




Rise and fall of the phacopids: the morphological history of a successful trilobite family

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Typescript received 23 October 2022; accepted in revised form 29 June 2023

Abstract: Phacopidae were a successful family of the Silurian–Devonian period. Although their diversity trends are well identified, their shape evolution is unknown; their morphology often considered to be conservative. We have quantified these morphologies using geometric morphometrics (landmarks) and investigated their evolution using morphological disparity indices. Results identified morphological variations between the genera, and through time. Phacopids differ from each other by the position of the facial suture linked to the size of the visual complex, the shape of the genal angle and the elongation of both cephalon and pygidium. The morphological disparity of cephalata was high from the Silurian, contrary to that of pygidia. Subsequently, the morphological disparity increased in the Early Devonian with the development of narrow cephalata and triangular pygidia. Morphological disparity was greater in the Emsian for both cephalata and pygidia, more than 50 myr after the

origination of phacopids. It constituted a perfect example illustrating that a peak of biodiversity does not necessarily happen in the early history of a clade. Subsequently, a strong decrease of morphological disparity occurred in the Middle Devonian, in conjunction with sea-level changes and anoxic events. Taxonomic richness and morphological disparity declined strongly in the Givetian, in a non-random extinction affecting particularly blind genera. The morphological disparity remained low in the Frasnian despite progressive eye reduction influenced by environmental changes. An extensive recovery occurred in the Famennian with an important increase of both taxonomic and morphological diversity. The Hangenberg event caused the final extinction of phacopids.

Key words: Phacopidae, Palaeozoic, morphological disparity, diversification, extinction.

PHACOPIDAE are a family that is frequently found in sedimentary rocks deposited on the Silurian–Devonian epicontinental platforms and were thus an important component of the marine benthos. They are represented worldwide, especially in Europe and North Africa. This family originated at the end of the Ordovician (Campbell 1967; Lespérance & Sheehan 1988; Adrain 2013), probably from the Pterygomtopidae family (Ludvigsen & Chatterton 1982). The oldest phacopid was the late Ordovician *Sambreusaspis* Lespérance in Lespérance & Sheehan, 1988 (Ramsköld & Werdelin 1991) discovered in Belgium. Phacopids diversified, first slowly with a few genera in the Silurian, then more importantly in the Devonian, to reach their highest diversity in the Middle Devonian (Crônier *et al.* 2011). Although initially they occupied the Iapetus ocean margins, they quickly spread worldwide (Ramsköld & Werdelin 1991). While the Phacopidae was one of the few trilobite families to survive the Frasnian–Famennian extinction, they vanished at the

end of the Devonian with the Hangenberg event (Chlupác 1994; Lerosey-Aubril & Feist 2012). Throughout their long evolutionary history, phacopids survived several environmental perturbations (Walliser 1996, pp. 225–250; House 2002; Calner 2008; Qie *et al.* 2019) including the second of the five ‘big’ mass extinctions described by Raup & Sepkoski (1982): the Kellwasser events (Bug-gisch 1991; Carmichael *et al.* 2019). Some events positively influenced their diversity as for example the Pragian regression, which led to the Pragian diversification of phacopids as well as many other trilobite clades (Chlupác 1994; Bault *et al.* 2022a). Other events had negative effects, such as the Late Devonian events, which led to the extinction of many genera (Feist 1991).

Phacopids occupied numerous habitats of the Late Devonian epicontinental platforms from the shallow depths to beyond the photic zone, and they showed strong bathymetrical and palaeogeographical affinities (McKellar & Chatterton 2009; Crônier & François 2014).

Their morphology and behaviour were affected by environmental changes, particularly at the Frasnian–Famennian boundary characterized by the development of blind forms living in deeper-water environments and/or endobenthic lifestyle (Feist *et al.* 2009).

Phacopidae was first established by Hawle & Corda (1847). This family is characterized by a glabella broadening markedly forward with lateral glabellar furrows S2 and S3 obsolescent, and S1 often transglabellar leading to an ‘intercalating ring’, genal angles rounded without genal spines, and a visual complex often well-developed. The phacopid pygidium is well rounded, semi-circular or trapezoidal, without lateral or marginal spines (Harrington *et al.* 1959). The morphological diversity among Phacopidae is expressed especially in the shape of both the vincular furrow and visual complex and in the course of the facial suture (Fig. 1). These characters are

considered important for systematic considerations (Crônier *et al.* 2011). Chlupáč (1977) identified two sub-families: Phacopidellinae Delo, 1935, characterized by a cephalic doublure without a vincular furrow, and Phacopinae Reed, 1905, characterized by a cephalic doublure with a deep and continuous vincular furrow.

Environmental changes are reflected in the variations of the exoskeleton of trilobites and their evolutionary history, which is essentially adaptive. Therefore, they represent an exceptional model to analyse trends and macroevolutionary processes (Foote 1989, 1990, 1991a, 1993; Gerber & Hopkins 2011; Webster & Zelditch 2011). Besides, studies on the taxonomic diversity of trilobites already highlighted the importance of phacopids, being for example the major component of Devonian Trilobite Evolutionary Faunas (Bault *et al.* 2022a). However, in recent decades, morphological disparity has proven to be

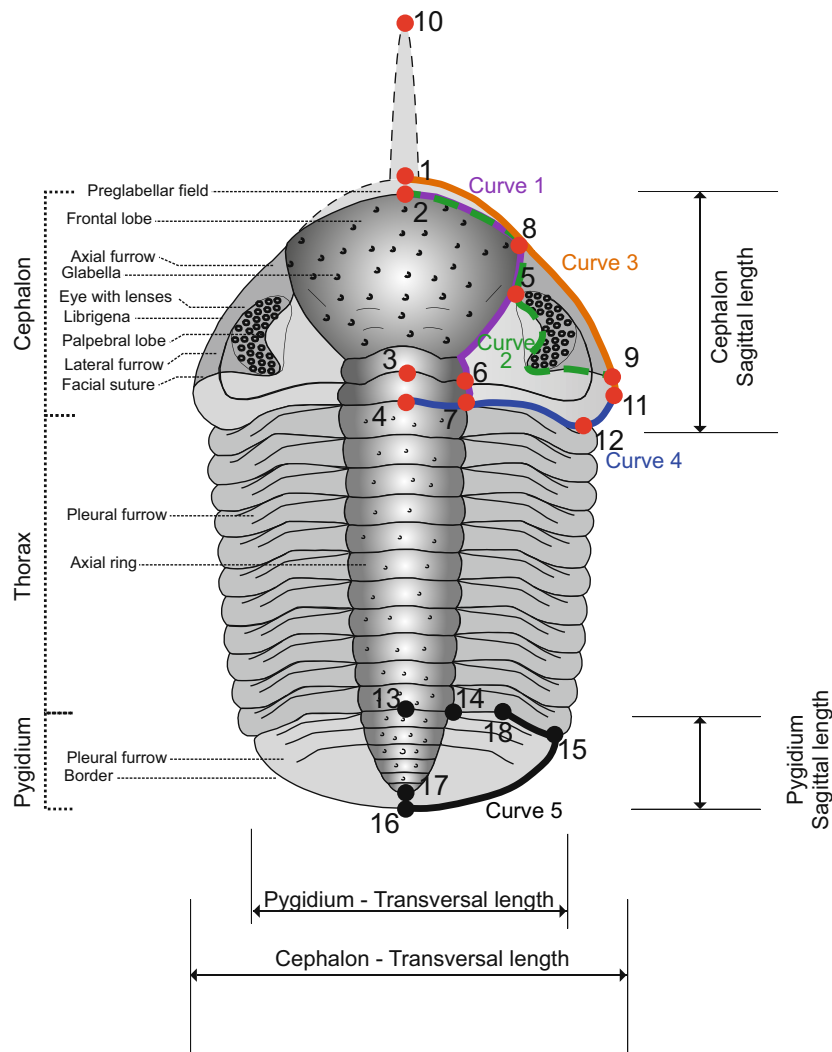


FIG. 1. Schematic showing 12 landmarks and 4 semi-landmark curves of 30 points defined on the cephalon and 8 landmarks and 1 semi-landmark curve of 24 points on the pygidium. Modified from Crônier (2013).

a successful, alternative biodiversity metric (Roy & Foote 1997). Concerning trilobites, morphological disparity analyses have focused on very few families or subfamilies, such as Pterocephaliidae (Hopkins 2013) but not on this major group of Phacopidae.

Therefore, the present study aims to investigate the morphological evolution of all phacopids from their origination in the Late Ordovician to the end of Devonian, by analysing their cephalic and pygidial shapes at the genus level by means of geometric morphometrics. Here, morphological disparity is investigated for the first time at a global scale, and using the stage for a temporal scale.

MATERIAL AND METHOD

Datasets

To explore the morphology of the Phacopidae, we have compiled two datasets to investigate the two main structures (largest, most often collected and/or illustrated) of the trilobite exoskeleton: the cephalon and the pygidium (Whittington *et al.* 1997).

The dataset is at the genus taxonomic rank and at the stage chronostratigraphic level. Our dataset includes almost all known genera of Phacopidae. However, because of the low number of genera before the Devonian, the Silurian has been treated as a unique time bin. For each genus, a representative specimen was selected, most often the holotype of the type species, unless the illustrations were insufficient. Because of the lack of illustration, the species of six genera were not the same for both cephalon and pygidium: *Nephranomma* Erben, 1952, *Pedinopariops* Struve, 1970, *Prokops* Chlupáč, 1971, *Struveaspis* Alberti, 1966, *Teichertops* Struve, 1992, and *Weyerites* Crônier & Feist, 2000. A total of 77 cephalon and 70 pygidia representing different genera were analysed, all at a holaspid stage (Appendix S1). For each genus, FAD and LAD (first and last appearance datum, respectively) are noted.

The classification used for this dataset follows Jell & Adrain (2002). Updates since this publication were taken into account, such as the replacement of *Cultrops* Struve, 1995 with *Struvephacops* (Ghobadi Pour, 2015) as well as the description of new genera: *Morocops* (Basse, 2006), *Enigmapyge* (Feist *et al.*, 2016), *Magreanops* (Van Viersen & Vanherle, 2018), and *Feistops* (Crônier *et al.*, 2020), *Acutiphacops* Feist & Klapper, 2022, *Cronierella* Feist & Klapper, 2022, *Girardina* Feist & Klapper, 2022, and *Occitanella* Feist & Klapper, 2022 (Feist & Klapper, 2022). The Late Devonian *Phacops* Emmerich, 1839 being significantly different from older specimens (Crônier *et al.* 2011), we separated the Late Devonian specimens into a distinct genus named: Late Devonian *Phacops*. Moreover, the Pterygometopid

Calyptaulax Cooper, 1930, was also included. The Pterygometopidae family is considered to be the sister group of Phacopidae (Ludvigsen & Chatterton 1982) and *Calyptaulax* was used as an outgroup in phylogenetic analyses of phacopids (McKellar & Chatterton 2009; Oudot *et al.* 2019). Nevertheless, some poorly known, poorly illustrated and/or hard to find genera were excluded (*Portlockia* McCoy, 1846, *Somatrikelon* McMurtrie, 1819, *Hottonops* Van Viersen *et al.* 2017 and *Loreleiops* Van Viersen *et al.* 2017 without illustration in both datasets; *Enygmapyge* Feist *et al.*, 2016, without cephalon in 'cephalon' dataset; *Adastocephalum* Mitchell, 1919, *Afrops* Alberti, 1983, *Burtonops* Struve, 1990, *Cryphops* Richter & Richter, 1926, *Spinicryphops* Crônier & Feist, 2000, *Struvephacops* Ghobadi Pour, 2015, *Tangbailaspis* Xiang & Zhang in Zhang, 1983, and *Zaplaops* Baldi & Blasco in Baldi *et al.*, 1976, without pygidium in 'pygidium' dataset). For each genus, the FAD and LAD are noted.

McKellar & Chatterton (2009) proposed a distribution of genera and sub-genera into tribes, based on the work of Flick & Struve (1984), Haas (1998) and Struve (1970, 1972, 1976, 1982, 1989, 1990, 1992, 1995). This distribution is in disagreement with the previous work of Chlupáč (1977); numerous members belonging to Phacopidellinae or Phacopinae are in the same tribe. Moreover, not all phacopid taxa listed in the exhaustive list of Jell & Adrain (2002), were taken into consideration by McKellar & Chatterton (2009).

Landmarks and geometric morphometrics

To describe the 2D morphology of cephalon and pygidia, we used a geometric morphometric approach based on homologous *loci* named landmarks (Bookstein 1991; Rohlf & Marcus 1993; Adams *et al.* 2004; Mitteroecker & Gunz 2009; Zelditch *et al.* 2012). This method is commonly used on trilobites for macroevolutionary and developmental studies (Gerber & Hopkins 2011, Webster & Zelditch 2011; Oudot *et al.* 2019; Bault *et al.* 2022b). The *x* and *y* coordinates of 12 landmarks and 4 semi-landmark curves of 30 points each on the cephalon, as well as 6 landmarks and one semi-landmark curve of 24 points on the pygidium were digitized (Fig. 1, for landmark definition see Table S1) using the software TPSDig 2.32 (Rohlf 2006, 2015). For the cephalon, the semi-landmark curves represent respectively the glabella shape, the facial suture shape and the cephalic outline (Fig. 1). For the pygidium, the semi-landmark curve represents the pygidial outline. The landmark 2D coordinates were exported in the standard TPS file format (Rohlf 2012; Data S1, S2).

To remove effects of size, position and orientation, all configurations of landmarks were superimposed by means

of a generalized Procrustes analysis (GPA) (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; Dryden & Mardia 1998; O'Higgins 2000; Zelditch *et al.* 2012) and projected to a linear tangent space at the full Procrustes mean (Kendall 1984; Rohlf 1999). A Procrustes sliding was applied to the semi-landmark curves (Gunz & Mitteroecker 2013).

To quantify morphological variation, a principal component analysis (PCA; Ringnér 2008; Abdi & Williams 2010) was performed on the variance–covariance matrix of Procrustes residual coordinates. To illustrate the largest shape changes over the morphospace, series of virtual shapes are reconstructed by doing a back transformation from the PC scores for PC1 and PC2, which are the two major principal components (PCs) in terms of shape variance explained.

Additionally, in order to identify morphological changes related to eye-reduction or blindness in the cephalon, and their effect to the pygidium, blind and ocellated genera were illustrated separately over the morphospace. Also, a one-side nonparametric, permutational ANOVA on all PC axes was performed using the Wilks' lambda test to assess statistically if a shape difference exists between blind and sighted trilobites. The ANOVA was performed on PCA axes instead of original Procrustes coordinates because the scores of each axis are uncorrelated and the number of dimensions corresponds to the degree of freedom (Rohlf 1993; Polly 2017).

To assess the robustness of the quantified morphospaces based on the selected specimens, two biases that can influence the quantification of trilobite shapes have been evaluated: the distribution of within-genus interspecies variation and the measurement error of a single specimen. In order to evaluate the impact of the selected specimen representing a genus, we also quantified 10 specimens from 10 different species for the genus *Morocops*. Furthermore, one randomly selected cephalon was also digitized 10 times to identify the part of variation attributed to measurements (Bartlett & Frost 2008). To compare the variation between the different subgroups (i.e. measurement error, inter-specific variability and inter-generic variability) we measured the variance of the distance to the centroid size of each subgroup.

Morphological analyses were computed using R v3.6.2 (R Core Team 2013); and the packages geomorph (v3.2.1; Adams & Otárola-Castillo 2013) and epaleo (v0.8.41; available from CM).

Morphological disparity indices

To quantify phacopid morphological disparity changes through time, we used several disparity indices, which described different aspects of the morphospace occupation

(Foote 1991b; Ciampaglio *et al.* 2001; Wills 2001; Guillerme *et al.* 2020). These disparity indices have already been used for trilobites (Foote 1990, 1993; Hopkins 2013). Disparity indices have been estimated for the Silurian as a whole and for each stage of the Devonian.

Two indices were used to estimate the size of the morphospace. The sum of range (SoR), corresponding to the total range of morphologies, and the sum of variance (SoV) corresponding to the average dissimilarity between morphologies. The overall first-order nearest neighbour distance (NND) was computed to characterize the density of the morphospace. Finally, the mean values per stage for PC1 and PC2 were computed to identify potential shift in morphospace filling through time.

Confidence intervals on the computed disparity values were obtained with a bootstrap approach, by iteratively calculating SoR, SoV and NND (1000 times) from random resampling with replacement of the individual points in the morphospace (Foote 1993). The 2.5 and 97.5 percentile values of the resulting bootstrapped distribution of each disparity metric are used as lower and upper confidence intervals. Morphological indices were performed with the package epaleo (v0.8.41; CM) in R (v3.6.2; R Core Team 2013).

Diversity

The phacopid diversity is estimated as the raw count of genera providing cephalia in a time bin, as only *Enygmopyge* (Famennian), *Portlockia* (Pragian) and *Somatrikelon* (Eifelian) did not record cephalia to study. The count of pygidia and cephalia is compared with morphological disparity indices to identify periods of coupled taxonomic and morphological diversification or contrariwise, decoupled trends.

RESULTS

Global morphospace

The measurements errors and the interspecific variation tests indicated a much smaller (one order of magnitude) variation than the inter-generic variation discussed thereafter (Fig. S1), therefore indicating a negligible impact on our genus level analysis.

Cephalon shape. The first four principal components explain 67% of the total shape variance (Fig. 2): PC1 (29.3%), PC2 (19.2%), PC3 (13.0%) and PC4 (5.1%). PC1 depicts changes in the position of the facial suture and the visual complex. The higher the PC1 value, the more the suture is close to the lateral margin and more

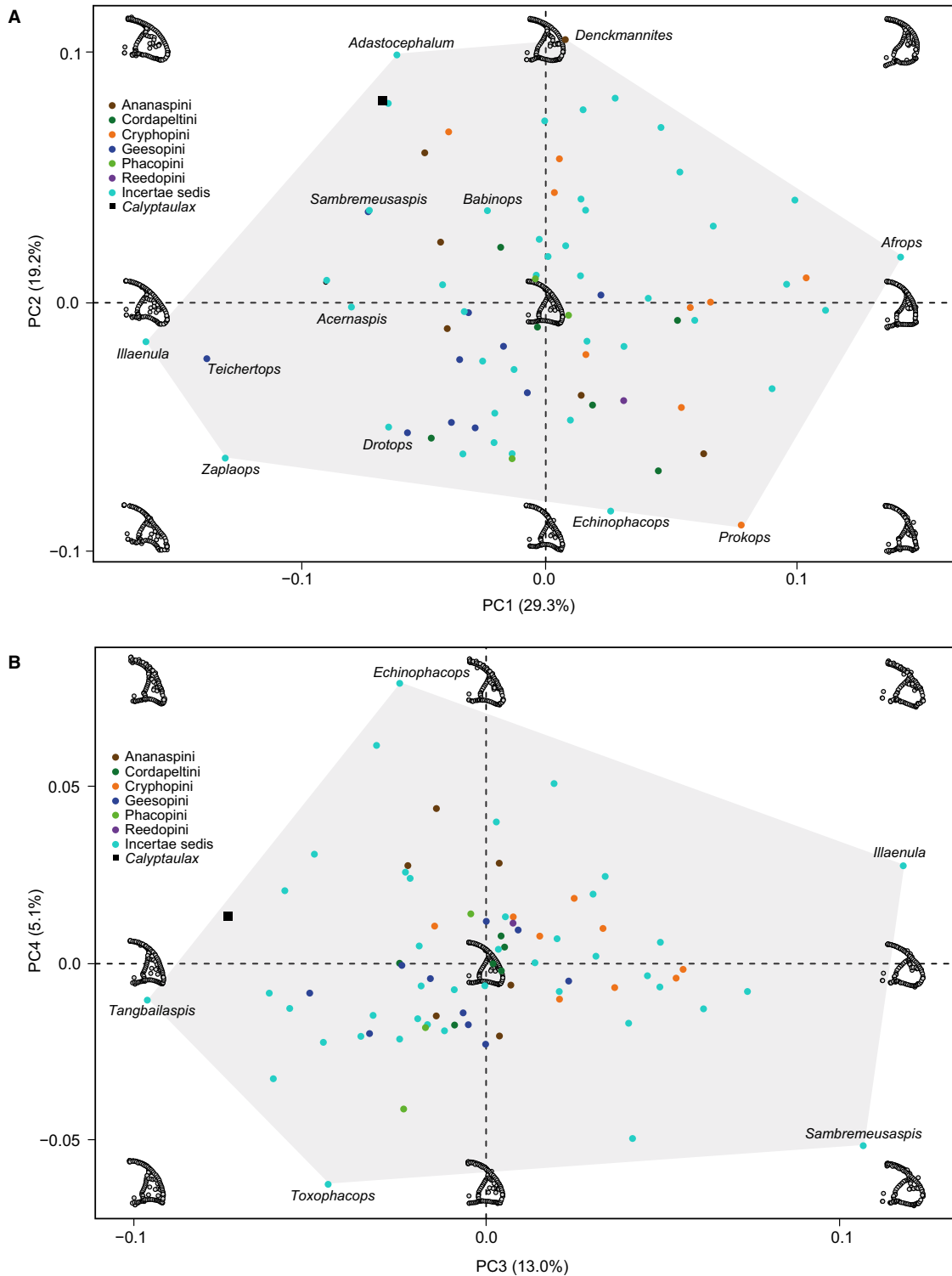


FIG. 2. Global morphospace for phacopid cephalae computed by performing a PCA based on Procrustes residuals. A, the first two axes, PC1 and PC2, explain 49% of the variance. B, PC3 and PC4 axes explain 18% of the variance. Tribes according to McKellar & Chatterton (2009): Ananaspini Haas, 1998 (brown); Cordapeltini Struve, 1989 (dark green); Cryphopini Struve, 1989 (orange); Geesopini Flick & Struve, 1984 (dark blue); Phacopini Flick & Struve, 1984 (light green); Reedopini Struve, 1989 (purple); and *incertae sedis* (light blue). The pterygometopid *Calyptaulax* is represented by a black square. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaping to landmark data.

the visual complex is reduced (Fig. 2A). PC1 also shows changes associated with the width/length ratio: narrow (transversal) cephalia in negative values to elongated (tr.) cephalia in positive values. The second axis PC2 depicts a stretched genal angle in negative values and a rounded genal angle in positive values. Where the PC2 is high, the facial suture is more distant from the lateral margin. Consequently, the filling of the morphospace (Fig. 2A) is roughly triangular reflecting the influence of the three cephalic parameters (width/length ratio, facial suture/visual complex location, and the shape of the genal angle). The bottom-left part of the morphospace corresponds to elongated cephalia with a stretched genal angle, the bottom-right part to narrow cephalia with a more reduced visual complex and the top-central part to intermediate shapes with a rounded genal angle. The distribution of genera is fairly homogeneous in the morphospace, with the exception of three outliers characterized by low PC1 and low PC2 values: *Illaeula* Chlupáč, 1977, *Teichertops* and *Zaplaops*. The label of each morphospace point is given in Figure S2. The pterygometopid *Calyptaulax* has a low PC1 value and one of the highest PC2 values placing it in the phacopid morphospace. The oldest phacopid *Sambreusaspis* had also a low PC1 value but an average PC2 value.

Along the PC3 (Fig. 2B), the cephalic variations are associated with the genal angle shape and the cheek proportion. Cephalia with an elongated genal angle and larger cheeks relative to the cephalic shield are positioned in negative values, and cephalia with rounded genal angle and smaller cheeks relative to the cephalic shield are in positive values. Along the PC4, the cephalic variations are associated with elongated genal angle (low PC4 values) or rounded genal angle (high PC4 values). The distribution of genera is relatively fairly homogeneous in the morphospace with the exception of two outliers characterized by high PC3 values: *Illaeula* and *Sambreusaspis*. Because genal spines are rare among phacopids, their presence is not clearly shown by the four first PCA axes. The genera developing such spines, such as *Acernaspis* Campbell 1967, *Babinops* Feist & Becker, 1997, *Drotops* Struve, 1990, and *Viaphacops* Maksimova, 1972, are located in the centre part of the morphospace with the phacopids without genal spines.

Pygidium shape. The first four axes (Fig. 3) explain 88% of the total shape variance: PC1 (56.3%) PC2 (20%), PC3 (7.1%) and PC4 (4.5%). The first axis PC1 (Fig. 3A) depicts changes in the pleural field proportion and the lateral border angle. The lower the PC1, the more the pleural field is important and the lateral border angle acute. The second axis PC2 depicts changes associated with the position of the greatest width: backward in negative values to forward in positive values. A higher PC2 value indicates a

higher width/length ratio. The distribution of genera is fairly homogeneous in the morphospace. *Calyptaulax* (with the highest PC1 value) is slightly distinct from phacopids with a high PC2 value. *Echinophacops* Zhou, 1983, is differentiated from other phacopids by high PC1 and low PC2 values corresponding to a long pygidium.

Along the PC3 and PC4 axes (Fig. 3B), the pygidial variations are associated with the position of the rachis relative to the pygidial posterior border and the lateral outlines. The rachis is more (low PC3 and PC4 values) or less (high PC3 and PC4 values) close to the posterior border of the pygidium. Most of the genera are located in the right part of the morphospace, whereas *Calyptaulax* is characterized by the highest PC3 values. While no complete cephalon of *Enigmapyge* is known yet, the pygidium of this genus has notably high PC1, PC3 and PC4 values that correspond with an elongated (sag.) pygidium with a short (sag.) rachis and a maximum pygidial width located backward with a linear lateral border.

Tribes. The phacopid tribes were widespread in the morphospace and they mingle with each other. Nevertheless, some trends exist: Cryphopini is mostly restricted to positive PC1 values of the cephalon (Fig. 2A) and negative PC1 values of the pygidium (Fig. 3A). Conversely, Geosopini occupies negative PC1 and PC2 values of the cephalon and positive PC1 values of the pygidium.

Blindness

Absence of eyes affected the shape of phacopid cephalia (Procrustes ANOVA: $p = 0.001$, $r^2 = 0.07$). With two exceptions, the blind and reduced-eyed trilobites are clustered in the highest PC1 values, while the oculated trilobites are gathered in the negative and slightly positive PC1 values (Fig. 4A). The distribution of these blind taxa is due to the presence of forms with a facial suture close to the anterolateral margin. However, the two blind genera *Nephranops* Richter & Richter, 1926, and *Illaeula* have lower PC1 values characterized by a wide (tr.) cephalic shield. In addition, blind taxa are mostly restricted to positive PC3 values and average PC4 values due to the presence of forms with a rounded genal angle and a facial suture close to the anterolateral margin.

The blindness observed in cephalia did not imply a different morphology of pygidia (Procrustes ANOVA: $p = 0.153$, $r^2 = 0.03$). However, the pygidia associated with blind cephalia are all gathered in the part of PC1 with the lowest values (Fig. 4B). This indicates that blind phacopids did not display a rounded lateral border or a large pleural field. The type of vision had no effect on PC2, PC3 and PC4.

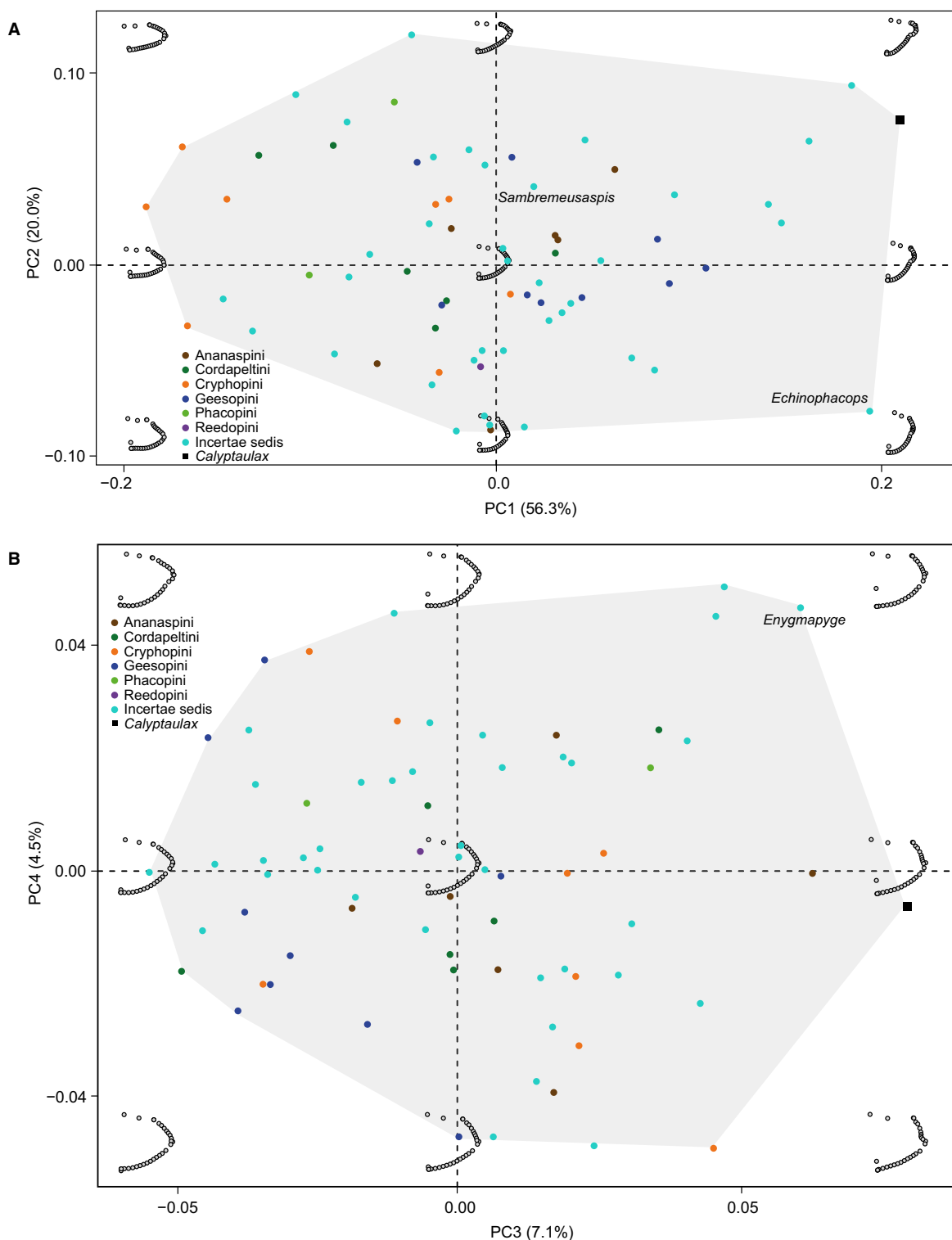


FIG. 3. Global morphospace for phacopid pygidia computed by performing a PCA based on Procrustes residuals. A, the first two axes PC1 and PC2 explain 76% of the variance. B, PC3 and PC4 axes explain 12% of the variance. Tribes *sensu* McKellar & Chatterton (2009): Ananaspini Haas, 1998 (brown); Cordapeltini Struve, 1989 (dark green); Cryphopini Struve, 1989 (orange); Geesopini Flick & Struve, 1984 (dark blue); Phacopini Flick & Struve, 1984 (light green); Reedopini Struve, 1989 (purple); and *incertae sedis* (light blue). The pterygometopid *Calyptaulax* is represented by a black square. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaping to landmark data.

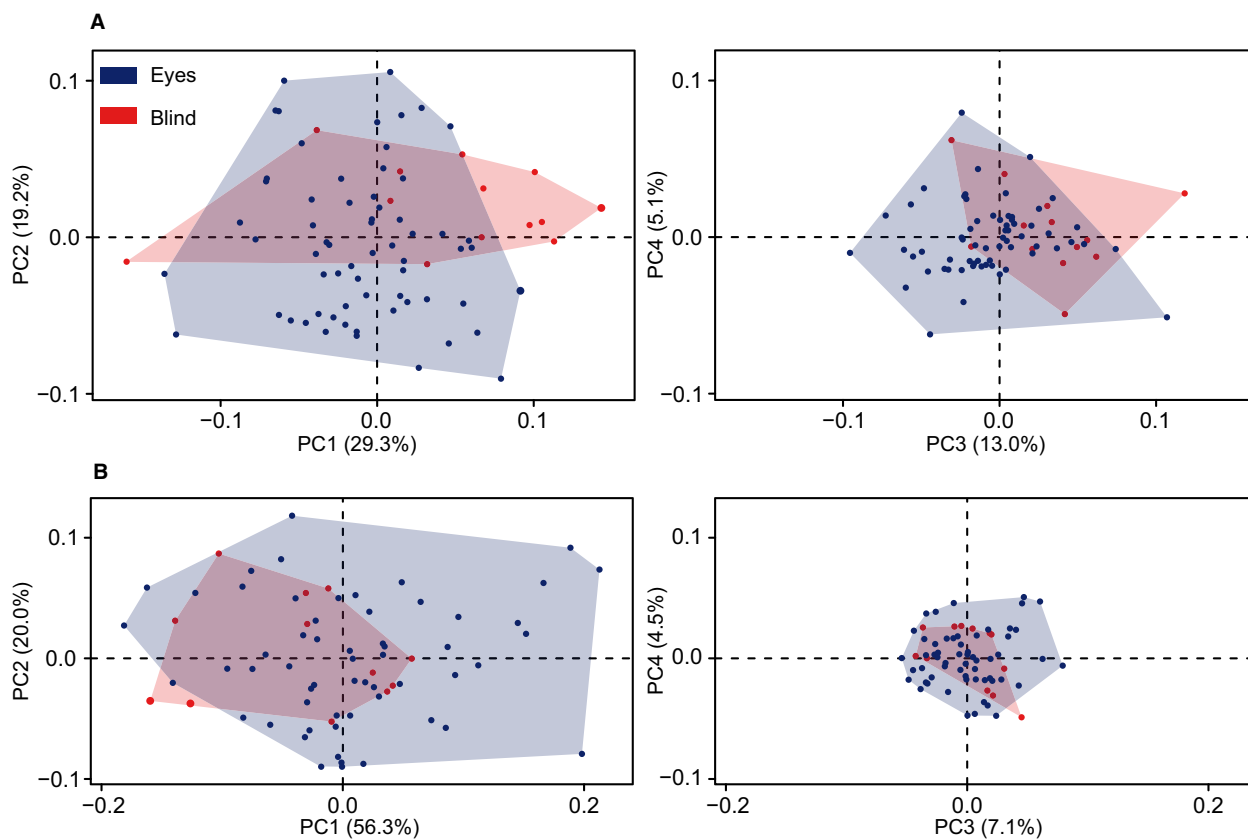


FIG. 4. Location of cephalae (A) and pygidia (B) according to visual abilities of phacopids in the global morphospace defined on the first four principal component axes performed on Procrustes residuals, respectively PC1 vs PC2 and PC3 vs PC4.

Diversity through time

Taxonomic richness. Phacopids were poorly diversified in the Silurian but their taxonomic richness increased almost continuously until the Eifelian (Fig. 5). Only a slight decrease occurred in the Pragian. In the Givetian, the diversity decreased strongly from 26 to 12 genera. This decline continued in the Frasnian before a substantial increase in the Famennian, when 19 genera lived. No phacopids survived into the Carboniferous.

Disparity of cephalae. From the Late Ordovician to the Pragian, the morphospace occupation moved toward higher PC1 and lower PC2 values (i.e. toward a facial suture closer to the lateral margin and a smaller cephalic shield; Fig. 6). The Middle–Late Ordovician pterygometopid *Calyptaulax* and the oldest phacopid *Sambreusaspis* are located at the top-left extremity of the morphospace (Fig. 7). *Calyptaulax* is characterized by a glabella with a hypertrophied frontal lobe anteriorly with well-developed S3 and a subtriangular pygidium. In the Silurian, the phacopid shapes extended with the emergence of more rounded cephalae and a facial suture closer to the anterolateral border such as in *Denckmannites* Wedekind, 1914,

and *Orygmatus* Sandford, 2000. The morphospace enlarged progressively in the Early Devonian with new morphologies in the Pragian: cephalae characterized by a narrow (tr.) cephalic shield associated with anterolateral facial sutures. The appearance of *Afrops* at the right edge (i.e. high PC1 values) of the morphospace illustrated this trend. In the Emsian, the morphospace is almost entirely occupied except for the left part of the all-phacopids distribution. Thus, SoR increased (Fig. 5). At the same time, NND and SoV tend to decrease.

During the Middle Devonian, the morphospace occupation moved toward the opposite side, the left part of the morphospace. The morphological disparity strongly decreased meantime. However, the reduction of the occupied part of the morphospace was initially only low in the Eifelian (Fig. 7). Shapes with a facial suture located close to the lateral border, such as the blind *Altaesajania* Maksimova, 1978a, and *Angulophacops* Maksimova, 1978b, are no longer present and disappeared at the Emsian–Eifelian boundary. Conversely, no new genera appeared. The Eifelian was also characterized by the lowest NND despite the presence of two outliers *Illaenula* and *Teichertops*. These outliers were located in the left part of the all-phacopids distribution during the Eifelian.

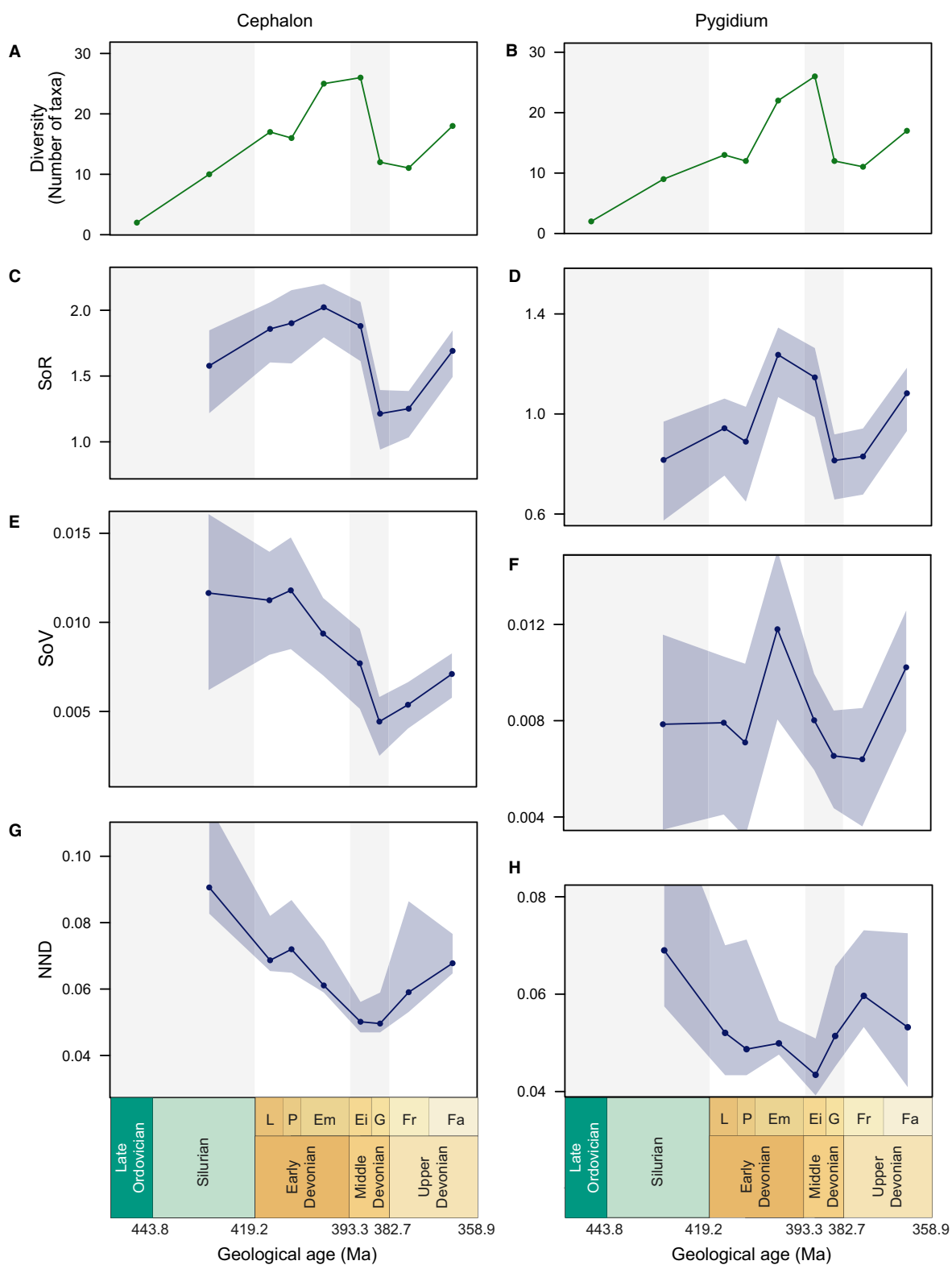


FIG. 5. Fluctuations of the morphological disparity and taxonomic diversity of phacopids through time, respectively based on the cephalon and the pygidium. A–B, number of studied genera for: A, cephalon; B, pygidium. C–H, morphological disparity of the cephalon (C, E, G) and pygidium (D, F, H): C–D, sum of range (SoR); E–F, sum of variance (SoV); G–H, nearest neighbour distance (NND); solid lines correspond to mean values from 1000 bootstrap replicates and shaded areas represent 95% confidence intervals. See text for explanations of the indices. Ages from Cohen *et al.* (2013) v2023/06.

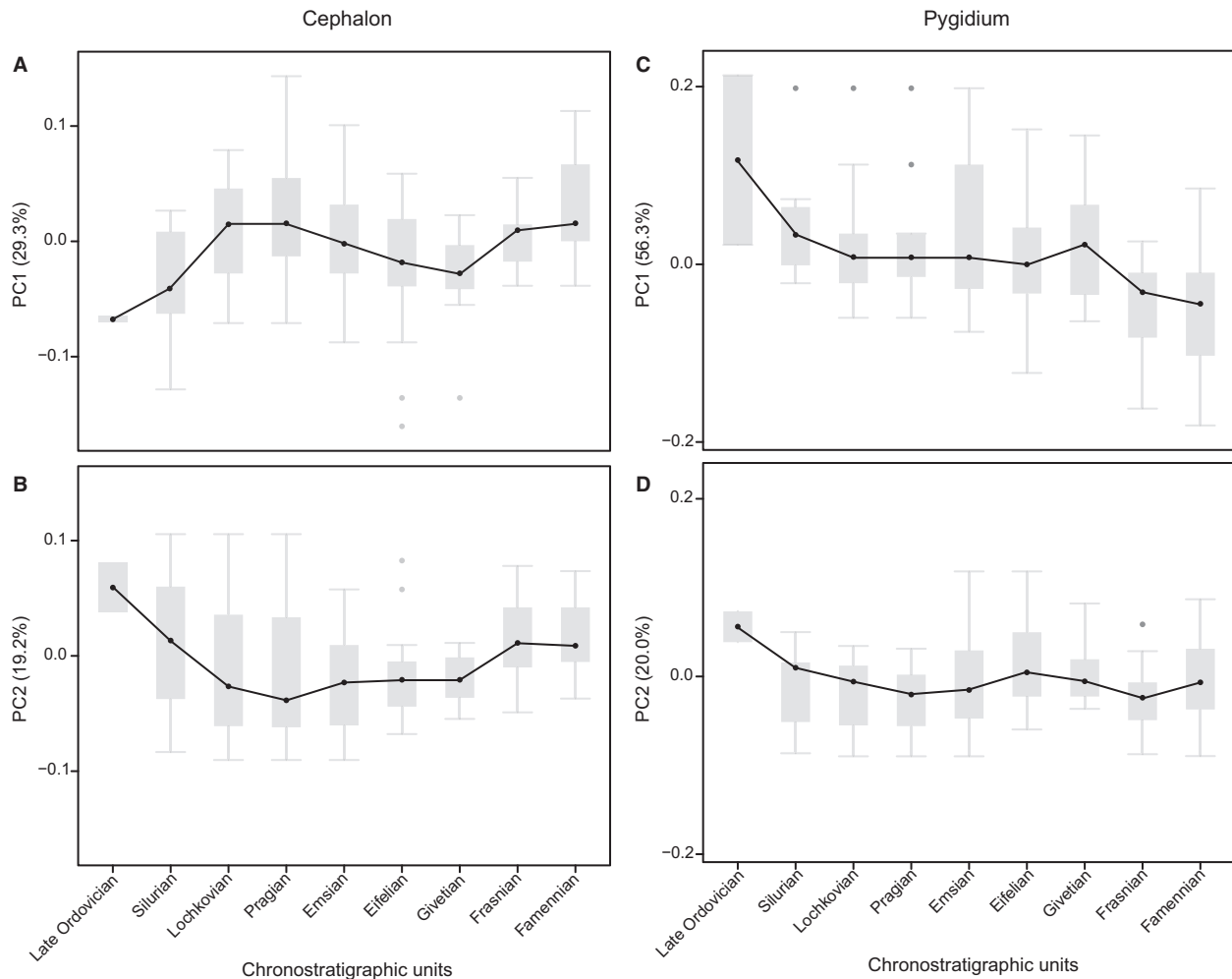


FIG. 6. Location of the morphospace occupation on PC1 and PC2 through time. A–B, average values of PC1 and PC2 for the cephalon. C–D, average values of PC1 and PC2 for the pygidium.

Subsequently, the morphospace collapsed in the Givetian because of the extinction of genera such as *Nandanaspis* Zhang & Yin in Yin & Li, 1978, *Eocryphops* Richter & Richter, 1931, *Plagiolaria* Kegel, 1952 and *Reedops* Richter & Richter, 1925. Their morphology implied a facial suture near the anterolateral border and a rounded genal angle. Afterwards, *Geesops* Struve, 1982, and *Nyterops* Struve, 1972, disappeared at the end of the Givetian. They are characterized by a cephalon with acute genal angles and a posterior section of the facial suture close to the posterior border. The occupied part of the morphospace is limited to the bottom-left part of the all-phacopids distribution (Fig. 7).

Finally, during the Late Devonian, the morphospace occupation shifted again to higher PC1 and PC2 values, due to the presence of more elongated cephalic shapes and facial sutures closer to the posterior border. The morphological disparity increased for the first time since the Emsian. Nevertheless, the morphospace occupation

remain reduced in the Frasnian but with a displacement of the occupied part of the morphospace. This displacement is partly due to the successive origination of *Acuticryphops* Crônier & Feist, 2000, and *Trimeroccephaloides* Feist *et al.*, 2009, which spread toward higher PC2 values of the morphospace with their anterolateral facial sutures and a narrow cephalon with rounded genal angles. The appearance of *Girardina* and *Occitanella*, characterized by the presence of eyes and a rounded genal angle, explains the displacement toward higher PC2 values. New genera appeared in the Famennian, such as *Dianops* Richter & Richter, 1923, *Ductina* Richter & Richter, 1931, *Struveops* Crônier & Feist, 2000, and *Trimeroccephalus* McCoy, 1849. They contributed to the partial refilling of the morphospace on its right side. These taxa exhibit a facial suture closest to the lateral margin border, a small (tr.) cheek, and a rounded genal angle. In the Famennian, the morphological disparity strongly expanded with an increase of SoR and SoV, while NND decreased slightly.

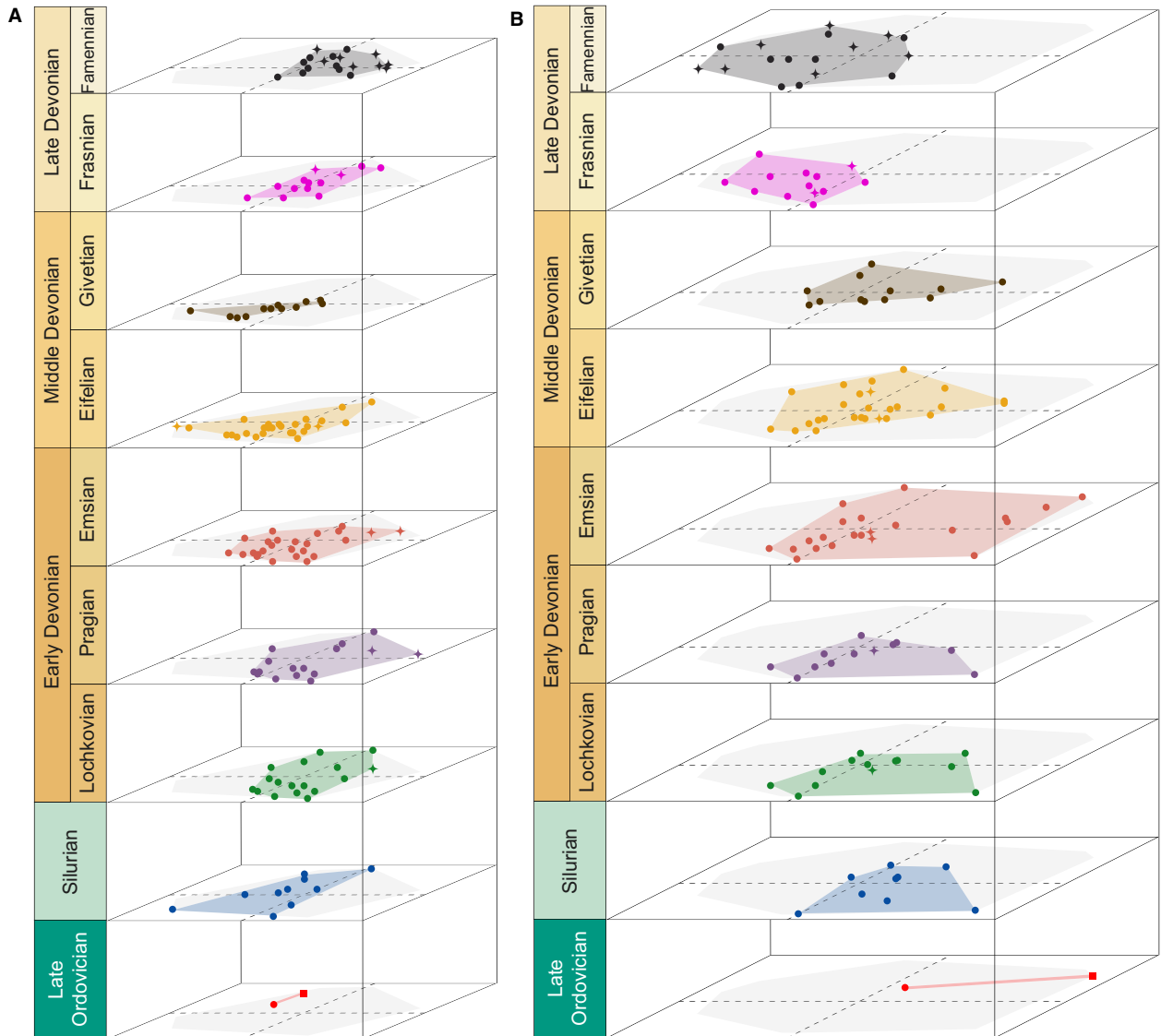


FIG. 7. Morphological occupation of the cephalon (A) and pygidium (B) through time (PCA based on Procrustes residuals). Circles represent eyed phacopids, crosses represent blind phacopids and the square represent the pterygometopid *Calyptaulax*.

Disparity of pygidia. From the Late Ordovician to the Silurian, the morphospace occupation moved toward lower PC1 and PC2 values to stay stable until the Pragian (Fig. 6). *Calyptaulax*, with its subtriangular pygidium, is located on one end of the morphospace (Fig. 7). In the Silurian, the phacopid shapes developed with the presence of more enlarged (tr.) pygidia with a larger pleural field. This morphospace occupation (mainly the bottom-middle right part) persisted until the Pragian. Thus, the morphological disparity remained almost stable, except for a decrease in NND (Fig. 5). In the Emsian, the morphological disparity of phacopids strongly increased to reach its highest value. This is the result of innovations occurring with the origination of *Austerops* McKellar & Chatterton, 2009, *Rhinophacops* Kaneko, 1990, and *Toxophacops*

Zhou & Campbell, 1990, for instance. This corresponds to a triangular pygidial shape and a weakly curved posterior border. The morphospace became filled and almost fully occupied except for the extreme left part.

During the Middle Devonian, the morphospace occupation shifted slightly to opposite values, in other words, to higher PC1 values; there was no real displacement on PC2 (Fig. 6). Both SoR and SoV decreased while NND increased after an initial diminution (Fig. 5). The occupied part of the morphospace was still relatively expanded in the Eifelian, with only the disappearance of taxa in the top-right and the bottom-right parts of the morphospace (Fig. 7). Indeed, *Echinophacops* and *Rhinophacops* were no longer present and disappeared at the Emsian–Eifelian boundary. These Asian genera are characterized by

narrow (tr.) pygidia with small pleural fields. Subsequently, the morphospace collapsed in the Givetian, particularly because of the extinction of *Morocops*, *Signatops* Příbyl & Vaněk, 1971, and *Viaphacops* in the left part of the morphospace. Therefore, the occupied part of the morphospace was limited to the right part of the all-phacopids distribution (Fig. 7).

Finally, during the Upper Devonian, the morphospace occupation shifted again to reach the lowest PC1 values whereas, once again, there is no real displacement on PC2 (Fig. 6). At the same time, SoR increased although the morphospace occupation remained reduced in the Frasnian, with low SoV and NND (Fig. 5). Contrary to the cephalon (characterized by lowest morphological disparity in the Givetian) the minimal occupation of the pygidial morphospace happened later, in the Frasnian (see SoV). Only wider displacement of the occupied part of the morphospace to the left occurred. This displacement is due to the appearance of genera characterized by an elongated (tr.) pygidium, such as *Acuticryphops*, *Chlupacops* Feist *et al.*, 2016 and Late Devonian *Phacops*. In the Famennian, new genera appeared, such as *Dianops* Richter & Richter, 1923, *Trifoliops* Crônier, 2003, *Trimeroccephalus* McCoy, 1849, and *Weyerites*, and contributed to a partial refilling of the morphospace. All of these taxa exhibit an elongated (tr.) pygidium. The morphological disparity strongly increased to reach values that are amongst the highest seen in phacopid history.

DISCUSSION

Morphological disparity

Phacopids did not exhibit a large morphological variation. This absence of strong differences among phacopid genera and tribes explains the difficulties encountered in determining their systematic structure (McKellar & Chatterton 2009). The choice of method and landmarks could influence the morphological variation measured (Van Bocxlaer & Schultheiß 2010; Webster & Sheets 2010; Zelditch *et al.* 2012). Nonetheless, the set of landmarks used catch most of trilobite morphology (Fig. 1; Bault *et al.* 2022b). The low morphological variability points towards morphological near-stasis in this group, although some important variations remain clearly identifiable. The low degree of variation is unexpected as phacopids have invaded many different environments during their evolutionary history (Chlupáč 1975; Crônier & François 2014; Bault *et al.* 2022a). Competition with other coexisting trilobite orders and/or strong developmental constraints may have hampered phacopids from exploring a large range of morphologies (Oyston *et al.* 2015). A stabilizing selection toward specific tasks may also explain the

relative morphological stasis (Hansen & Houle 2004; Tendler *et al.* 2015). For instance, the conservation of the *Olenus*-like morphology among the Olenids throughout the early Palaeozoic has been interpreted as the persistence of their habitats (Fortey 2000). However, phacopids had a conservative morphology throughout their evolutionary history whilst inhabiting the whole onshore–offshore profile (Bault *et al.* 2022a), indicating that other factors could explain such a tendency. The fact that phacopids did not develop extravagant morphologies probably suggests that their ‘basic’ morphology was better adapted to environmental variations, and invasion of new ecological niches did not require morphological novelties.

Only one genus differs strongly from the others: *Echinophacops* is the only phacopid which developed prominent marginal spines on the cephalon (Zhou 1983). The cephalic morphology of this genus is qualified as ‘marginal cephalic spines’ (*sensu* Fortey & Owens 1990). *Echinophacops* occurs with ammonoids, conodonts, brachiopods, gastropods and corals (Hua-Zhang & Cook 2003) in Lower Devonian calcareous sandstones of the Zhusileng Formation (China), representative of subtidal environments (Zhou & Campbell 1990). In this kind of environment, spinose asteropygines, another Phacopida subfamily, also proliferated at the same time (Morzadec 1992, 2001). Other phacopids co-occurred with *Echinophacops* in the same horizon (i.e. *Rhinophacops* and *Toxophacops*), as well as *Zhusilengops* Zhou & Campbell, 1990, and *Atopophacops* Zhou & Campbell, 1990, above the Zhusileng Formation (Zhou & Campbell 1990). Contrary to *Echinophacops*, these genera did not have spines. Nevertheless, an intermediate morphology existed between taxa with long spines (i.e. *Echinophacops mirabilis* Zhou, 1983), and taxa without spines, such as *Rhinophacops schlizoma* Zhou, 1983. The pygidium of *Echinophacops* also differed from other phacopids, which makes the entire exoskeleton of this genus special.

Among other genera, very few have a very differentiated morphology like that of *Enigmafyge* from the Famennian of Algeria (Feist *et al.* 2016). Although incompletely preserved, its cephalon shows all the characteristics of a phacopid. Nonetheless, its pygidium is unusual among this family in having a large pygidial margin and a short (sag.) pygidial axis ending at a considerable distance from the posterior edge (Feist *et al.* 2016). The morphology of the cephalon of *Teichertops* and *Zaplaops* was also uncommon. These two genera are represented by very few specimens in the literature and deformation of the landmarked fossils is possible. The specimen of *Teichertops* was found in black marls (Struve 1970) where distortions often happen (Webster & Hughes 1999). The usual shape of the pygidium of *Teichertops* tends to confirm this assumption although the cephalon and the pygidium of the same taxon show a different distribution

in morphospace (Bault *et al.* 2022b). For its part, *Zaplaops* could be a junior synonym of *Ananaspis* Campbell, 1967 (Holloway & Rustán 2012), which is not an outlier. This latter genus is characterized by an elongated cephalon as in *Zaplaops* (negative PC1 value) but without a downward genal field (average PC2 value), probably a consequence of a distortion. *Acernaspis*, *Adrisiops*, *Babinops*, *Drotops* and *Viaphacops* are the five genera differentiated by an elongated genal angle. Genal spines could develop from this configuration, as it is the case for *Babinops* (Feist & Becker 1997), *Viaphacops* (Eldredge 1973) and *Drotops armatus* (Struve 1995). Usually, phacopids had a genal spine during the early stages of their development, but these spines then reduced (Crônier & Feist 1997; Crônier *et al.* 1999; Crônier & Courville 2003). Contrary to the Early Devonian tendency among Trilobita (Bault *et al.* 2022b), this development of genal spines among phacopids was not a temporal trend because taxa with such morphology existed throughout the evolutionary history of phacopids. Only the presence of the strongly spinose *Echinophacops* coincided with the Early and Middle Devonian trends in spiny marine faunas, mainly in response to increasing predation (Brett & Walker 2002; Brett 2003). The presence of such genal spines could also favour stabilization on soft substrates (Brett 2003).

Except the few taxa described above, most phacopid genera show only slight differences between them. The main variation concerns the position of the facial suture, which corresponds to a line of weakness facilitating the moulting process (Daley & Drage 2016; Drage 2019). This allows the separation between the cranidium and the free cheeks during ecdysis (Drage 2019). Among trilobites, the phacopids have a proparian suture, the posterior section of which intersects the lateral cephalic margins in front of the genal angles (Harrington *et al.* 1959). The position of this facial suture constituted a trade-off between the ability to moult and a resistance to burrowing loads (Esteve *et al.* 2021). Although the facial sutures are non-functional during the holaspide period in phacopids (Speyer 1985), they are functional during the larval and juvenile periods (Crônier & Feist 1997; Crônier *et al.* 1998, 2005; Crônier & Courville 2003), exposing them to such a trade-off. Among phacopids, the size of the visual complex influences the location of the facial suture. Blindness or reduced-eyes imply a facial suture situated close to the lateral margin. Indeed, the reduction and marginal 'migration' of the visual complex caused the displacement of the associated dorsal facial sutures (Feist 1995). Consequently, the facial sutures of blind taxa are located on the anterolateral margins, relating to a macro-evolutionary paedomorphic process (Feist 1995; Crônier & Courville 2003; Crônier *et al.* 2005; Crônier 2013). This 'migration' occurred, even though cephalons with marginal facial sutures seem to become less resistant to stress

related to burrowing (Esteve *et al.* 2021). Such a characteristic challenges the assumed endobenthic behaviour of blind phacopids, but the ankylosed facial suture of holaspide phacopids and their moulting by disarticulation of the cephalothoracic joint (Drage 2019) could be a response to that issue. In addition to the facial suture displacement along with the visual complex reduction, blind phacopids have a less curved genal angle, with the exception of *Illaenula*. A marginal facial suture and weakly arched genal angles characterized blind phacopids but these characteristics are also found among some sighted genera. There were reduced-eye trilobites such as *Eocryphops* (Holloway 2005), that showed the suture displacement. Blind trilobites are not associated with a particular morphology of the pygidium as was the case for the cephalon. Nevertheless, the morphology of blind phacopids was limited to a particular shape of pygidium: those with high width/length ratios.

The second most important morphological variation in phacopids concerned the curvature of the genal angle and the cheek width. Large cheeks give a vaulted form to the cephalon. This kind of cephalic shape is found in other clades such as harpetids, and is thought to have prevented the trilobite from sinking into mud (Richter 1920; Feist & Clarkson 1989). Many phacopids with the most vaulted cephalons lived indeed in a muddy environment; for example, *Echidnops taphomimus* (Rustán & Balseiro 2016), *Illaenula struvei* (Basse & Müller 2000), *Nephranomma sweeti* (Sandford 2003), *Orygmatos yanyeani* (Sandford 2000), *Teichertops soetenicus* (Struve 1970) and *Zaplaops zaplensis* (Baldis *et al.* 1976). However, some trilobites with a vaulted cephalon occurred in limestone deposits; such as *Lochkovella misera* (Chlupáč 1977). Consequently, the type of substrate is not the only factor influencing the shape of the cephalon. Although all phacopids are characterized by a similar shape of glabella, narrower (tr.) at the base and wider (tr.) at the front, there were glabellar changes associated with cephalic changes. The glabella is wider at its front with a less curved genal angle for a vaulted cephalon. The base/frontal part width ratios are partly due to the putative predatory/scavenger habit of phacopids, a forwardly expanding glabella allowing ingestion of higher volumes (Fortey & Owens 1999). However, Bruton & Haas (2003) claimed that phacopids were more likely to be filtering detritus. This pattern contrasts with the morphological changes observed during the ontogeny for which the maximal width of the glabella/minimal width of the glabella ratio increased while the genal spines, and so the curvature of the genal angle, reduced (Crônier & Fortey 2006; Crônier 2007).

The elongation of the pygidium was also a major variation in phacopids. Some genera had an elongated pygidium with a width/length ratio greater than 2 (e.g. *Trifoliops*) while others had a ratio less than 1, such as

Enygmopyge (Feist *et al.* 2016). It is noticeable that the genera with the most elongated (tr.) pygidium are not the same as those with the largest cephalon. The pygidium shape was probably less suitable for stabilizing the organism on the seafloor. The morphology of organisms being the result of trade-offs between different tasks (Shoval *et al.* 2012; Ou *et al.* 2020), the pygidial organization probably favoured functions other than the balance of the trilobite. For example, enrolment influenced both cephalon and pygidium morphology, but it had probably a stronger effect on the pygidium, which was dedicated to fewer tasks (Oudot *et al.* 2019; Suárez & Esteve 2021). Consequently, there is a decoupling at the level of innovations between cephalon and pygidia. Finally, although the length of the pygidial axis also changes between different phacopids, only a short (sag.) postaxial area characterized the phacopid family, except *Enygmopyge* as discussed above.

Evolutionary history

The shape of the pterygometopid *Calyptaulax*, a sister group of phacopids (Oudot *et al.* 2019), is located close to the edge of phacopid morphologies with a facial suture close to the posterior border. Its shape is not completely different from phacopid morphologies, being close to the shape of the oldest phacopid *Sambreusaspis*. Hence, the assumption that Pterygometopidae is a sister taxon of phacopids seems relevant (Ludvigsen & Chatterton 1982). Similarities between ontogenetic trajectories of this genus and some phacopids (Jacobs & Carlucci 2019) reinforce this hypothesis. *Calyptaulax* had a facial suture (and therefore the eyes) near to the posterior border furrow, and a vaulted cephalon (Clarkson & Tripp 1982). From similar ancestral character states, phacopids developed from the Late Ordovician onwards leading to an increase of their morphological disparity. Although the oldest phacopid, *Sambreusaspis*, exhibited a general morphology similar to that of *Calyptaulax*, the facial sutures of phacopids are relatively close to the lateral margin in the Silurian. This was particularly the case for *Denckmannites*, *Lochkovella* and *Orygmotos*, the first reduced-eye phacopids (Chlupáč 1977; Sandford 2000; Crônier & Courville 2003). An eye reduction in trilobites could be linked to migration and an adaptation to deeper environments (Feist *et al.* 2009; Feist 2019). While *Acernaspis* and *Paciphacops* Maksimova, 1972, lived in shallow environments (Waisfeld *et al.* 1988; Owen *et al.* 2008; Rustán *et al.* 2011), *Denckmannites*, *Lochkovella* and *Orygmotos* lived in a relatively deep environment. The observed morphological change seems to be related to the invasion of this environmental niche. However, *Calyptaulax* proliferated in a deep environment (Owen & Parkes 2000; Carlucci &

Westrop 2012), indicating that this large-eyed morphology is not inconsistent with the habitat of a basin environment. On its side, the pygidium of phacopids lengthened compared to its probable ancestral morphology.

The morphological disparity trends corresponding to the cephalon and to the pygidium shapes, are partly uncorrelated. The constant increase of the morphospace occupancy from the Silurian until the Emsian observed in the cephalon is more irregular in the pygidium. This period was more favourable to the origination of novelties in other trilobite families, such as proetids, scutelluids and dalmanitids than in phacopids (Chlupáč 1994). The taxonomic diversity increase in the Lochkovian was associated with only a slight increase of morphological disparity. Therefore, no important innovations occurred, the new morphologies remained close to those of the Silurian. Origination of new species brought morphologies close to those already existing. Nevertheless, the cephalon morphospace shifted throughout the Silurian and the Early Devonian. There was probably a slight directional selection linked to a change of phenotypic optimums. From the Silurian to the Pragian, environmental conditions fluctuated, including a decrease in the sea-level, cooling and sedimentological changes (Haq & Schutter 2008; Scotese *et al.* 2021) and probably affected morphological evolution of phacopids. Most of the phacopids developed a narrower cephalon with eyes upward through this period.

During the Pragian–Emsian diversification, the taxonomic richness of phacopids increased, as did many trilobite families (Chlupáč 1994; Bault *et al.* 2021, 2022a). This boost of diversity was linked to the increase in morphological disparity for both cephalon and pygidia. Competition and niche partitioning within Phacopidae and with other trilobites in this period of diversification may have strengthened the morphological diversification (Cross *et al.* 2022; Bault *et al.* 2022b). Nevertheless, no important novelties characterized the development of new phacopids. Only the blind genus *Afrops* exhibits a new cephalon morphology, with a small cephalic shield without an elongated genal angle (Alberti 1983). For pygidia, the main innovation involved a triangular shape as in *Rhinophacops schizoloma* (Kaneko 1990) or the elongated (tr.) pygidium as in *Morocops granulops* (Chatterton *et al.* 2006). Nevertheless, the Emsian was the age of maximum disparity for both cephalon and pygidia. Contrary to most of the trilobites, for which the peak of morphological disparity occurred usually after the peak of diversity (Foote 1993), phacopids showed a different pattern. The Emsian morphological disparity peak occurred earlier than the maximum diversity, which followed in the Eifelian (Crônier & Courville 2003). Decoupling between morphological disparity and taxonomic diversity is common in the fossil record (Foote 1993) but has often been

linked to extinctions (Bapst *et al.* 2012; Hopkins 2013; Wan *et al.* 2021). In this case, the Eifelian anoxic events, associated with sea-level changes, may have affected morphological disparity more than diversity. This pattern differs from mass extinction events for which the impacts are stronger on the diversity component (Villier & Korn 2004; Oyston *et al.* 2015). The decrease of morphological disparity might have been caused either by a loss of ecological habitats (Valentine 1995; Oyston *et al.* 2015) or by an increase in developmental constraint (Gould 1991; Oyston *et al.* 2015).

Another feature of the morphological diversification of this family is that its peak was reached in the later part of its evolutionary history. This was the opposite of the common trend among Palaeozoic clades, which often have a maximum of disparity early in their evolutionary history (Hughes *et al.* 2013). Hopkins & Smith (2015) argued that evolutionary dynamics changed through time and were not necessarily higher in the first period of their existence. New ecological opportunities, such as those in the Devonian, could generate an increase of the evolutionary rate and thus, a morphological disparity rise.

An important extinction phase occurred in the Givetian with a strong decrease of both diversity and morphological disparity. The sea-level changes and the anoxia of the Middle Devonian events (Walliser 1996, pp. 225–250; House 2002) affected all trilobites (Lerosey-Aubril & Feist 2012; Bault *et al.* 2022a). The phacopids did not escape these environmental events and lost more than 60% of their genera. The mid-Givetian Taghanic event was the most devastating for them (Feist 1991; Crônier & Courville 2003). This crisis caused a collapse of the morphospace occupation, characteristic of non-random extinctions (Ciampaglio *et al.* 2001). On the contrary, the density of the morphospace was not disturbed by these events, implying a marginal or lateral extinction (Korn *et al.* 2013). Interestingly, a lateral extinction of the morphospace affected the cephalon with the disappearance of genera with well-rounded genal angles and anterolateral facial sutures such as *Eocryphops* and *Nandanaspis*. Therefore, the morphospace shifted during the Middle Devonian, while a rather marginal extinction with no strong change in the morphospace range affected the pygidium morphospace. The Taghanic extinction event led to the disappearance of genera with a cephalon characterized by an anterolateral facial suture. Therefore, in the late Givetian all phacopids had large eyes. Nevertheless, reduced-eyed trilobites did survive these environmental changes in other families such as Tropicoryphidae (Feist 2003). Abiotic causes were not the only possible explanations for the Middle Devonian morphological variations: increasing predation at that time may have reshaped the phacopid morphospace (Brett & Walker 2002; Bault *et al.* 2022a). Meanwhile, two of the largest genera of the family

appeared: *Drotops* and *Hypsiopariops* (Struve, 1982 (Struve 1995)). Indeed, the Early and Middle Devonian were times of giant organisms including trilobites (Klug *et al.* 2014). This trend can hardly be explained by single environmental parameters although a latitudinal influence cannot be excluded (Klug *et al.* 2014). *Drotops* and *Hypsiopariops* lived in the mid-latitudes of Morocco (Struve 1995), exactly the range of gigantism occurrences.

In the Frasnian, morphological disparity remained low. This stage has long been thought to be poorly diversified, despite Feist & Klapper (2022) proposing four new phacopid genera. Nevertheless, this was the least populated period in phacopid history. Generic diversity mainly increased in middle and late Frasnian times. Nevertheless, the stagnation of morphological disparity was accompanied by important morphological changes. For cephalon, morphospace occupancy shifted to the area indicating the acquisition of an anterolateral facial suture, underlying the Late Devonian trend towards blindness (Feist 1995, 2019; Crônier & Courville 2003; Crônier *et al.* 2011). This trend was also noticed in other families (Feist & Clarkson 1989; Lerosey-Aubril & Feist 2012; Schoenemann 2018). As for the Silurian, the existence of blind phacopids was associated with a life in deeper environments (Feist *et al.* 2009; Feist 2019). The successive transgressions and the long-term sea-level rise in the second part of the Devonian forced the trilobites to adapt to these new environments (Lerosey-Aubril & Feist 2012; Crônier & François 2014). Whatever the water depth, an endobenthic habit or a turbid environment with low luminosity could also imply an eye-reduction (Feist *et al.* 2009). Rustán *et al.* (2011) had precisely identified an increase of endobenthic behaviour among phacopids in the Devonian due to increasing predation. Concomitantly with the progressive modification of the eye and the displacement of the facial suture on the cephalon, the pygidium changed to a more elongated shape in phacopids. The morphological innovations still developed in the same direction in the Famennian. The combination of lateral facial sutures and an elongated pygidium contributed to increase the morphological disparity, particularly for the pygidium. Subsequent to the disastrous Kellwasser events at the Frasnian–Famennian boundary (Bugisch 1991; Bond & Wignall 2008), trilobites recovered and invaded various habitats and areas (Crônier & François 2014). As the result of this dispersal, morphological disparity increased, as was the case with the appearance of new niches in the Pragian. Some phacopids recolonized shallower environments and developed large eyes, such as *Omegops* (Crônier & François 2014).

The evolutionary history of phacopids stopped at the end of the Devonian with the disappearance of the whole order Phacopida (Bault *et al.* 2022a). Their extinction was the consequence of the Hangenberg event consisting of

sea-level changes, carbon cycle perturbation and temperature oscillations (Kaiser *et al.* 2016). All phacopids vanished regardless of their shape, but the predominance of reduced-eyed and blind taxa inhabiting more distal environments probably doomed them. Indeed, this event was devastating for non-occulated and reduced-eyed trilobites, including Proetida (Lerosey-Aubril & Feist 2012).

CONCLUSION

Phacopidae originated at the end of the Ordovician and rapidly diversified. They had a morphology close to their sister taxon Pterygomtopidae, with a glabella broadening forward and a proparian facial suture. Some genera had an unusual morphology but most of them had rather a similar shape with minor morphological changes. The main morphological variations among phacopids were the position of the facial suture, the shape of the genal angle and the elongation of both cephalon and pygidium. For cephalon, most morphologies already existed in the Silurian but the morphological diversity increased in the Devonian. Innovations and novelties were particularly favoured by the colonization of new habitats offered by Pragian environmental changes. The maximum of morphological disparity occurred in the Emsian, late in the evolutionary history of the phacopids. Their diversity peak occurred later, in the Eifelian. The Middle Devonian events strongly affected the phacopids, leading to a decrease of more than half of the morphological and taxonomic diversity in the Givetian. These extinctions were non-random, particularly affecting trilobites with reduced-eyes. Although morphological disparity remained low in the Frasnian, some morphological changes occurred. The facial suture migrated toward the anterolateral margins related to the eye-reduction and blindness and the pygidium elongated laterally. Eye reduction was achieved during environmental changes, especially sea-level changes. These trends continued in the Famennian, during which a recovery caused an increase in both diversity and morphological disparity. However, the Hangenberg event at the Devonian–Carboniferous boundary led to the disappearance of this representative trilobite family during the Devonian.

Acknowledgements. Our work benefited from the constructive remarks and the language corrections provided by G.D. Edgecombe (Natural History Museum, London). The authors also thank the reviewers Brian D.E. Chatterton (University of Alberta, Edmonton) and Lukáš Laibl (Charles University, Prague) who greatly improved this work and the English writing. Financial support was provided by the Région Hauts-de-France and the project ECOS Sud-MINCYT A17A01 (Argentina). This work is a contribution to the IGCP 652 ‘high-resolution Paleozoic geologic timescale’, and to the French CNRS UMR 8198 Evo-Eco-Paleo.

Author contributions. **Conceptualization** V Bault (VB); **Data Curation** VB; **Formal Analysis** VB, C Monnet (CM); **Funding Acquisition** C Crônier (CC), B Waisfeld (BW); **Investigation** VB; **Methodology** VB, CC, CM, D Balseiro (DB), F Serra (FS), BW, A Bignon (AB), JJ Rustán (JJR); **Project Administration** VB, CC; **Resources** VB, CM; **Software** CM; **Validation** VB; **Vizualization** VB; **Writing – Original Draft** VB; **Writing – Review & Editing** VB, CC, CM, DB, FS, BW, AB, JJR.

Editor. Xi-Guang Zhang

SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1111/pala.12673>):

- Table S1.** Description of landmarks and semi-landmark curves.
Figure S1. Evaluation of the measurement process bias and the intra-generic variation. A, phacopid cephalon morphospace. B, within sample variance.
Figure S2. Global morphospace for phacopid cephalon (A) and pygidium (B) computed by performing a PCA based on Procrustes residuals. Numbers correspond to the ID of each genus (Appendix S1).
Appendix S1. Dataset of all phacopid genera and *Calyptaulax* Cooper, 1930, used in this analysis.
Appendix S2. List of the publications used to compile the phacopid dataset.
Data S1. Cephalon TPS coordinates for all landmarks and semi-landmarks curves for each specimen used in the study.
Data S2. Pygidium TPS coordinates for all landmarks and semi-landmarks curves for each specimen used in the study.

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