 elongation (sag.) is a major axis of shape variation.

507 The three studied morphospaces are characterized by the presence of morphological  
508 clusters. The palaeoecology, measured here as the bathymetry and the diet factors, has only a  
509 weak effect on the trilobite morphology because different categories overlapped, and cannot  
510 explain such identified morphotypes (Fig. 6, Table 2). Hopkins (2014) already noticed a weak  
511 bathymetry influenced on the trilobite morphology excepted during the Ordovician and the  
512 Late Devonian when Proetida lived in shallow environments and Phacopida in deeper ones.  
513 The absence of real links between the trilobite morphologies and the water depth contrasts  
514 with the structure of the morphological disparity in ammonoids (Neige *et al.* 1997). As  
515 nektonic organisms, the ammonoids colonized the water column from the platform to the

516 basin with typical morphologies related to the pressure, which is not the case for benthic  
517 trilobites found only on the sea floor of the platform.

518 The diet influenced on the shape of trilobites as it contributed to morphological variations  
519 in modern arthropods (Lunardi *et al.* 2017). The distinct glabellar shapes recognized in our  
520 analyses (Fig. 6) are already identified in previous studies and are interpreted as an indicator  
521 of feeding habits (Fortey & Owens 1999). The expanded glabella anteriorly with wide frontal  
522 lobes observed in our study was interpreted as predator feeding habits, which are associated  
523 with the ingestion of bulky food (Fortey & Owen 1999). However, some predator/scavenger  
524 taxa showed a glabellar shape with narrower anterior frontal lobes, a morphology attributed to  
525 particle feeding trilobites. Difference of feeding habits for a same dorsal morphology is  
526 explained by the fact that morphologies changes in connection with diet mostly concerned  
527 especially the ventral structure, i.e., the hypostome (Fortey & Owens 1999). Filter chamber  
528 feeding trilobite needed a large cephalic shield to filter suspension particules in the water.  
529 Consequently, these trilobites presented the larger preglabellar field (Fig. 6). However, a large  
530 cephalic shield can also be used to avoid sinking into the mud (Richter 1920) and would not  
531 be related to feeding habits. Although pygidium shape did not played a role in trilobite  
532 feeding, particle feeding trilobites occupied only a small area of the morphospace.

533 The visual abilities, estimated here from the shape of the visual surfaces, have an important  
534 effect on the global trilobite morphology. Devonian trilobites with well-developed eyes  
535 occupied the global morphospace whereas blind and reduced-eye trilobites occupied only a  
536 small part of this morphospace (Fig. 6). Moreover, blind and reduced-eye trilobites occupied  
537 the same small part of the morphospace, except for taxa with narrow frontal lobes anteriorly  
538 (Fig. 6, Table 2). During the Devonian, pedomorphic evolutionary trends have been  
539 observed in Late Devonian taxa showing progressive eye reduction between closely related  
540 species that eventually leads to blindness (Feist & Clarkson 1989; Feist 1995; Crônier &

541 [Courville 2003](#); [Schoenemann 2018](#)). Such eye reduction implies morphological changes as  
542 the enlargement of fixigenae observed among Proetida or the 'displacement' of the facial  
543 suture towards the outer margins observed among Phacopida ([Feist 1995](#); [Crônier & Courville](#)  
544 [2003](#)). Consequently, Phacopida with reduced eyes are mainly confined to the part of the  
545 morphospace characterized by a suture closer to the lateral border (i.e., higher PC1 values,  
546 Fig. 6D).

547 In addition to diets and habitats, the trilobite morphologies are known to be influenced by  
548 their lifestyle, such as living in low-oxygen habitats ([Fortey 2004](#)) or the enrolment type  
549 ([Suárez & Esteve 2021](#)). In the same way, the competition between species is also a driver of  
550 diversification recognized in arthropods ([Eberle et al. 2014](#)).

551

#### 552 *Morphological evolution through time*

553 The trilobite morphospace occupation evolved during the Devonian in North Africa. A  
554 minimum occupancy in the morphospace occurred at the beginning of the Early Devonian,  
555 inherited from the end of the Silurian (Fig. 4). Only one cephalic and pygidial morphotypes  
556 and two **central cephala** morphotypes were encountered; the difference between cephala and  
557 **central cephala** being due to a lack of cephalic record. These morphologies were adapted to all  
558 depth/bathymetry and vision abilities but not to a particle feeding behaviour. Despite a  
559 reduced shape variability, trilobites were not restricted to any depth or type of vision. These  
560 morphologies coincided with the expansion of Phacopida disparity (Fig. 5A) and their  
561 dominance during the Lochkovian in North Africa ([Bault et al. 2021](#)).

562 During the Pragian, the morphological disparity increased and new morphologies were  
563 explored, i.e., cephala with an opistoparian facial suture and a narrow (tr.) frontal lobe. These  
564 new morphologies are assigned to Proetida (Fig. 5A) which developed in North Africa ([Bault](#)  
565 [et al. 2021](#)) and exhibited their maximal dispersion at the global scale at this time ([Foote](#)



566 1993). Moreover, exoskeletons with spines proliferated, i.e., pygidia with spines developed as  
567 well as cephalons with genal spines, which became more diverse and extended towards shapes  
568 with very long genal spines. Pygidia with a narrow (tr.) outline assigned to Corynexochida  
569 appeared too (Fig. 5C). Cephalons with a thick preglabellar field appeared in both Proetida and  
570 Phacopida morphologies without link with environmental depth (Fig. 6A-C) contrary to the  
571 Ordovician (Fortey & Wilmot 1991). Genal spines and preglabellar field appeared at the same  
572 time in different lineages showing a common trajectory in morphospace through time.  
573 However, Phacopida explored morphologies with sagittal spines but not Proetida suggesting  
574 that different causes could influence different lineages. The diversification of morphologies  
575 with the appearance of novelties in the Pragian coincided with new ecological opportunities  
576 due to the sea-level fall (Chlupáč 1994). The extension of the carbonate platform toward  
577 offshore environment offered new habitats leading to the morphospace expansion toward the  
578 middle shelf and to a trilobite radiation. Similarly, the predator/scavenger trilobites showed an  
579 increasing morphospace occupation possibly linked to a food partitioning and to an  
580 interspecific competition (Schluter 2000; Grant & Grant 2006). The increase of enrolment  
581 type in the Devonian was also a source of morphological disparity (Suárez & Esteve 2021).  
582 More generally, the diversification phases could be partly attributed to interspecific  
583 competition in arthropods (Eberle *et al.* 2014). The diversification of many clades in the Early  
584 Devonian (Alroy *et al.* 2008; Klug *et al.* 2010; Fan *et al.* 2020), may have an influence on the  
585 predator morphology with the arrival of new preys (Cattau *et al.* 2017). This advantageous  
586 feeding strategy could induce a radiation of predator/scavenger trilobites and at the opposite,  
587 particle feeding trilobites decreased maybe because an increasing competition of more  
588 efficient organisms. Despite new morphologies explored in the Pragian, those already present  
589 during the Lochkovian remained majority.

590 During the Emsian, all the main morphologies persisted with the maximum dispersion in  
591 the morphospace with the development of cephalia with long genal spines and especially with  
592 a wide (tr.) frontal lobe (Fig. 3). Only shape losses regarding the narrowest (tr.) pygidia  
593 occurred, leading to a decrease of morphological disparity. In trilobites, spinose exoskeletons  
594 were interpreted as passive morphological defences by some authors (Fortey 2004; Pates &  
595 Bicknell 2019). In a context of the Devonian Nekton Revolution (Klug *et al.* 2010), the  
596 emergence of morphologies with spines can be interpreted as a new answer to an increase of  
597 the predation. However, this hypothesis seems unlikely because some potential predators  
598 appeared only from the Emsian like ammonoids or chondrichthyans (Becker *et al.* 2019) or  
599 developed in the end of the Devonian like fishes (Derycke 2017). In addition, the  
600 morphologies with spines disappeared in the Middle Devonian and Frasnian, contrary to other  
601 shapes, which remained in the Famennian (Fig. 4). Nevertheless, these disappearances could  
602 be attributed to the inefficiency of spines against the large jaws predators of the Late  
603 Devonian (Brett 2003). The diversification of morphologies in the Early Devonian could be  
604 partly related to novel feeding habits, i.e., particle feeding habits with the appearance of  
605 glabella with a short (sag.) preglabellar field in trilobites (Fortey 2014). In addition, only  
606 exoskeletons with genal spines were attributed to this diet as well as in North Africa during  
607 the Devonian as in other areas and at other times (Fortey & Owens 1999). In their  
608 evolutionary history during the Early Devonian, trilobites explored morphospace with much  
609 of the subsequent variation in their cephalic features compared to their pygidial features.  
610 Accordingly, the pygidial characters display much overlap of taxonomic groups in the  
611 morphospace, while the cephalic characters show more distinct morphospace occupation at  
612 the order level.

613 The morphospace occupation persisted during the Eifelian with all the cephalic, central  
614 cephalia and pygidial morphotypes despite environmental changes implying sea-level and oxic

615 condition changes (Kaufmann 1998). Only the morphologies appeared during the Pragian  
616 were rarer, especially MCp2 for cephalon and MPg3 for pygidia (Fig. 4).

617 The Givetian was characterized by an important loss of morphology. The disappearance of  
618 some orders, i.e., Lichida and Corynexochida (Bault *et al.* 2021) led respectively to the loss of  
619 exoskeletons (i.e., cephalon and pygidia as well) with spines or the loss of cephalon with a long  
620 (sag.) glabella and of pygidia with a long (sag.) axis. However, Corynexochida was known in  
621 the lower Givetian of North Africa (Feist & Orth 2000) but only represented by a single  
622 pygidium; thus, the loss of the cephalic morphology occurred later although it is not possible  
623 to observe this in the morphospace. Between the different lineages, a common pattern of  
624 disappearance seems to exist and in particular, for both Proetida and Phacopida, which  
625 showed that the most affected trilobites were those with morphologies with protuberance like  
626 spines and preglabellar field implying a common origin of disappearance. The Givetian is  
627 known to be a period marked by a series of anoxic/hypoxic events associated with sea-level  
628 rise (Kaufman 1996; House 2002; Becker *et al.* 2016) and to have an important impact on the  
629 trilobite diversity (Feist 1991; Chlupáč 1994; Lerosey-Aubril & Feist 2012). The  
630 morphospace was reduced probably due to marginal or lateral extinctions (Foote 1991b; Korn  
631 *et al.* 2013). Morphologies with the lowest bathymetric extent such as the MCp2 and MCp3  
632 for cephalon and MPg3 for pygidia were the most impacted and they disappeared (Fig. 6A-C).  
633 Indeed, these morphologies have never been encountered in a deep environment, which could  
634 be a disadvantage in a context of rising sea level. In addition, the morphologies that remained  
635 were versatile and exhibited different vision abilities (Fig. 6). Accordingly, these  
636 morphologies were more adapted to environmental changes. The morphologies persisted  
637 during the Givetian corresponded to morphologies already present in the Ludlow and  
638 represent persistent morphologies.

639 The dispersion in the morphospace decreased in the Frasnian to reach only one  
640 morphotype for cephalia (MCp1) and for pygidia (MPg2). Nevertheless, the absence of  
641 additional morphotypes (i.e., MCp3 and MCp4 without spines or short genal spines) for  
642 cephalia in Proetida is due to the lack of sampled specimens in our dataset. Some Proetida  
643 were encountered in the upper Frasnian of North Africa (Feist 2002). The Frasnian is marked  
644 by an increase of the morphological disparity characterized by the reappearance of  
645 morphologies with numerous spines. These morphologies occurred within the dark-grey  
646 hypoxic limestone levels of the Kellwasser deposits related to relative deep-sea conditions  
647 (Feist 2002). Trilobite morphologies did not show significant shape losses and seem to have  
648 been little affected by the Kellwasser Events that occurred at the Frasnian/Famennian  
649 boundary and was one of five major extinction events in the history of life on Earth (McGhee  
650 1988, 1996; Racki 2005, 2020). The main shape change was the disappearance of  
651 morphologies with spines except genal spines in Cyrtosymbolinae (Proetida). Unfortunately,  
652 only the central cephalia and the pygidia for the Famennian Proetida are available in North  
653 Africa and they are therefore not included in the cephalic morphospace. As for the Givetian  
654 and the Frasnian, only the versatile morphologies related to depth conditions and vision  
655 abilities persisted during the Famennian. Only Proetida and Phacopida crossed the Frasnian-  
656 Famennian boundary both at the global and at the North Africa regional scale (Chlupáč 1994;  
657 Lerosey-Aubril & Feist 2012; Bault *et al.* 2021). These two orders are characterized by the  
658 maximal morphological variation in the Devonian morphospace in North Africa (Fig. 4). Such  
659 variability is known to be helpful to cope the environmental changes in other clades (Kolbe *et*  
660 *al.* 2011; González-Suárez & Revilla 2012; Huang *et al.* 2015; Austin & Dunlap 2019).  
661 Across all these events, from the Eifelian to the Famennian, there were irregular shape losses  
662 among trilobites but no extensive morphological innovation occurred after mass extinctions  
663 despite potential availability of the ecospace (Erwin 2015).

664 The notable extinction at the end of the Famennian, i.e., the Hangenberg event led to the  
665 demise of Phacopida whereas Proetida survived (Feist 1991; Lerosey-Aubril & Feist 2012;  
666 Bault *et al.* 2021). During this event, a severe shape loss but selective occurred which only  
667 affected Phacopida and their cephalo. Such selective patterns were previously identified in  
668 other organisms such as ammonoids where the morphology of clymeniids was more affected  
669 than that of goniatitids (Korn *et al.* 2013). If Phacopida and Proetida showed different  
670 morphologies of cephalo, they exhibited similar morphologies of pygidia, suggesting that the  
671 pygidia were the structures with the less extinction selectivity contrary to the cephalo.

672

### 673 *Morphospace divergence in the light of morphological constraints*

674 Location of cephalo, central cephalo and pygidia in the morphospaces showed a different  
675 relative distribution of specimens: for instance, Corynexochida and Phacopida that occupied  
676 the same part of the central cephalon morphospace, occupied distinct parts of the pygidium  
677 morphospace (Fig. 5B-C). This is explained by the relatively independence of the evolution of  
678 the studied structures known as tagmas (Hughes 2003) even if some covariations between  
679 these different structures exist due to enrolment (Oudot *et al.* 2019). Functional morphology,  
680 consequently functional modularity, explains why some orders showed overlapping  
681 morphologies for cephalo or pygidia but different shapes for other structures. Modularity was  
682 implied in the developmental process of trilobites indicating a developmental constraint on  
683 the morphology. Not all combination of characters were possible due to intrinsic constraints  
684 that channel the morphological evolution like physical or developmental constraints (Arnold  
685 1992; Gould 2002; Gerber 2014; Briggs 2017). For trilobites from the Devonian of North  
686 Africa, it was not possible to develop a sagittal spine without genal spines in the cephalon  
687 (high PC1 and low PC2 scores; Fig. 3A). Ontogenetic studies underlined a progressive  
688 enlargement (tr.) of the glabella during the development, especially in Phacopida due to a

689 change in the food niche (Crônier & Feist 1997; Crônier & Fortey 2006; Jacobs & Carlucci  
690 2019). Thus, feeding constraints during the development probably led to the absence of  
691 trilobites with a very narrow (tr.) glabella at an adult stage (high PC2 scores; Fig. 3B) in our  
692 dataset.

693 Some taxa exhibit intermediate morphologies between the morphotypes indicating that  
694 physical constraints did not hampered the existence of these morphologies (Fig. 3). The  
695 density distribution of morphologies in morphospace can reflect the positions of clusters with  
696 high-fitness interpreted as ‘adaptive peak’, separated by ‘valleys’ with few morphologies,  
697 driven by competition, trophic specialization or behaviour (McGhee 2007; Polly 2017). The  
698 trade-offs between different tasks led to adaptive landscape and therefore to phenotypic  
699 clusters (Shoval *et al.* 2012; Tandler *et al.* 2015). Thus, the overall dispersion of taxa was  
700 restricted to some areas of the morphospace with some empty areas and with a heterogeneous  
701 distribution for the Devonian time slice. This explains why some morphologies were absent  
702 during the Devonian such as a narrow (tr.) pygidium associated with a long (sag.) axis while  
703 such morphologies were present during the Cambrian, in the genus *Balcoracania* for example  
704 (Pocock 1970). Consequently, intrinsic factors alone cannot explain the absence of these  
705 morphologies and two other factors can be identified: the environmental conditions were not  
706 favourable to these morphologies or these morphological areas were simply never explored  
707 again after their disappearance. In the case of *Balcoracania*, this genus was found in very  
708 shallow environment, like lagoon or estuaries, during the Cambrian (Paterson *et al.* 2007) but  
709 trilobites deserted this environment during the Devonian of North Africa, suggesting an  
710 environmental explanation for the absence of a narrow (tr.) pygidium. The evolution of such  
711 parameter may be a trade-off between selection on factors such as function,  
712 ecology/environment, or development.

713 Our study shows same trends of covariation of different characteristics and the most  
714 obvious covariation concerns the cephalon for which a common pattern of morphological  
715 changes occurred. For both Proetida and Phacopida, some arrangements of the cephalon were  
716 needed to develop spines: the glabellar shape became less curved with a narrow (tr.) frontal  
717 lobe (lower PC1 and PC2 scores, Fig. 3A). Morphological covariations are known in trilobites  
718 and were mainly due to physical and developmental constraints (Hughes 2003; Crônier &  
719 Feist 1997; Gerber & Hopkins 2011; Webster & Zelditch 2011; Oudot *et al.* 2019).

720

## 721 CONCLUSION

722 In the Devonian, North African trilobites showed substantial morphological variations in their  
723 cephala, **central cephala** and pygidia. The morphological disparity concerned the width (tr.) of  
724 the glabella, the location of facial sutures, the elongation (sag.) of pygidia and the presence of  
725 spines. Both abiotic and biotic factors such as depth of water conditions, feeding habits and  
726 visual abilities seems to have only a weak effect on the global trilobite morphology. Trilobites  
727 with well-developed eyes occupied the global morphospace whereas blind and reduced-eye  
728 trilobites occupied only a small part of this morphospace.

729 North African trilobites have experienced significant morphological fluctuations from the  
730 Early to the Late Devonian. During the Devonian, the trilobites exhibited cases/examples of  
731 convergence in the visual surfaces or and spines and, a development of ‘rare’ morphologies  
732 such as the very spiny shapes of the Pragian-Emsian. The morphological disparity was low at  
733 the end of the Silurian and the Lochkovian. The trilobites occupied a relatively small part of  
734 the morphospace. Subsequently, the disparity increased considerably in the Pragian with the  
735 appearance of several new morphologies. Then, the disparity reached a maximum in the  
736 Emsian. The trilobites occupied the global morphospace and exhibited additional new  
737 morphologies, although some areas of the morphospace remained empty because some

738 morphologies did not develop in the Devonian. The morphological disparity persisted until  
739 the Eifelian, decreased considerably in the Givetian, and reached a minimum in the Late  
740 Devonian with a density more important for the Famennian than for the Frasnian. The  
741 trilobites developed no novelties anymore. This significant decrease in the morphological  
742 disparity occurred during a period characterized by numerous environmental events implying  
743 habitat changes with sea-level fluctuations and anoxic/hypoxic conditions. Some taxa (i.e.,  
744 morphologies) were more resilient to these environmental changes and persisted during the  
745 Devonian because of their adaptation to different bathymetry and their visual ability.  
746 Similarly, Phacopida and Proetida survived to most of the events thanks to their large  
747 morphospace occupation, and they were characterized by an evolutionary trend toward a  
748 progressive eye reduction leading to blindness.

749

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755

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1114 **Figures**

1115

1116 **Figure 1.** (A) Location of Morocco and Algeria (white star) on a palinspastic map (Cao et al.  
1117 2017), with continent positions and shapes for the Emsian. (B) Geographical location of  
1118 studied area with the Devonian outcrops (in bold; modified from Hollard 1968).

1119

1120 **Figure 2.** Complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight  
1121 landmarks for cephalon (in red), plus eight for central cephalon (in blue), and seven for  
1122 pygidium; and some linear measurements. Modified from Crônier (2013).

1123

1124 **Figure 3.** Location of: A, 328 cephala; B, 959 central cephala; and C, 605 pygidia from the  
1125 Devonian of North Africa in the global morphospace defined according to the two first  
1126 principal component axes performed on Procrustes residuals. Black dots represent the  
1127 reconstructed virtual shape, see Fig. S8 for more details. Coloured representative  
1128 morphotypes are displayed.

1129

1130 **Figure 4.** Location of morphotypes of: A, cephala; B, central cephala; and C, pygidia from  
1131 the Devonian of North Africa in the global morphospace defined according to the two first  
1132 principal component axes performed on Procrustes residuals, represented for each Devonian  
1133 stage. Coloured morphotypes according to Figure 3. D, Morphological disparity estimated by  
1134 the sum of variance (SoV) through time of cephala (blue), central cephala (red), and pygidia  
1135 (green). Ages from Cohen et al. (2013, updated with the version of 3/2020).

1136



1137 **Figure 5.** Location of: A, cephalia; B, **central cephalia**; and C, pygidia from the Devonian of  
1138 North Africa in the global morphospace defined according to the two first principal  
1139 component axes performed on Procrustes residuals for each order.

1140

1141 **Figure 6.** Location of: A, D, G, cephalia; B, E, H, **central cephalia**; and C, F, I, pygidia from  
1142 the Devonian of North Africa in the global morphospace defined according to the two first  
1143 principal component axes performed on Procrustes residuals for three factors: (A-C)  
1144 bathymetry; (D-F) visual abilities and (G-I) feeding habits. See supplementary figures S5, S6  
1145 and S7 for more details.

1146

1147 **Table 1.** Description of landmarks.

1148

1149 **Table 2.** P-values of the Procrustes ANOVA with permutation procedures to assess shape  
1150 covariation according to bathymetry, visual abilities and feeding habits as factors.

1151 **Supplemental figures**

1152

1153 **Figure S1.** Results of analyses performed to verify if topological issues occurred with our  
1154 set of landmarks. Correlation circles of landmarks showing the most contributing variables  
1155 for: A, cephalata; B, **central cephalata**; and C, pygidia. Morphospace defined according to the  
1156 two first principal component axes performed on Procrustes residuals using cephalon  
1157 specimens without (D) landmarks 13 and 16 and (E) landmarks 10 and 12.

1158

1159 **Figure S2.** Clusters identify by a Hierarchical Cluster Analysis (HCA) performed with the  
1160 Euclidian distance measure and Ward's linkage algorithm on the PC's scores for all  
1161 specimens, and the global morphospace defined according to the two first principal  
1162 component axes performed on Procrustes residuals for: A, cephalata; B, **central cephalata**; and  
1163 C, pygidia.

1164

1165 **Figure S3.** Location of: A, 328 cephalata; and B, 605 pygidia from the Devonian of North  
1166 Africa in the global morphospace defined according to the third and the fourth principal  
1167 component axes performed on Procrustes residuals.

1168

1169 **Figure S4.** Location of: A, cephalata; B, **central cephalata**; and C, pygidia from the Devonian of  
1170 North Africa in the global morphospace defined according to the two first principal  
1171 component axes performed on Procrustes residuals, represented for each Devonian stage. The  
1172 number of specimens is indicated for each stage. Ages from [Cohen \*et al.\* \(2013, updated with](#)  
1173 [the version of 3/2020\)](#).

1174

1175 **Figure S5.** Location of the morphotypes of: A, cephalia; B, **central cephalia**; and C, pygidia  
1176 from the Devonian of North Africa in the global morphospace defined according to the two  
1177 first principal component axes performed on Procrustes residuals for bathymetry. Ages from  
1178 [Cohen \*et al.\* \(2013, updated with the version of 3/2020\)](#).

1179

1180 **Figure S6.** Location of the morphotypes of: A, cephalia; B, **central cephalia**; and C, pygidia  
1181 from the Devonian of North Africa in the global morphospace defined according to the two  
1182 first principal component axes performed on Procrustes residuals for vision abilities. Ages  
1183 from [Cohen \*et al.\* \(2013, updated with the version of 3/2020\)](#).

1184

1185 **Figure S7.** Location of the morphotypes of: A, cephalia; B, **central cephalia**; and C, pygidia  
1186 from the Devonian of North Africa in the global morphospace defined according to the two  
1187 first principal component axes performed on Procrustes residuals for feeding habits. Ages  
1188 from [Cohen \*et al.\* \(2013, updated with the version of 3/2020\)](#).

1189

1190 **Figure S8.** Reconstruction of virtual shapes of cephalia according respectively to the two first  
1191 principal component axes PC1 and PC2 performed on Procrustes residuals.

1192

1193 **Appendix. Supplementary data**

1194

1195 **Appendix S1.** Dataset of Silurian and Devonian trilobites from Morocco and Algeria.

1196

1197 **Appendix S2.** References used in the dataset, including 65 publications with sufficient  
1198 chronostratigraphic information to calibrate occurrences at the stage and substage levels, and  
1199 taxonomic information to form an up-to-date taxonomy. These references constitute a  
1200 relatively complete fossil record of the Silurian and Devonian in North Africa.

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