Morphological disparity trends in Devonian trilobites from North Africa

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

Key words: trilobite, North Africa, Devonian, morphological disparity, evolution, environmental change.

Appearing as early as the Cambrian Explosion, trilobites diversified quickly to reached their maximum diversity at the end of the Cambrian (Westrop & Adrain 1998) and underwent an irregular decline from then to the end of the Permian (Sepkoski & Sheehan 1983; Foote 1993; Fan et al. 2020). The Devonian in particular marked an important step of this decline. Despite an important diversity increase in the Early Devonian, a protracted decrease at all taxonomic ranks (family, genus, species) occurred during the Middle Devonian up to the disappearance of three of the five orders (i.e. Odontopleurida, Harpetida and Corynexochida; using the Adrain (2011) classification updated by Lamsdell & Selden (2015) concerning the superfamily Aulacopleuroidea) in the Late Devonian during the Kellwasser events (Feist 1991; Chlupáč 1994; Crónier & Van Viersen 2007; Lerosey-Aubril & Feist 2012; Bault et al. 2021). In addition to this loss in diversity, the visual abilities and the life environments of trilobites changed, especially after the Frasnian–Famennian boundary (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Therefore, the Devonian is a critical period in the evolutionary history of trilobites. This interval of time also records major biotic and abiotic changes, such as the Devonian Nekton Revolution (Klug et al. 2010), the development of vascular land plants (Pawlik et al. 2020), exceptional sea-level highstands, widespread epicontinental shallow seas, greenhouse climates (Tinn et al. 2020) and several anoxic/hypoxic events and rapid sea level fluctuations (House 2002; Becker et al. 2016).

Another important morphological indicator of evolutionary success or failure is disparity, as measured by the occupancy of morphospace (Foote 1997; Wills 2001; Erwin 2007, Minelli 2016, Guillerme et al. 2020). Success in diversity does not necessarily go together with success in disparity. Many taxa show high diversity with low disparity, while others are highly diverse but also exhibit high disparity (Minelli 2016). Taxonomic richness and morphological disparity are complementary metrics which can be decoupled (Foote 1991a, 1991b, 1993). Such decoupled changes in taxonomic diversity and morphological disparity can suggest different proxies for understanding the ecological impact of an extinction event for example (Wan et al. 2021). Morphological disparity of trilobites has been extensively documented in the Cambrian and the Ordovician (Foote 1991a; Smith & Lieberman 1999; Webster 2007; Hopkins 2013; Jacobs &
Carlucci 2019). However, Devonian studies are rare and often dedicated to developmental and ontogenetic topics exploring the intrinsic factors of morphological change (e.g. Crónier et al. 1998; Crónier 2013; Oudot et al. 2019). However, if biotic and abiotic factors are known to contribute to diversification, they also contributed to the morphological disparity (Crónier et al. 2004; Hopkins & Gerber 2017). Some relationships have been noticed or demonstrated between trilobite shape and ecological affinity, such as bathymetric conditions (Hopkins 2014), feeding habits (Fortey & Owens 1999) or life habits (Fortey 2014). Although the environmental influence on the morphological disparity has rarely been evaluated, Hopkins (2014) emphasized the effect of bathymetry, substrate and latitude on trilobite shape for the entire Palaeozoic. As the result of these environmental effects, the morphological disparity can be dependent on the geographical location of populations through time (Hopkins & Webster 2009; Abe & Liebermann 2012; Esteve et al. 2017). These recent studies have been done at the global scale or focusing on only one family. Nevertheless, for Devonian trilobites, no studies have been performed on the total richness available throughout a span time for a relatively well-constrained area.

In Devonian sediments, the environmental and ecological changes are particularly well exhibited in North Africa where trilobites were especially well represented and diverse (Lebrun 2018; Bault et al. 2021). This area is one of the richest in terms of Devonian trilobites with five orders and 15 families (Bault et al. 2021), corresponding to all known worldwide Devonian orders and the majority of families (Crónier & Van Viersen 2007). In addition to its fossil record, this area is also particularly well known for its stratigraphy and its palaeoenvironmental context (Massa 1965; Hollard 1967; Wendt & Belka 1991; Becker et al. 2004; Abbache et al. 2019; among others). It allows us to establish the relationship between trilobites as characterized by their shape, and their habits and palaeoenvironmental affinities. Moreover, the Devonian events are all clearly identifiable in this area (Kaufmann 1998).

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

**MATERIAL AND METHOD**

**Trilobite data and frameworks**

We compiled a dataset to investigate the morphology of Silurian and Devonian trilobites from Morocco and Algeria (Fig. 1). At this time, this area was situated on the continental margin of the Gondwana at a latitude between 30° and 45°S (Scotese & Golonka 1992; Golonka 2002). It was a favourable place for the settlement of benthic communities such as trilobites (Morzade 2001; McKellar & Chatterton 2009). All figures of specimens illustrated over the last 80 years with sufficient quality have been directly exploited for shape analysis (Appendix S1). The morphology of trilobites is here quantified by focusing on their most important structures: the cephalon, glabella and pygidium (Fig. 2). The glabella is a subset of the cephalon and it is here analysed with the occipital ring and preglabellar field as the ‘central cephalon’. The cephalon is studied as a whole, including the central cephalon landmarks, for morphological analysis. A first dataset contains 328 complete cephalas, 959 complete central cephalas and 605 complete pygidias; each structure being studied independently. This dataset includes all well-preserved and illustrated specimens during the last 80 years from 65 publications (Appendix S2). Only dorsal views were used and the right-side from each structure was selected unless the left-side was more complete; in this case, a mirror image was used to correspond to the right side. A second dataset contains 30 complete specimens of 30 different species for which both the cephalon and the pygidium were simultaneously preserved.

For each specimen, taxonomy, age (stage) as well as ecological characteristics were also included in the dataset. Firstly, genera were classified by environmental affinity (i.e. water depth conditions) (Fortey 1975; Turvey 2005; Crónier & Van Viersen 2007). Bathymetrical affinity for each genus was determined as the environment where it mainly occurred. Because these data were not available for each occurrence, we interpolated it with the data from other papers with the same stratigraphic context or from genera with the same affinity. Four categories are identified along the bathymetric profile: (1) the shoreface environment characterized by shallow and proximal conditions; (2) the upper offshore or inner shelf environment characterized by relatively shallow waters; (3) the median offshore or middle shelf environment characterized by relatively deep deposits; and (4) the lower offshore or outer shelf environment located below effective
storm wave base. It is important to note that depth categories were based on sedimentological evidence and not trilobite shape, to avoid analytical bias.

Secondly, genera were classified by their diet. We referred to Fortey & Owens (1999) to determine the feeding habits of genera based on hypostome features. Three diet categories are recognized in our database: 'Predator/Scavenger', which ingested small prey; 'Particle feeding', which fed on nutrients; and 'Filter chamber', which brought sedimentary material into suspension before selecting out edible particles (Fortey & Owens 1999). It should be noted that the estimates of feeding habits are only assumptions and evidence in the fossil record is rare. For instance, only two examples confirmed as particle feeders are known (Zhu et al. 2014; Gutiérrez-Marco et al. 2017). Feeding habits are still an ongoing debate and advances in biomechanics (Bicknell et al. 2018, 2021) will help to refine the trilobite diets.

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

Landmark data

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

The shape of the cephalon is here described by a set of 15 landmarks and one curve of 24 equally spaced semi-landmarks between landmark 2 and landmark 7 (Fig. 2; Table 1). For the central cephalon, seven landmarks plus the semi-landmark curve were digitized (Fig. 2; Table 1). Similarly, seven landmarks were digitized for pygidia (Fig. 2; Table 1). Landmarks were positioned in key locations to summarize the complexity of morphologies. The semi-landmarks were processed directly and not slid. Specimens with missing landmarks were excluded. The $x$ and $y$ coordinates of 2D landmarks and semi-landmarks were digitized (Fig. 2) with TPSdig v.2.32 (Rohlf 2010, 2015). The landmark 2D coordinates were then exported in the standard TPS file format (Rohlf 2012) (Data S1, Data S2).

Because we analysed specimens from different lineages, shapes can be very different with extreme landmark locations and thus, geometric morphometric methods could not be applied (Zelditch et al. 2012). In our case this issue concerns only the cephala where landmarks 10, 11 and 12 can exhibit topological changes in their relative position to other landmarks (Fig. 2; Table 1). The Pinocchio effect (Chapman 1990; Thulman 2019) can also affect landmarks 13 and 16 (Fig. 2; Table 1). To assess the impact of these issues, we removed these landmarks to see whether or not the morphospace is affected by these biases. To assess the possible impact of each landmark, we calculated the Pearson’s correlation coefficient between each landmark dimension and the major ordination axes and their statistical significance by means of the

**Fig. 2.** Complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight landmarks for cephalon (in red), plus eight for central cephalon (in blue), and seven for pygidium; also some linear measurements. Modified from Crönier (2013).
envfit function of the vegan R-package (Oksanen et al. 2020). The graphical output of these correlations as arrows proportional to these correlations on the PCA-based morphospace leads to a so-called correlation circle. In our case, this analysis shows that none of these 'suspicious' landmarks (10, 11, 12, 13 and 16) have an influence larger than the other landmarks (Fig. S1). Thus, our morphospaces are not being determined by topological issues or a Pinocchio effect.

**Shape analysis**

Standardization of the landmark data (superimposition) to remove variability due to differences in size, placement and orientation, was performed by means of a generalized Procrustes analysis (GPA), which minimizes the sum of square distances between equivalent landmarks (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O’Higgins 2000; Zelditch et al. 2012). Curves of semilandmarks are slid by means of the minimum Procrustes distance (Perez et al. 2006; Gunz & Mitteroecker 2013) and the superimposed landmarks are projected to the tangent space at the full Procrustes mean (Rohlf 1999; Kendall 1984).

For each of the three studied structures (cephalon, central cephalon and pygidium), we performed a principal components analysis (PCA; Ringnæs 2008; Abdi & Williams 2010) to reduce the high-dimensionality of the superimposed landmarks to fewer variables (eigenvectors), along which the shape variation is maximal. Each specimen can be represented by relatively few variables and can be plotted in a PCA-space (morphospace) defined by principal component axes (PCs), which are ordered by decreasing percentage of the total shape variance. The morphospace is centred on the average shape (consensus) where each point represents a specimen shape and its position reflects the relative shape similarities and differences between specimens. Finally, among the studied specimens, series of virtual shapes were reconstructed by doing a back transformation from the PC scores for PC1 and PC2 to illustrate the largest shape changes over the morphospace. Shape analysis was computed in the R scientific environment (v.3.6.2; R Core Team 2013) and the packages geomorph (v.3.2.1; Adams & Otárola-Castillo 2013) and epaleo (v.0.8.41; CM, unpub.), as well as PAST (v.3.24; Hammer et al. 2001). Figures were created from R outputs.

To identify some morphological clusters or morphotypes (Fig. S2), we performed a hierarchical cluster

### Table 1. Description of landmarks.

| Structure                  | Landmark | Definition                                                                 |
|----------------------------|----------|----------------------------------------------------------------------------|
| Central cephalon only      | 1        | Anteriormost point of sagittal cephalic length without spine               |
| Cephalon (including central part) | 2        | Anteriormost point of sagittal glabellar length                            |
|                            | 3        | Intersection between sagittal axis and occipital furrow                    |
|                            | 4        | Posteriormost point of sagittal cephalic length                           |
|                            | 5        | Maximum transverse glabellar width                                        |
|                            | 6        | Intersection between occipital furrow and dorsal furrow                   |
|                            | 7        | Intersection between posterior border and dorsal furrow                    |
|                            | 8        | Anteriormost end of eye                                                   |
|                            | 9        | Posteriormost end of eye                                                  |
|                            | 10       | Intersection between anterior facial suture and anterior lateral border    |
|                            | 11       | Intersection between posterior branch of facial suture and posterior or lateral border furrow |
|                            | 12       | Anteriormost point of sagittal (or ex-sagittal) cephalic length with spine |
|                            | 13       | Lateral external most point of eye                                        |
|                            | 14       | Maximum transverse cephalic width                                         |
|                            | 15       | Extremity of genal angle or spine                                         |
| Pygidium                   | 16       | Anteriormost point of sagittal pygidial length                            |
|                            | 17       | Intersection between anterior pygidial border and dorsal furrow           |
|                            | 18       | Maximum transverse pygidial width without spines                         |
|                            | 19       | Posteriormost point of sagittal pygidial length without spines           |
|                            | 20       | Posteriormost point of sagittal pygidial axis length                      |
|                            | 21       | Maximum transverse pygidial width with or without spines                 |
|                            | 22       | Posteriormost point of sagittal or ex-sagittal pygidial length (with spines) |
analysis (HCA) with the package epaleo on the principal component scores by using the Euclidean distance measure and Ward’s linkage algorithm. See Everitt et al. (2011) or Murtagh & Contreras (2012) for more details on these methods.

**Morphospace analysis**

Morphospaces were established for the complete data set of all specimens independently for cephalas, central cephalas and pygidia. They were explored to evaluate the morphospace occupation first by the previously defined morphotypes, and then by the orders (using Adrain (2011) classification updated by Lamsdell & Selden (2015) concerning Proetida). Moreover, to investigate trilobite shape changes through time, the structure morphospace was also plotted for different chronostratigraphic stages. This allows us to visualize how the different groups are distributed in the morphospace, to identify which morphotypes or orders are impacted by morphological change and how, and to identify key morphologies among trilobites for a given stage which were related to a successful diversification or disappearance.

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

Additionally, the morphospace was explored according to the inference of the potential influence on morphospace variation of three different factors related to life modes known to be changing with Devonian events: bathymetry, feeding habits and visual ability (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Effect of eye reduction was investigated for all the structures, including those without eyes (i.e. central cephalon and pygidium). Eye reduction may affect other parts of trilobites by imposing a rearrangement of structures, such as the suture line position (and so fixigena) in Phacopida or Proetida. This analysis was done by mapping each factor of each individual onto the morphospace. We computed a one-side nonparametric, permutational ANOVA on the PC axes to test statistically if a shape difference exists according to these factors, we highlighted the different categories of our factors on PCA. Morphospace analyses were also computed with R v.3.6.2 and PAST v.3.24.

**RESULTS**

**Global morphological space**

For cephalas, the PCA yields 77 principal components (PCs), five of which explained 83.4% of the variance in shape of the studied trilobites: PC1, 47.1%; PC2, 15.6%; PC3, 11.9%; PC4, 4.7%; and PC5, 4.1%. The remaining components accounted for less than 4% each. The morphological interpretation of the shape changes associated with PC1 and PC2 is depicted by only a few differences in the shape of the studied trilobites: PC1, 47.1%; PC2, 15.6%; PC3, 11.9%; PC4, 4.7%; and PC5, 4.1%. The remaining components accounted for less than 4% each. The morphological interpretation of the shape changes associated with PC1 and PC2 is depicted by overlying reconstructed shapes at various locations of the morphospace (Fig. 3A). PC1 depicts the presence or not of genal spines and sagittal spine, the shape change of the glabella and the postrostral position (i.e. opistoparian, proparian or gonatoparian; Fig. 2) of the facial suture. High scores of PC1 show the presence of long genal or sagittal spines, a wide (transverse; tr.) glabella at its base and an opistoparian facial suture with its terminal end to the posterior border (Fig. 3A). At the opposite end, low PC1 scores show cephala without spines, a wide (tr.) glabella at the frontal lobe and a proparian facial suture with its terminal end to the lateral border. PC2 depicts the presence or absence of spines and the postrostral position of the facial suture too (Fig. 3A). However, the main shape change seems to be depicted by the shape of the occipital ring. Low scores of PC2 show a wide (tr.) occipital ring, while high scores of PC2 show a narrow (tr.) occipital ring. PC3 contrasts two different morphologies with spines (Fig. 3A). High scores of PC3 show a long sagittal spine without genal spine, while low scores of PC3 show genal spines without sagittal spine. Finally, low scores of PC4 indicate narrow (tr.) librigena, while high scores show wide (tr.) librigena.

The set of individual cephalas is grouped into five morphotypes along the first two principal component axes, with only few individuals between them (Fig. S2A; Fig. 3A). HCA shows five main morphotypes corresponding to five main morphotypes (Fig. S2). The most common shapes are depicted by negative PC1 and null PC2 scores (Fig. 3A). These shapes assigned to Morphotype 1 (MCp1) correspond to cephalas without sagittal and genal spines, with a wide frontal lobe (tr.) and a
proparian facial suture (Fig. 3A). MCp1 changes to a similar glabellar shape and facial suture position but with presence of genal spines (MCp3), and of sagittal spine (MCp2), depicted by high PC1 and PC2 scores. Other morphotypes are depicted by low PC1 and PC2 scores (MCp5) to high PC1 and low PC2 scores (MCp4). These two morphotypes (4 and 5) correspond to cephalas with a proparian or opistoparian facial suture, with a frontal lobe narrower (tr.) than in the other morphotypes, such that the basal part of the glabella is wider (tr.) than the frontal lobe. The main difference between MCp4 and MCp5 is the presence of genal spines in MCp4. For all types of glabella (i.e. wide or narrow frontal lobe (tr.), MCp1 and MCp5), cephalas can exhibit spines but it requires narrower (tr.) glabellar furrows without an inflated frontal lobe (Morphotypes 2, 3 and 4).

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

The set of individual central cephalas is grouped into two morphotypes (MCn1 and MCn2; Fig. S2B), mainly along the first principal component axis PC1 (Fig. 3B). Negative PC1 and null PC2 scores depict a common shape (Fig. 3B). This shape (assigned to MCn1) corresponds to central cephalas with a wide (tr.) frontal lobe compared to the glabellar base and without preglabellar field anteriorly (Fig. 3B). Positive PC1 and null PC2 scores depict another common shape (Fig. 3B). This shape is assigned to MCn2 and corresponds to central cephalas with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B).

For pygidia, the PCA yields 14 PCs, four of which explained 89.9% of the variance in shape of the studied trilobites: PC1, 42.5%; PC2, 22.2%; PC3, 14.2%, and PC4, 11.0%. The remaining components accounted for less than 5% each. PC1 (Fig. 3C) shows that the main shape change contrasts narrow (tr.) pygidia (low scores) to wide (tr.) pygidia (high scores). PC2 depicts the sagittal (sag.) length of the pygidial axis, PC3 depicts the presence of lateral and sagittal spines and PC4 depicts the

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**FIG. 3.** Location of: A, 328 cephalas; B, 959 central cephalas; and C, 605 pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal components. Black dots represent the reconstructed virtual shapes, see Figure S8 for more details. Coloured representative morphotypes are displayed.
curve of the pygidial border (Fig. S3B). Along PC3 and PC4, most of the shapes show individuals with no spines. Only few individuals located in the low PC3 scores have small pygidial spines. These pygidial spines are generally short and never longer (sag.) than the pygidium itself. High scores on PC4 indicate a maximal (tr.) length below the anteriormost point of sagittal pygidial length and conversely low scores indicate a maximal (tr.) length above the anteriormost point of sagittal pygidial length (Fig. S3B). No pygidia are present in the area of the morphospace that depicts pygidia with a very narrow (tr.) and a long (sag.) pygidial axis (i.e. low PC1 and PC2 scores).

The set of individual pygidia is grouped into three morphotypes (Fig. S2C). The most common shapes, assigned to MPg1 and MPg2, are depicted by rather null scores of PC1 (Fig. 3C). These shapes correspond to pygidia with a medium size and with either a long (MPg1) or a medium length of pygidial axis (MPg2). MPg3 is depicted by low PC1 and high PC2 scores (Fig. 3C). The shapes associated with this cluster correspond to pygidia with a narrow (tr.) and a short (sag.) pygidial axis (MPg3).

**Morphospace occupation by time**

The changes in occupancy/filling of the morphospaces (i.e. the morphological disparity) through time are illustrated in Figure 4 for the three structures. For cephala, the morphological space was characterized by a reduced occupation from the Ludlow to the Lochkovian, followed by widespread occupation in the second part of the Early Devonian. During Ludlow time, the filling of morphological space was limited (Fig. 4A) and was restricted to MCP1 and MCP5. The location of morphotypes through time is given in Figure S4A. At this time, the morphological dissimilarity among specimens (i.e. SoV) was low. Then, the morphological disparity remained reduced in the Lochkovian and restricted to only one cephalon assigned to a new morphotype (MCP4) in the early Lochkovian and three cephalon to MCP1 in the late Lochkovian (Fig. 4A). After this low disparity period, the disparity in the Pragian covered almost all the morphospace, with the only exception of some cephalon with sagittal spines (MCP2) (Fig. 4A; Fig. S4A). This morphology appeared during Emsian when the morphospace reached its maximal coverage and SoV was the highest.

The transition to the Middle Devonian (Fig. 4A; Fig. S4A) did not coincide with an important loss of morphological disparity for the central cephalon and the pygidium but the cephalon was more affected with the disappearance of MCP2. This morphology loss is confirmed by the strong decrease of SoV. Only cephala characterized by low PC2 scores disappeared. These cephala exhibit sagittal spines. However, the morphotypes 2, 3 and 4 disappeared from North Africa in the late Eifelian (Fig. 4A; Fig. S4A). These morphotypes correspond to cephala with spines. If MCP1 and MCP5 persisted in the early Givetian, MCP1 disappeared in the middle Givetian and MCP5 in the late Givetian. In the Late Devonian, only MCP1 reappeared.

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

As for cephala and central cephala, the morphological space for pygidia was characterized by a widespread occupation of shapes during the late Early Devonian (Fig. 4C; Fig. S4C). From the Ludow to the Lochkovian, the morphological space slightly increased by the apparition of MPg1 which is characterized by a long (sag.) pygidial axis (Fig. 4C; Fig. S4C). After this low disparity period, the morphological space reached a maximal occupation by continuing the previous morphologies but also by developing new one, MPg3, (low PC1 scores) with narrow (tr.) pygidia from the Pragian to the Emsian (Fig. 4C; Fig. S4C). In this morphological space, MPg1 with long (sag.) pygidial axis developed but without co-occurring with pygidia with a long (sag.) axis and a narrow (tr.) outline. Morphologies with spines and a curved pygidial border were also developed (low PC3 and PC4 scores). Narrowest (tr.) pygidia occurred only in the Pragian, never again. The pygidium had the most important SoV increase of all the tagmata, but it started to decrease in the Emsian.

The transition to the Middle Devonian did not coincide with a loss of morphological disparity; the three main morphotypes remain present (Fig. 4C; Fig. S4C). The reduction of the morphological space occurred during the late Eifelian. All the extreme shapes disappeared:
FIG. 4. Location of morphotypes of A, cephalon; B, central cephalon; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal components, represented for each Devonian stage. Coloured morphotypes according to Figure 3. D, morphological disparity estimated by the sum of variance (SoV) through time of cephalon (blue), central cephalon (red), and pygidia (green). Ages from Cohen et al. (2013, updated with the version of 3/2020).
narrow (MPg3) and wide (tr.) pygidia disappeared as well as long (MPg1) and short (sag.) pygidial axis and pygidia with curved pygidial border (Fig. 4C; Fig. S4C). If the pygidia with spines persisted in the Eifelian, they disappeared in the Givetian with the collapse of the morphospace as underlined by the SoV decrease; only one pygidium morphotype is represented, the MPg2. A slight expansion of the morphological space occurred during the Frasnian but remained relatively restricted compared to the Early Devonian. Only wide (tr.) pygidia were present. During the Famennian, the morphological space was a little bit more widespread and not so scarce but remained in the same occupation ranges until the latest Famennian when a reduction of the morphological space occurred. In contrast, SoV slightly declined in the Famennian. Only MPg2 persisted into the Late Devonian (Fig. 4C; Fig. S4C).

Morphospace occupation by taxonomic order

For cephala, the morphospace shows a reduced overlap between Phacopida and Proetida, two orders that each occupied a vast area (Fig. 5A). Lichida appeared as a somewhat intermediate order (Fig. 5A). Corynexochida is the only order with a restricted area (Fig. 5A). The main cephalic shape differences between these lineages are related to the position of the facial suture and the relative width (tr.) of the frontal lobe. Proetida were distinguished by an opistoparian facial suture and a wide (tr.) glabellar lobe equal to the frontal lobe (MCp4 and MCp5). Proetida have no sagittal spines and no or short genal spines (according to PC3 scores close to zero; Fig. S3A). At the opposite end of the spectrum, Phacopida are distinguished by a wide (tr.) frontal lobe (according to high scores of PC2) and mainly without spines (morphotype 1, according to low scores of PC1). All of the Phacopida specimens have a proparian facial suture, no genal spines but some of them are characterized by the presence of sagittal spines. Corynexochida are distinguished by a prominent frontal lobe and no long (sag.) spines (MCp1). Finally, Lichida are characterized by a wide (tr.) frontal lobe similar to that of Phacopida and an opistoparian facial suture like Proetida. As Proetida and Corynexochida, Lichida have no sagittal spines and no or short (sag.) genal spines (according to PC3 scores close to zero).

For central cephala, six orders are documented (Fig. 5B). The morphospace shows important overlap between Trinucleida, Phacopida, Proetida, Corynexochida and Lichida (Fig. 5B). Phacopida and Proetida remain the two orders that occupied vast areas sharing a moderate overlap (Fig. 5B). Proetida are characterized mainly by

FIG. 5. Location of: A, cephala; B, central cephala; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal components for each order.
MCn2 with a wide (tr.) preoccipital and occipital rings, while Phacopida are characterized mainly by MCn1. Corynexochida are characterized only by MCn1 with a wide (tr.) frontal lobe and no preglabellar field. Trinucleida are characterized by an intermediate morphology between wide (tr.) frontal lobe (MCn1) and wide (tr.) preoccipital and occipital rings (MCn2). Lichida is another order with a vast area but sharing an important overlap with Phacopida. As for cephala, Lichida are characterized by an intermediate morphology between wide (tr.) frontal lobe and no preglabellar field. Trinucleida are characterized only by MCn1 with a wide (tr.) preoccipital and occipital rings, except for MCn2 without preglabellar field. Phacopida are characterized mainly by MCn1. MCn2 excluding the morphologies with a preglabellar field. Harpetida is the only order with an isolated area with no overlap. They are characterized by narrow (tr.) central cephala with a broad preglabellar field.

For pygidia, the morphospace shows a large overlap of most orders. However, Phacopida and Corynexochida are quite separate (Fig. 5C). The main pygidial shape differences between lineages are related to the width (tr.) of pygidia and the length of the pygidal axis. Proetida are distinguished by a wide (tr.) pygidium with a medium-size pygidal axis (MPg2). For Phacopida, Phacopida can have a wide (tr.) pygidium with a medium-size pygidal axis (MPg1). However, most of them have a wide (tr.) pygidium with a long (sag.) pygidal axis (MPg1). Corynexochida is characterized by a relatively important shape variation in which the pygidal axis length or the pygidium (tr.) width seem to be not discriminant (MPg1, MPg2 and MPg3).

Morphospace occupation by vision

For cephala, central cephala and pygidia (Fig. 6D–F), the morphospace shows a widespread area for large-eyed trilobites, while reduced-eye trilobites show a more restricted area. Blind trilobites show a restricted area (Fig. 6E–F). Nevertheless, the results of the ANOVA (Table 2) show significant p-values (p < 0.05) suggesting a shape difference between all vision groups according to visual abilities except between two compared groups of pygidia represented by reduced-eyed and blind taxa. These datasets (i.e. cephala, central cephala, pygidia) reveal a differentiation between visual abilities. For cephala, reduced-eyes trilobites are not represented in MCp2, MCp4 and MCp5 and they are characterized by shape without spines or with very small spines. For central cephala, both blind and reduced-eye trilobites are represented by both MCn1 and MCn2. However, for MCn2, reduced-eye trilobites did not constitute a subset of the large-eyed trilobites but had their own unique morphology with a wide (sag.) preglabellar field contrasting with MCn1 for which they showed no new morphology (Fig. 6E).

For pygidia, only MPg2 corresponds to blind or reduced-eyes trilobites, while all other morphotypes are represented by large eyes trilobites.

Morphospace occupation by feeding habits

As for central cephala and pygidia (Fig. 6G–I), the cephala morphospace shows a widespread area for one group, predator/scavenger habits, while particle feeding and filter chamber habits have restricted areas. The results of the ANOVA (Table 2) show significant p-values (p < 0.001) suggesting a shape difference between all diet groups according to feeding habits; only two compared groups of pygidia, represented by particle feeding and predator/scavenger taxa, show a p-value < 0.05. For cephala, particle-feeding trilobites were mainly restricted to MCp4, characterized by no genal spines, with a single specimen...
exception within MCp3 (Fig. 6G). In terms of morphology, predators and/or scavengers were distinguished from particle feeding trilobites, although some of these differences were minor; for example in MCp4, the facial suture was slightly different for trilobites in the two diet categories. For central cephala, particle-feeding trilobites were also characterized by narrow (tr.) frontal lobes occurring mainly in MCn2 (Fig. 6H). In contrast, predator/scavenger trilobites occupied all of the morphospace. The more extensive dataset of central cephala produced the partition of trilobites with filter chambers, which had very large preglabellar field and narrow (tr.) frontal lobes. For pygidia, particle-feeding trilobites included only the morphotype MPg2 (Fig. 6I). They also have no spines, and occupy only the centre of the PC3–PC4 morphospace.

**DISCUSSION**

*Relationships between morphological spaces and proxies*

The maximum morphological disparity in trilobites with many different morphologies for both cephala and pygidia was documented in the Ordovician but remained...
significant in the Devonian (Foote 1993; Webster 2007).

During this Devonian time interval, and according to our results, the overall dispersion of taxa in the morphospace shows: (1) cephalon with spines or not, visual surfaces or not, proparian or opistoparian facial sutures, glabella with wide or narrow (tr.) anterior frontal lobes; and (2) pygidia with spines, wide or narrow (tr.) outlines and different lengths (sag.) of pygidial axis. The type of suture was already an important criterion to segregate trilobite morphologies in the early Palaeozoic (Foote 1991a) although their ecological or life-history-strategy significance is uncertain (Hopkins 2014). The position of facial sutures corresponded to a trade-off between burrowing and moulting, and could be an advantage for developing an infaunal lifestyle (Esteve et al. 2021). The presence of spines is identified as contributor to overall morphological variation for pygidia too, for which elongation (sag.) is a major axis of shape variation.

The three studied morphospaces are characterized by the presence of morphological clusters. Palaeoecology, measured here as bathymetry and diet factors, has only a weak effect on the trilobite morphology because different categories overlapped, and cannot explain such identified morphotypes (Fig. 6; Table 2). Hopkins (2014) recognized a weak bathymetric influence on trilobite morphology except during the Ordovician and the Late Devonian when Proetida lived in shallow environments and Phacopida in deeper ones. The absence of real links between trilobite morphology and water depth contrasts with the structure of the morphological disparity in ammonoids (Neige et al. 1997). As nektic organisms, the ammonoids colonized the water column from the platform to the basin with typical morphologies related to the pressure, which is not the case for benthic trilobites found only on the sea floor of the platform.

Diet influenced the shape of trilobites in the same way that it has contributed to morphological variations in modern arthropods (Lunardi et al. 2017). The distinct glabellar shapes recognized in our analysis (Fig. 6) have already been identified in previous studies and are interpreted as an indicator of feeding habits (Fortey & Owens 1999). The glabella expanded anteriorly with wide frontal lobes observed in our study was interpreted by Fortey & Owens (1999) as an adaptation to the ingestion of bulky food among predator trilobites. However, some predator/scavenger taxa showed a glabellar shape with narrower anterior frontal lobes, a morphology attributed to particle feeding trilobites. Differences in feeding habits for the same dorsal morphology can be explained by the fact that morphology changes in connection with diet mostly concerned especially the ventral structure (the hypostome) (Fortey & Owens 1999). Filter chamber feeding trilobites needed a large cephalic shield to filter particles suspended in the water. Consequently, these trilobites presented a larger preglabellar field (Fig. 6). However, a large cephalic shield can also be used to avoid sinking into the mud (Richter 1920) and in this case would not be related to feeding habit. Although pygidium shape did not play a role in trilobite feeding, particle-feeding trilobites occupied only a small area of the morphospace.

The visual abilities, estimated here from the shape of the visual surfaces, have an important effect on the overall trilobite morphology. Devonian trilobites with well-
developed eyes occupied the whole morphospace whereas blind and reduced-eye trilobites occupied only a small part of it (Fig. 6). Moreover, blind and reduced-eye trilobites occupied the same small part of the morphospace, except for taxa with narrow frontal lobes anteriorly (Fig. 6; Table 2). During the Devonian, paedomorphic evolution trends have been observed in Late Devonian taxa showing progressive eye reduction between closely related species that eventually leads to blindness (Feist & Clarkson 1989; Feist 1995; Crónier & Courville 2003; Schoenemann 2018). Such eye reduction implies morphological changes as the enlargement of fixigenae observed among Proetida or the ‘displacement’ of the facial suture towards the outer margins observed among Phacopida (Feist 1995; Crónier & Courville 2003). Consequently, Phacopida with reduced eyes are mainly confined to the part of the morphospace characterized by a suture closer to the lateral border (i.e. lower PC1 values; Fig. 6D).

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

**Morphological evolution through time**

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

During the Pragian, the morphological disparity increased and new morphologies were explored; cephala with an opistoparian facial suture and a narrow (tr.) frontal lobe emerged. These new morphologies are assigned to Proetida (Fig. 5A) which developed in North Africa (Bault et al. 2021) and exhibited their maximal dispersion at the global scale at this time (Foote 1993). Moreover, exoskeletons with spines proliferated (on pygidia as well as the genal spines on cephala) becoming more diverse and extending towards shapes with very long genal spines. Pygidia with a narrow (tr.) outline assigned to Corynexochida appeared too (Fig. 5C).

Cephala with a thick preglabellar field appeared in both Proetida and Phacopida morphologies, without link to environmental depth (Fig. 6A-C) unlike in the Ordovician (Fortey & Wilmot 1991). Genal spines and preglabellar field appeared at the same time in different lineages showing a common trajectory in morphospace through time. However, Phacopida explored morphologies with sagittal spines but not Proetida suggesting that different causes could influenced different lineages. The diversification of morphologies with the appearance of novelties in the Pragian coincided with new ecological opportunities due to the sea-level fall (Chlupáè 1994). The extension of the carbonate platform towards the offshore environment offered new habitats, leading to morphospace expansion toward the middle shelf and to a trilobite radiation. Similarly, the predator/scavenger trilobites showed an increasing morphospace occupation possibly linked to a food partitioning and to an interspecific competition (Schluter 2000; Grant & Grant 2006). The increase of enrollment type in the Devonian was also a source of morphological disparity (Suárez & Esteve 2021).

More generally, the diversification phases could be partly attributed to interspecies competition in arthropods (Eberle et al. 2014). The diversification of many clades in the Early Devonian (Alroy et al. 2008; Klug et al. 2010; Fan et al. 2020), may have an influence on the predator morphology with the arrival of new prey (Cattau et al. 2017). This advantageous feeding strategy could have induced a radiation of predator/scavenger trilobites and, conversely, particle feeding trilobites may have decreased because of increasing competition from more efficient organisms. Despite the new morphologies explored in the Pragian, those already present during the Lochkovian remained in the majority.

During the Emsian, all the main morphologies persisted with the maximum dispersion in the morphospace with the development of cephala with long genal spines and especially with a wide (tr.) frontal lobe (Fig. 3). Only shape losses regarding the narrowest (tr.) pygidia occurred, leading to a decrease of morphological disparity. In trilobites, spinose exoskeletons have been interpreted as passive morphological defences by some authors (Fortey 2004; Pates & Bicknell 2019). In the context of the Devonian Nekton Revolution (Klug et al. 2010), the emergence of morphologies with spines can be interpreted as a new answer to an increase in predation. However, this hypothesis seems unlikely because some potential predators, such as ammonoids and chondrichtyans, appeared only from the Emsian (Becker et al. 2019) or developed in the end of the Devonian, like fishes (Derycke 2017). In addition, the morphologies with spines disappeared in the Middle Devonian and Frasnian, in contrast to other shapes, which still existed in the Famennian (Fig. 4). Nevertheless, these disappearances
could be attributed to the inefficiency of spines against the large-jawed predators of the Late Devonian (Brett 2003). The diversification of morphologies in the Early Devonian could be partly related to novel feeding habits (i.e. particle feeding habits) with the appearance of glabella with a short (sag.) preglabellar field in trilobites (Fortey 2014). Indeed, this diet is the only one attributed to exoskeletons with genal spines (Fortey & Owens 1999).

In their evolutionary history during the Early Devonian, trilobites explored morphospace with much of the subsequent variation in their cephalic features compared to their pygidial features. Accordingly, the pygidial characters display much overlap of taxonomic groups in the morphospace, while the cephalic characters show more distinct morphospace occupation at the order level.

The morphospace occupation persisted during the Eifelian with all the cephalic, central cephalia and pygidial morphotypes despite environmental changes implying sea-level and oxic condition changes (Kaufmann 1998). Only the morphologies that had appeared during the Pragian were rarer, especially MCp2 for cephalia and MPg3 for pygidia (Fig. 4).

The Givetian was characterized by an important loss of morphology. The disappearance of some orders (i.e. Lichida and Corynexochida) (Bault et al. 2021) led respectively to the loss of exoskeletons (i.e. cephalia and pygidia as well) with spines or the loss of cephalia with a long (sag.) glabella and of pygidia with a long (sag.) axis. However, Corynexochida was known in the lower Givetian of North Africa (Feist & Orth 2000) but only represented by a single pygidium; thus, the loss of the cephalic morphology occurred later although it is not possible to observe this in the morphospace. Between the different lineages, a common pattern of disappearance seems to exist and in particular for both Proetida and Phacopida, in which the most affected trilobites were those with morphologies with protuberance such as spines and a preglabellar field, implying a common origin of disappearance. The Givetian is known to be a period marked by a series of anoxic/hypoxic events associated with sea-level rise (Kaufmann 1998; House 2002; Becker et al. 2016) and to have an important impact on the trilobite diversity (Feist 1991; Chlupáč 1994; Lerosey-Aubril & Feist 2012). The morphospace was probably reduced due to marginal or lateral extinctions (Foote 1991b; Korn et al. 2013). Morphologies with the lowest bathymetric extent, such as the MCp2 and MCp3 for cephalia and MPg3 for pygidia, were the most impacted and they disappeared (Fig. 6A–C). Indeed, these morphologies have never been encountered in a deep environment, which could be a disadvantage in the context of rising sea level. In addition, the morphologies that remained were versatile and exhibited different visual abilities (Fig. 6). Accordingly, these morphologies were more adapted to environmental change. The morphologies that persisted during the Givetian corresponded to morphologies already present in the Ludlow and represent persistent morphologies.

The dispersion in the morphospace decreased in the Frasnian to reach only one morphotype for cephalia (MCp1) and for pygidia (MPg2). Nevertheless, the absence of additional morphotypes (i.e. MCp3 and MCp4 without spines or short genal spines) for cephalia in Proetida may be due to the lack of sampled specimens in our dataset. Some Proetida were encountered in the upper Frasnian of North Africa (Feist 2002). The Frasnian is marked by an increase of the morphological disparity characterized by the reappearance of morphologies with numerous spines. These morphologies occurred within the dark-grey hypoxic limestone levels of the Kellwasser deposits related to relative deep-sea conditions (Feist 2002). Trilobite morphologies did not show significant shape losses and seem to have been little affected by the Kellwasser events that occurred at the Frasnian–Famennian boundary, marking one of five major extinction events in the history of life on Earth (McGhee 1988, 1996; Racki 2005, 2020). The main shape change was the disappearance of morphologies with spines except genal spines in Cyrtosymbolinae (Proetida). Unfortunately, only the central cephalia and the pygidia for the Famennian Proetida are available in North Africa and they are therefore not included in the cephalic morphospace. As for the Givetian and the Frasnian, only the versatile morphologies related to depth conditions and vision abilities persisted during the Famennian. Only Proetida and Phacopida crossed the Frasnian–Famennian boundary both at the global and at the North Africa regional scale (Chlupáč 1994; Lerosey-Aubril & Feist 2012; Bault et al. 2021). These two orders are characterized by the maximal morphological variation in the Devonian morphospace in North Africa (Fig. 4). Such variability is known to be helpful to cope the environmental changes in other clades (Kolbe et al. 2011; González-Suárez & Revilla 2013; Huang et al. 2015; Austin & Dunlap 2019). Across all of these events, from the Eifelian to the Famennian, there were irregular shape losses among trilobites but no extensive morphological innovation occurred after mass extinctions despite potential availability of the ecospace (Erwin 2015).

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

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

Location of cephala, central cephala and pygidia in morphospace showed a different relative distribution of specimens for instance, Corynexochida and Phacopida that occupied the same part of the central cephalon morphospace, occupied distinct parts of the pygidium morphospace (Fig. 5B–C). This is explained by the relative independence of the evolution of the studied structures, known as tagmas (Hughes 2003), even if some covariations between these different structures exist due to enrolment (Oudot et al. 2019). Functional morphology explains why some orders show overlapping morphologies for cephala or pygidia but different shapes for other structures. Modularity was implied in the developmental process of trilobites indicating a developmental constraint on the morphology. Not all combinations of characters were possible due to intrinsic constraints that channel the morphological evolution, such as physical or developmental constraints (Arnold 1992; Gould 2002; Gerber 2014; Briggs 2017). For trilobites from the Devonian of North Africa, it was not possible to develop a sagittal spine without genal spines in the cephalon (high PC1 and low PC2 scores; Fig. 3A). Ontogenetic studies underlined a progressive enlargement (tr.) of the glabella during the development, especially in Phacopida, due to a change in the food niche (Crönier & Feist 1997; Crönier & Fortey 2006; Jacobs & Carlucci 2019). Thus, feeding constraints during development probably led to the absence of trilobites with a very narrow (tr.) glabella at an adult stage (high PC2 scores; Fig. 3B) in our dataset.

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

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

**CONCLUSION**

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

North African trilobites experienced significant morphological fluctuations from the Early to the Late Devonian. During the Devonian, the trilobites exhibited cases/examples of convergence in the visual surfaces or and spines and, a development of ‘rare’ morphologies such as the very spiny shapes of the Pragian–Emian. The morphological disparity was low at the end of the Silurian and the Lochkovian. The trilobites occupied a relatively small part of the morphospace. Subsequently, the disparity increased considerably in the Pragian with the appearance of several new morphologies; reaching a maximum in the Emsian. Trilobites occupied the global
morphospace and exhibited additional new morphologies, although some areas of morphospace remained empty because some morphologies did not develop in the Devonian. The morphological disparity persisted until the Eifelian, decreased considerably in the Givetian, and reached a minimum in the Late Devonian with a greater density in the Famennian than the Frasnian. The trilobites developed no further novelties. This significant decrease in morphological disparity occurred during a period characterized by numerous environmental events implying habitat changes with sea-level fluctuations and anoxic/hypoxic conditions. Some taxa (i.e. morphologies) were more resilient to these environmental changes and persisted throughout the Devonian because of their adaptation to different bathymetry and their visual ability. Similarly, Phacopida and Proetida survived most of the events thanks to their large morphospace occupation; they were characterized by an evolutionary trend towards a progressive eye reduction leading to blindness.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12623):

Appendix S1. Dataset of Silurian and Devonian trilobites from Morocco and Algeria. IDs correspond to TPS data in files Data S1 and Data S2.

Appendix S2. References cited in Appendix S1.

Data S1. TPS data for cephalon and central cephalon landmarks (ID 0–993).

Data S2. TPS data for pygidium landmarks (ID 0–630).

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

Fig. S2 Clusters identified by a hierarchical cluster analysis (HCA) performed with the Euclidean distance measure and Wards linkage algorithm on the PCs scores for all specimens, and the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for: A, cephalon; B, central cephalon; C, pygidia.

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

Fig. S4 Location of: A, cephalon; B, central cephalon; C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals, represented for each Devonian stage. The number of specimens is indicated for each stage. Ages from Cohen et al. (2013; v.3/2020).

Fig. S5 Location of the morphotypes of: A, cephalon; B, central cephalon; C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for bathymetry. Ages from Cohen et al. (2013; v.3/2020).

Fig. S6 Location of the morphotypes of: A, cephalon; B, central cephalon; C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for vision abilities. Ages from Cohen et al. (2013; v.3/2020).

Fig. S7 Location of the morphotypes of: A, cephalon; B, central cephalon; C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for feeding habits. Ages from Cohen et al. (2013; v.3/2020).

Fig. S8 Reconstruction of virtual shapes of cephalon according respectively to the two first principal component axes PC1 and PC2 performed on Procrustes residuals.

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