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### ► To cite this version:

Valentin Bault, Catherine Crônier, Claude Monnet, Diego Balseiro, Fernanda Serra, et al.. Rise and fall of the phacopids: the morphological history of a successful trilobite family. *Palaeontology*, 2023, 66 (5), pp.e12673. 10.1111/pala.12673 . hal-04412795

**HAL Id: hal-04412795**

**<https://hal.science/hal-04412795>**

Submitted on 23 Jan 2024

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1 **RISE AND FALL OF THE PHACOPIDS: THE MORPHOLOGICAL**  
2 **HISTORY OF A SUCCESSFUL TRILOBITE FAMILY**

3

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26

27 **Abstract:**

28 Phacopidae was a successful family of the Silurian–Devonian period. Although their diversity  
29 trends are well identified, their shape evolution is unknown, often considered to have a  
30 conservative morphology. Their morphologies were quantified by using geometric  
31 morphometrics (landmarks) and their evolution was investigated by morphological disparity  
32 indices. Results identified morphological variations between the genera, and through time.  
33 Phacopids differ from each other by the position of the facial suture linked to the size of the  
34 visual complex, the shape of the genal angle and the elongation of both cephalon and  
35 pygidium. The morphological disparity of cephalon was high since the Silurian, contrary to that  
36 of pygidia. Subsequently, the morphological disparity increased in the Early Devonian with  
37 the development of narrow cephalon and triangular pygidia. Morphological disparity was  
38 **greater** in the Emsian for both cephalon and pygidia, more than 50 Myr after the origination of  
39 phacopids. It constituted a perfect example illustrating that a peak of biodiversity did not  
40 **happen necessarily** in the early history of a clade. Subsequently, **a** strong decrease of  
41 morphological disparity occurred in the Middle Devonian, in conjunction **with** sea-level  
42 changes and anoxic events. Taxonomic richness and morphological disparity declined  
43 strongly in the Givetian. It was a non-random extinction affecting particularly blind genera.  
44 The morphological disparity remained low in the Frasnian despite **p**rogressive eye reduction  
45 influenced by environmental changes. An extensive recovery occurred in the Famennian with  
46 **an** important increase of both taxonomic and morphological diversity. The Hangenberg event  
47 caused the final extinction of phacopids.

48

49 **Key words:**

50 Phacopidae, Palaeozoic, morphological disparity, diversification, extinction

51

52 PHACOPIDAE is a family that is frequently found in sedimentary rocks deposited on the  
53 Silurian-Devonian epicontinental platforms and thus was an important component of the  
54 marine benthos. They are represented worldwide, especially in Europe and North Africa. This  
55 family originated at the end of the Ordovician (Campbell 1967; Lespérance & Sheehan 1988;  
56 Adrain 2013), probably from the Pterygometopidae family (Ludvigsen & Chatterton 1982).  
57 The oldest phacopid was the late Ordovician *Sambreusaspis* Lespérance in Lespérance &  
58 Sheehan 1988 (Ramsköld & Werdelin 1991) discovered in Belgium. Phacopids diversified,  
59 first slowly with a few genera in the Silurian, then more importantly in the Devonian, to reach  
60 their highest diversity in the Middle Devonian (Crônier *et al.* 2011). Although initially they  
61 occupied the Iapetus ocean margins, they quickly spread worldwide (Ramsköld & Werdelin  
62 1991). While the Phacopidae was one of the few trilobite families to survive the Frasnian–  
63 Famennian extinction, they vanished at the end of the Devonian with the Hangenberg event  
64 (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Throughout their long evolutionary history,  
65 phacopids survived several environmental perturbations (Walliser 1996, pp 225–250; House  
66 2002; Calner 2008; Qie *et al.* 2019) including the second of the five ‘big’ mass extinctions  
67 described by Raup & Sepkoski (1982), i.e., the Kellwasser events (Buggisch 1991;  
68 Carmichael *et al.* 2019). Some events positively influenced their diversity as for example the  
69 Pragian regression, which led to the Pragian diversification of phacopids as well as many  
70 other trilobite clades (Chlupáč 1994; Bault *et al.* 2022a). Other events had negative effects,  
71 such as the Late Devonian events, which led to the extinction of many genera (Feist 1991).

72 Phacopids occupied numerous habitats of the Late Devonian epicontinental platforms from  
73 the shallow depths to beyond the photic zone, and they showed strong bathymetrical and  
74 palaeogeographical affinities (McKellar & Chatterton 2009; Crônier & François 2014). Their  
75 morphology and behaviour were affected by environmental changes, particularly at the

76 Frasnian–Famennian boundary characterized by the development of blind forms living in  
77 deeper-water environments and/or endobenthic lifestyle (Feist *et al.* 2009).

78 Phacopidae was first established by Hawle & Corda (1847). This family is characterised by  
79 a glabella broadening markedly forward with lateral glabellar furrows S2 and S3 obsolescent,  
80 and S1 often transglabellar leading to an ‘intercalating ring’, genal angles rounded without  
81 genal spines, and a visual complex often well-developed. The phacopid pygidium is well  
82 rounded, semicircular or trapezoidal, without lateral or marginal spines (Harrington *et al.*  
83 1959). The morphological diversity among Phacopidae is expressed especially in the shape of  
84 both the vincular furrow and visual complex and in the course of the facial suture (Fig. 1).  
85 These characters are considered important for systematic considerations (Crônier *et al.* 2011).  
86 Chlupáč (1977) identified two sub-families, i.e., Phacopidellinae Delo, 1935 characterised by  
87 a cephalic doublure without a vincular furrow and Phacopinae Reed, 1905 characterised by a  
88 cephalic doublure with a deep and continuous vincular furrow.

89 Environmental changes are reflected in the variations of the exoskeleton of trilobites and  
90 their evolutionary history, which is essentially adaptive. Therefore, they represent an  
91 exceptional model to analyze trends and macroevolutionary processes (Foote 1989, 1990,  
92 1991a, 1993, Gerber & Hopkins 2011, Webster & Zelditch 2011). Besides, studies on the  
93 taxonomic diversity of trilobites already highlighted the importance of phacopids, being for  
94 example the major component of Devonian Trilobite Evolutionary Faunas (Bault *et al.*,  
95 2022a). However, in recent decades, morphological disparity has proven as a successful,  
96 alternative biodiversity metric (Roy & Foote, 1997). Concerning trilobites, morphological  
97 disparity analyses have focused on very few families or subfamilies, such as Pterocephaliidae  
98 (Hopkins 2013) but not on this major group of Phacopidae.

99 Therefore, the present study aims to investigate the morphological evolution of all  
100 phacopids from their origination in the Late Ordovician to the end of Devonian, by analysing

101 their cephalic and pygidial shapes at the genus level by means of geometric morphometrics.  
102 Here, morphological disparity is investigated for the first time at a global scale, and using the  
103 stage for a temporal scale.

104

## 105 MATERIAL AND METHODS

106

### 107 *Datasets*

108

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

112 The dataset is at the genus taxonomic rank and at the stage chronostratigraphic level.

113 Our dataset includes almost all known genera of Phacopidae. However, because of the low  
114 number of genera before the Devonian, the Silurian has been treated as a unique time bin. For  
115 each genus, a representative specimen was selected, most often the holotype of the type  
116 species, unless the illustrations were insufficient. Because of the lack of illustration, the  
117 species of six genera were not the same between cephalon and pygidium: *Nephranomma*  
118 [Erben, 1952](#), *Pedinopariops* [Struve, 1970](#), *Prokops* [Chlupáč, 1971](#), *Struveaspis* [Alberti, 1966](#),  
119 *Teichertops* [Struve, 1992](#) and *Weyerites* [Crônier & Feist, 2000](#). 79 cephalia and 72 pygidia  
120 representing different genera were analysed, all at a holaspid stage ([Appendix S1](#)). For each  
121 genus, FAD and LAD (First and Last Appearance Datum, respectively) are noted.

122 The classification used for this dataset follows [Jell & Adrain \(2002\)](#). Updates since this  
123 publication were taken into account such as the replacement for *Cultrops* [Struve, 1995](#) to  
124 *Struvephacops* ([Ghobadi Pour 2015](#)) as well as the description of new genera: *Morocops*  
125 ([Basse, 2006](#)), *Enigmapyge* ([Feist \*et al.\* 2016](#)), *Magreanops* ([VanViersen & Vanherle 2018](#))

126 and *Feistops* (Crônier *et al.* 2020), *Acutiphacops* Feist & Klapper, 2022, *Cronierella* Feist &  
127 Klapper, 2022, *Girardina* Feist & Klapper, 2022 and *Occitanella* Feist & Klapper, 2022  
128 (Feist & Klapper, 2022). The Late Devonian *Phacops* Emmrich, 1839 being significantly  
129 different from previous ones (Crônier *et al.* 2011), we separated the Late Devonian specimens  
130 into a distinct genus named: **Late Devonian** *Phacops*. Moreover, the Pterygometopid  
131 *Calyptaulax* Cooper, 1930 was also included. The Pterygometopidae family is considered as  
132 the sister group of Phacopidae (Ludvigsen & Chatterton 1982) and *Calyptaulax* was used as  
133 an outgroup in phylogenetic analyses of phacopids (McKellar & Chatterton 2009; Oudot *et al.*  
134 2019). Nevertheless, some poorly known and **poorly** illustrated genera were excluded  
135 (*Portlockia* McCoy, 1846 and *Somatrikelon* McMurtrie, 1819 without illustration in both  
136 datasets; *Enygmapyge* Feist *et al.*, 2016 without cephalon in ‘cephalon’ dataset;  
137 *Adastocephalum* Mitchell, 1919, *Afrops* Alberti, 1983, *Burtonops* Struve, 1990, *Cryphops*  
138 Richter & Richter, 1926, *Spinicryphops* Crônier & Feist, 2000, *Struvephacops* Ghobadi Pour,  
139 2015, *Tangbailaspis* Xiang & Zhang, 1983 in Zhang 1983, and *Zaplaops* Baldis & Blasco,  
140 1976 in Baldis *et al.* 1976 without pygidium in ‘pygidium’ dataset). For each genus, **the FAD**  
141 **and LAD** are noted.

142 McKellar & Chatterton (2009) proposed a distribution of genera and sub-genera in  
143 tribes based on the work of Flick & Struve (1984), Haas (1998) and Struve (1970, 1972, 1976,  
144 1982, 1989, 1990, 1992, 1995). This distribution is in disagreement with the previous work of  
145 Chlupáč (1977): numerous members belonging to Phacopidellinae or Phacopinae are in the  
146 same tribe. Moreover, **not** all **phacopid** taxa listed in the exhaustive list of Jell & Adrain  
147 (2002), have been taken into consideration **by McKellar & Chatterton (2009)**.

148

149 *Landmarks and geometric morphometrics*

150

151 To describe the 2D morphology of cephalon and pygidia, we used a geometric morphometric  
152 approach based on homologous **loci** named landmarks (Bookstein 1991; Rohlf & Marcus  
153 1993; Adams *et al.* 2004; Mitteroecker & Gunz 2009; Zelditch *et al.* 2012). This method is  
154 commonly used on trilobites for macroevolutionary **and developmental** topics (Gerber &  
155 Hopkins 2011, Webster & Zelditch 2011; Oudot *et al.* 2019; Bault *et al.* 2022b). The *x*- and *y*-  
156 coordinates of 12 landmarks and 4 semi-landmark curves of 30 points **each** on the cephalon,  
157 as well as 6 landmarks and one semi-landmark curve of 24 points on the pygidium were  
158 digitized (**Fig. 1**, for landmark definition see **Table S1**) using the software TPSDig 2.32  
159 (Rohlf 2006, 2015). For the cephalon, the semi-landmark curves represent respectively the  
160 glabella shape, the facial suture shape and the cephalic outline (**Fig. 1**). For the pygidium, the  
161 semi-landmark curve represents the pygidial outline. The landmark 2D coordinates were  
162 exported in the standard TPS file format (Rohlf 2012; **data S1 and S2**).

163 To remove effects of size, position and orientation, all configurations of landmarks were  
164 superimposed by means of a generalized Procrustes analysis (GPA) (Gower 1975; Rohlf &  
165 Slice 1990; Bookstein 1991; Dryden & Mardia 1998; O'Higgins 2000; Zelditch *et al.* 2012)  
166 and projected to a linear tangent space at the full Procrustes mean (Rohlf 1999; Kendall  
167 1984). A Procrustes sliding was applied to the semi-landmark curves (Gunz & Mitteroecker  
168 2013).

169 To quantify morphological variation, a principal component analysis (PCA; Ringnér 2008;  
170 Abdi & Williams 2010) was performed on the variance-covariance matrix of Procrustes  
171 residual coordinates. Series of virtual shapes were reconstructed to illustrate the shape  
172 changes **described in the results part** for PC1 and PC2, which are the two major principal  
173 components (PCs) in terms of shape variance explained.

174 Additionally, in order to identify morphological changes related to eye-reduction or  
175 blindness in the cephalon, **and their effect to** the pygidium, blind and ocellated genera were



176 illustrated separately over the morphospace. Also, an one-side nonparametric, permutational  
177 ANOVA on all PC axes was performed using the Wilks' lambda test to assess statistically if a  
178 shape difference exists between blind and sighted trilobites. The ANOVA was performed on  
179 PCA axes instead of original Procrustes coordinates because the scores of each axis are  
180 uncorrelated and the number of dimensions corresponds to the degree of freedom (Rohlf  
181 1993; Polly 2017).

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

192 Morphological analyses have been computed with the software R v. 3.6.2 (R Core Team  
193 2013); and the packages 'geomorph' (v. 3.2.1; Adams & Otárola-Castillo 2013) and 'epaleo'  
194 (v. 0.8.41; Monnet, unpub.).

195

### 196 *Morphological disparity indices*

197

198 To quantify phacopid morphological disparity changes through time, we used several  
199 disparity indices, which described different aspects of the morphospace occupation (Foote  
200 1991b; Ciampaglio *et al.* 2001; Wills 2001; Guillerme *et al.* 2020). These disparity indices

201 have already been used for trilobites (Foote 1990, 1993; Hopkins 2013). Disparity indices  
202 have been estimated for the Silurian as a whole and for each stage of the Devonian.

203 Two indices were used to estimate the size of the morphospace. The Sum of Range (SoR),  
204 corresponding to the total range of morphologies, and the Sum of Variance (SoV)  
205 corresponding to the average dissimilarity between morphologies. The overall first-order  
206 Nearest Neighbour Distance (NND) was computed to characterise the density of the  
207 morphospace. Finally, the mean values per stage for PC1 and PC2 were computed to identify  
208 potential shift in morphospace filling through time.

209 Confidence intervals on the computed disparity values were obtained with a bootstrap  
210 approach, by iteratively (1000 times) calculating SoR, SoV and NND from random  
211 resampling with replacement of the individual points in the morphospace (Foote 1993). The  
212 2.5 and 97.5 percentile values of the resulting bootstrapped distribution of each disparity  
213 metric are used as lower and upper confidence intervals. Morphological indices have been  
214 performed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.) on the software R v. 3.6.2  
215 (R Core Team 2013).

216

217 *Diversity*

218

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

224

225 **RESULTS**

226

## 227 *Global morphospace*

228

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

232 *Cephalon shape.* The first four principal components explain 67% of the total shape variance  
233 (Fig. 2): PC1 (29.3%), PC2 (19.2%), PC3 (13.0%) and PC4 (5.1%). PC1 depicts changes in  
234 the position of the facial suture and the visual complex. The higher the PC1 value, the more  
235 the suture is close to the lateral margin and more the visual complex is reduced (Fig. 2A). PC1  
236 also shows changes associated with the width/length ratio: narrow (transversal) cephalia in  
237 negative values to elongated (tr.) cephalia in positive values. The second axis PC2 depicts a  
238 stretched genal angle in negative values and a rounded genal angle in positive values. Where  
239 the PC2 is high, the facial suture is more distant from the lateral margin. Consequently, the  
240 filling of the morphospace (Fig. 2A) is roughly triangular reflecting the influence of the three  
241 cephalic parameters (width/length ratio, facial suture/visual complex location and the shape of  
242 the genal angle). The bottom-left part of the morphospace corresponds to elongated cephalia  
243 with a stretched genal angle, the bottom-right part to narrow cephalia with a more reduced  
244 visual complex and the top-central part to intermediate shapes with a rounded genal angle.  
245 The distribution of genera is fairly homogeneous in the morphospace, with the exception of  
246 three outliers characterised by low PC1 and low PC2 values: *Iliaenula* Chlupáč, 1977,  
247 *Teichertops* and *Zaplaops*. The label of each morphospace point is given in figure S2. The  
248 pterygometopid *Calyptaulax* has a low PC1 value and one of the highest PC2 values placing  
249 it in the phacopid morphospace. The oldest phacopid *Sambreusaspis* had also a low PC1  
250 value but an average PC2 value.

251 Along the PC3 (Fig. 2B), the cephalic variations are associated with the genal angle shape  
252 and the cheek proportion. Cephalia with an elongated genal angle and larger cheeks relative to  
253 the cephalic shield are positioned in negative values, and cephalia with rounded genal angle  
254 and smaller cheeks relative to the cephalic shield are in positive values. Along the PC4, the  
255 cephalic variations are associated with elongated genal angle (low PC4 values) or rounded  
256 genal angle (high PC4 values). The distribution of genera is relatively fairly homogeneous in  
257 the morphospace with the exception of two outliers characterised by high PC3 values:  
258 *Illaenula* and *Sambremeusaspis*. Because genal spines are rare among phacopids, its presence  
259 is not clearly showed by the four first PCA axes. The genera developing such spines like  
260 *Acernaspis* Campbell 1967, *Babinops* Feist & Becker, 1997, *Drotops* Struve, 1990 and  
261 *Viaphacops* Maksimova, 1972 are located in the centre part of the morphospace with the  
262 phacopids without genal spines.

263 *Pygidium shape*. The first four axes (Fig. 3) explain 88% of the total shape variance: PC1  
264 (56.3%) PC2 (20%), PC3 (7.1%) and PC4 (4.5%). The first axis PC1 (Fig. 3A) depicts  
265 changes in the pleural field proportion and the lateral border angle. The lower the PC1, the  
266 more the pleural field is important and the lateral border angle acute. The second axis PC2  
267 depicts changes associated with the position of the greatest width: backward in negative  
268 values to forward in positive values. A higher PC2 value indicates a higher width/length ratio.  
269 The distribution of genera is fairly homogeneous in the morphospace. *Calyptaulax* with the  
270 highest PC1 values is slightly distinct from phacopids with a high PC2 value. *Echinophacops*  
271 Zhou, 1983 is differentiated from other phacopids by high PC1 and low PC2 values  
272 corresponding to a long pygidium.

273 Along the PC3 and PC4 axes (Fig. 3B), the pygidial variations are associated with the  
274 position of the rachis relative to the pygidial posterior border and the lateral outlines. The  
275 rachis is more (low PC3 and PC4 values) or less (high PC3 and PC4 values) closed to the

276 posterior border of the pygidium. Most of the genera are located in the right part of the  
277 morphospace, whereas *Calyptaulax* characterised by the highest PC3 values. While no  
278 complete cephalon of *Enigmapyge* is known yet, the pygidium of this genus is noticeable by  
279 very high PC1, PC3 and PC4 values that correspond with an elongated (sag.) pygidium with a  
280 short (sag.) rachis and a maximum pygidial width located backward with a linear lateral  
281 border.

282 *Tribes*. The phacopid tribes were widespread in the morphospace and they mingle with each  
283 other. Nevertheless, some trends exist, Cryphopini being almost restricted in the positive PC1  
284 values of the cephalon (Fig. 2A) and negative PC1 values of the pygidium (Fig. 3A).  
285 Conversely, Geesopini occupies negative PC1 and PC2 values of the cephalon and positive  
286 PC1 values of the pygidium.

287

#### 288 *Blindness*

289

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

299 The blindness observed in cephalata did not imply a different morphology of pygidia  
300 (Procrustes ANOVA:  $p=0.153$ ,  $r^2=0.03$ ). However, the pygidia associated with blind cephalata

301 are all gathered in the part of PC1 with the lowest values (Fig. 4B). This indicates that blind  
302 phacopids did not display a rounded lateral border or a large pleural field. The type of vision  
303 had no effect on PC2, PC3 and PC4.

304

305 *Diversity through time*

306

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

312 *Disparity of cephalata.* From the Late Ordovician to the Pragian, the morphospace occupation  
313 moved toward higher PC1 and lower PC2 values (i.e. toward a facial suture closer to the  
314 lateral margin and a smaller cephalic shield; Fig. 6). The Middle–Late Ordovician  
315 pterygometopid *Calyptaulax* and the oldest phacopid *Sambreusaspis* are located to the top-  
316 left extremity of the morphospace (Fig. 7). *Calyptaulax* is characterised by a glabella with a  
317 hypertrophied frontal lobe anteriorly with well-developed S3 and a subtriangular pygidium. In  
318 the Silurian, the phacopid shapes extended with the emergence of more rounded cephalata and a  
319 facial suture closer to the anterolateral border such as in *Denckmannites* Wedekind, 1914 and  
320 *Orygmator* Sandford, 2000. The morphospace enlarged progressively in the Early Devonian  
321 with new morphologies in the Pragian: cephalata characterised by a narrow (tr.) cephalic shield  
322 associated with antero-lateral facial sutures. The appearance of *Afrops* at the right edge (i.e.  
323 high PC1 values) of the morphospace illustrated this trend. In the Emsian, the morphospace is  
324 almost entirely occupied except for the left part of all phacopid distribution. Thus, SoR  
325 increased (Fig. 5). In the same time, NND and SoV tend to decrease.

326 During the Middle Devonian, the morphospace occupation moved toward the opposite  
327 side, the left part of the morphospace. The morphological disparity strongly decreased  
328 meantime. However, the reduction of the occupied part of the morphospace was initially only  
329 low in the Eifelian (Fig. 7). Shapes with a facial suture located close to the lateral border, such  
330 as the blind *Altaesajania* Maksimova, 1978a and *Angulophacops* Maksimova, 1978b are no  
331 longer present and disappeared at the Emsian–Eifelian boundary. Conversely, no new genera  
332 appeared. The Eifelian was also characterised by the lowest NND despite the presence of two  
333 outliers *Illaenula* and *Teichertops*. These outliers were located in the left part of all phacopid  
334 distribution during the Eifelian. Subsequently, the morphospace collapsed in the Givetian  
335 because of the extinction of genera, such as *Nandanaspis* Zhang & Yin in Yin & Li, 1978,  
336 *Eocryphops* Richter & Richter, 1931, *Plagiolaria* Kegel, 1952 and *Reedops* Richter &  
337 Richter, 1925. Their morphology implied a facial suture near the antero-lateral border and a  
338 rounded genal angle. Afterwards, *Geesops* Struve, 1982 and *Nyterops* Struve, 1972  
339 disappeared at the end of the Givetian. They are characterised by a cephalon with acute genal  
340 angles and a posterior section of the facial suture close to the posterior border. The occupied  
341 part of the morphospace is limited to the bottom-left part of all phacopids distribution (Fig. 7).

342 Finally, during the Late Devonian, the morphospace occupation shifted again to higher  
343 PC1 and PC2 values, due to the presence of more elongated cephalic shapes and facial sutures  
344 closer to the posterior border. The morphological disparity increased for the first time since  
345 the Emsian. Nevertheless, the morphospace occupation remain reduced in the Frasnian but  
346 with a displacement of the occupied part of the morphospace. This displacement is partly due  
347 to the successive origination of *Acuticryphops* Crônier & Feist, 2000 and *Trimercephaloides*  
348 Feist et al., 2009, which spread toward higher PC2 values of the morphospace with their  
349 antero-lateral facial sutures and a narrow cephalon with rounded genal angles. The appearance  
350 of *Girardina* and *Occitanella* characterized by the presence of eyes and a rounded genal angle

351 explains the displacement toward higher PC2 values. New genera appeared in the Famennian,  
352 such as *Dianops* Richter & Richter, 1923, *Ductina* Richter & Richter, 1931, *Struveops*  
353 Crônier & Feist, 2000 and *Trimerocephalus* McCoy, 1849. They contributed to refill partially  
354 the morphospace in its right-part. These taxa exhibit the facial suture closest to the lateral  
355 margin border, a small (tr.) cheek and a rounded genal angle. In the Famennian, the  
356 morphological disparity strongly expanded with an increase of SoR and SoV while NND  
357 decreased slightly.

358 *Disparity of pygidia*. From the Late Ordovician to the Silurian, the morphospace  
359 occupation moved toward lower PC1 and PC2 values to stay stable until the Pragian (Fig. 6).  
360 *Calyptaulax* by its a subtriangular pygidium is located on one end of the morphospace (Fig.  
361 7). In the Silurian, the phacopid shapes developed with the presence of more enlarged (tr.)  
362 pygidia with a larger pleural field. This morphospace occupation (mainly the bottom-middle  
363 right part) persisted until the Pragian. Thus, the morphological disparity remained almost  
364 stable, except a decrease of NND (Fig. 5). In the Emsian, the morphological disparity of  
365 phacopids strongly increased to reach the highest values. Consequently, some innovations  
366 occurred with the origination of *Austerops* McKellar & Chatterton, 2009, *Rhinophacops*  
367 Kaneko, 1990 and *Toxophacops* Zhou & Campbell, 1990 for instance. It corresponds to a  
368 triangular pygidial shape and a weakly curved posterior border. The morphospace became  
369 filled and almost occupied except the extreme left part.

370 During the Middle Devonian, the morphospace occupation shifted slightly to opposite  
371 values, i.e., higher PC1 values; no real displacement on PC2 (Fig. 6). Both SoR and SoV  
372 decreased while NND increased after an initial diminution (Fig. 5). The occupied part of the  
373 morphospace was still relatively expanded in the Eifelian, with only the disappearance of taxa  
374 in the top-right and the bottom-right parts of the morphospace (Fig. 7). Indeed,  
375 *Echinophacops* and *Rhinophacops* were no longer present and disappeared at the Emsian–



376 Eifelian boundary. These Asian genera are characterised by narrow (tr.) pygidia with small  
377 pleural fields. Subsequently, the morphospace collapsed in the Givetian, particularly because  
378 of the extinction of *Morocops*, *Signatops* Příbyl & Vaněk, 1971 and *Viaphacops* in the left  
379 part of the morphospace. Therefore, the occupied part of the morphospace was limited to the  
380 right part of all phacopids distribution (Fig. 7).

381 Finally, during the Upper Devonian, the morphospace occupation shifted again to reach the  
382 lowest PC1 values whereas there is no real displacement on PC2 once again (Fig. 6). In the  
383 same time, the SoR increased although the morphospace occupation remained reduced in the  
384 Frasnian with low SoV and NND (Fig. 5). Contrary to the cephalon characterized by lowest  
385 morphological disparity in the Givetian, the minimal occupation of the pygidial morphospace  
386 happened later, in the Frasnian (see SoV). Only wider displacement of the occupied part of  
387 the morphospace to the left occurred. This displacement is due to the appearance of genera  
388 characterised by an elongated (tr.) pygidium, such as *Acuticryphops*, *Chlupacops* Feist *et al.*,  
389 2016 and Late Devonian *Phacops*. In the Famennian, new genera appeared such as *Dianops*  
390 Richter & Richter, 1923, *Trifoliops* Crônier, 2003, *Trimerocephalus* McCoy, 1849 and  
391 *Weyerites* for instance, and contributed to refill partially the morphospace. All taxa exhibit an  
392 elongated (tr.) pygidium. The morphological disparity strongly increased to reach among the  
393 highest values of the phacopid history.

394

## 395 **DISCUSSION**

396

### 397 *Morphological disparity*

398

399 Phacopids did not exhibit a large morphological variation. This absence of strong difference  
400 among phacopid genera and tribes explains the difficulties encountered to determine their

401 systematic structure (McKellar & Chatterton 2009). The choice of method and landmarks  
402 could influence the morphological variation measured (Van Bocxlaer *et al.* 2010; Webster &  
403 Sheets, 2001; Zelditch *et al.* 2012). Nonetheless, the set of landmarks used catch most of  
404 trilobite morphology (Fig. 1; Bault *et al.* 2022b). The low morphological variability points  
405 toward morphological near-stasis in this group, although some important variations remain  
406 clearly identifiable. The low degree of variation is unexpected as phacopids have invaded  
407 many different environments during their evolutionary history (Chlupáč 1975; Crônier and  
408 François, 2014; Bault *et al.* 2022a). Competition with other coexisting trilobite orders and/or  
409 strong developmental constraints may have hampered phacopids from exploring a large range  
410 of morphologies (Oyston *et al.* 2015). A stabilizing selection toward specific tasks may also  
411 explain the relative morphological stasis (Hansen & Houle, 2004; Tandler *et al.* 2015). For  
412 instance, the conservation of the *Olenus*-like morphology among the Olenids throughout the  
413 early Palaeozoic was interpreted as the persistence of their habitats (Fortey 2000). However,  
414 phacopids had a conservative morphology throughout their evolutionary history by inhabiting  
415 the whole onshore-offshore profile (Bault *et al.*, 2022a), indicating that other factors could  
416 explain such a tendency. The fact that phacopids did not develop extravagant morphologies  
417 probably suggests that their ‘basic’ morphology was better adapted to environmental  
418 variations, and invasion of new ecological niches did not require morphological novelties.

419 Only one genus differs strongly from the others: *Echinophacops* is the only phacopid  
420 which developed prominent marginal spines on the cephalon (Zhou 1983). The cephalic  
421 morphology of this genus is qualified as ‘marginal cephalic spines’ (sensu Fortey & Owens  
422 1990). *Echinophacops* occurred with ammonoids, conodonts, brachiopods, gastropods and  
423 corals (Hua-Zhang & Cook 2003) in the Lower Devonian from calcareous sandstones of the  
424 Zhusileng Formation (China), representative of subtidal environments (Zhou & Campbell  
425 1990). In this kind of environment, spinose asteropygines, another Phacopida subfamily,

426 proliferated also at the same time (Morzadec 1992, 2001). Other phacopids co-occurred with  
427 *Echinophacops* in the same horizon (i.e. *Rhinophacops* and *Toxophacops*), and *Zhusilengops*  
428 Zhou & Campbell, 1990 and *Atopophacops* Zhou & Campbell, 1990 above the Zhusileng  
429 Formation (Zhou & Campbell 1990). Contrary to *Echinophacops*, these genera did not have  
430 spines. Nevertheless, an intermediate morphology existed between taxa with long spines (i.e.,  
431 *Echinophacops mirabilis* Zhou, 1983) and taxa without spines: *Rhinophacops schlizoma*  
432 Zhou, 1983. The pygidium of *Echinophacops* also differed from other phacopids, which  
433 makes this genus special regarding its entire exoskeleton.

434 Among other genera, very few have a very differentiated morphology like *Enigmapyge*  
435 from the Famennian of Algeria (Feist *et al.* 2016). Although incompletely preserved, its  
436 cephalon shows all the characteristics of a phacopid. Nonetheless, its pygidium is unusual  
437 among this family with a large pygidial margin and a short (sag.) pygidial axis ending at a  
438 considerable distance from the posterior edge (Feist *et al.* 2016). The morphology of the  
439 cephalon of *Teichertops* and *Zaplaops* was also uncommon. These two genera are represented  
440 by very few specimens in the literature and a deformation of the landmarked fossils is  
441 possible. The specimen of *Teichertops* was found in black marls (Struve 1970) where  
442 distortions often happen (Webster & Hughes 1999). The usual shape of the pygidium of  
443 *Teichertops* tends to confirm this assumption although the cephalon and the pygidium of the  
444 same taxon show a different distribution in a morphospace (Bault *et al.* 2022b). For its part,  
445 *Zaplaops* could be a junior synonym of *Ananaspis* Campbell, 1967 (Holloway & Rustán  
446 2012), which is not an outlier. This latter genus is characterised by an elongated cephalon as  
447 in *Zaplaops* (negative PC1 value) but without a downward genal field (average PC2 value),  
448 probably a consequence of a distortion. *Acernaspis*, *Adrasiops*, *Babinops*, *Drotops* and  
449 *Viaphacops* are the five genera differentiated by an elongated genal angle. Genal spines could  
450 develop from this configuration, as it is the case for *Babinops* (Feist & Becker 1997),

451 *Viaphacops* (Eldredge 1973) and *Drotops armatus* (Struve 1995). Usually, phacopids had a  
452 genal spine during the early stages of their development, but these spines then reduced  
453 (Crônier & Feist 1997; Crônier et al. 1999; Crônier & Courville 2003). Contrary to the Early  
454 Devonian tendency among Trilobita (Bault *et al.* 2022b), this development of genal spines  
455 among phacopids was not a temporal trend because taxa with such morphology existed  
456 throughout the evolutionary history of phacopids. Only the presence of the strongly spinose  
457 *Echinophacops* coincided with the Early and Middle Devonian trends in spiny marine faunas,  
458 mainly in response to increasing predation (Brett & Walker, 2002; Brett 2003). The presence  
459 of such genal spines could also favour the stabilization on soft substrates (Brett 2003).

460 Except the few taxa described above, most phacopid genera showed slight differences  
461 between them. The main variation concerns the position of the facial suture, which  
462 corresponds to a line of weakness facilitating the moulting process (Daley & Drage 2016;  
463 Drage 2019). This allows the separation between the cranidium and the free cheeks during  
464 ecdysis (Drage 2019). Among trilobites, the phacopids have a proparian suture, the posterior  
465 section of which intersects the lateral cephalic margins in front of the genal angles  
466 (Harrington *et al.* 1959). The position of this facial suture constituted a trade-off between the  
467 ability to moult and a resistance to burrowing loads (Esteve *et al.* 2021). Although the facial  
468 sutures are non-functional during the holaspid period in phacopids, they are functional during  
469 the larval and juvenile periods (Crônier & Feist 1997; Crônier et al. 1998; Crônier &  
470 Courville, 2003; Crônier et al. 2005), exposing them to such a trade-off. Among phacopids,  
471 the size of the visual complex influences the location of the facial suture. Blindness or  
472 reduced-eyes imply a facial suture situated close to the lateral margin. Indeed, the reduction  
473 and marginal 'migration' of the visual complex caused the displacement of the associated  
474 dorsal facial sutures (Feist 1995). Consequently, the facial sutures of blind taxa are located on  
475 the anterolateral margins related to a macroevolutionary pedomorphic process (Feist 1995;

476 Crônier & Courville 2003; Crônier et al. 2005; Crônier 2013). This ‘migration’ occurred, even  
477 though cephalons with marginal facial sutures seem to become less resistant to stress related to  
478 burrowing (Esteve et al. 2021). Such characteristic challenges the assumed endobenthic  
479 behaviour of blind phacopids, but the ankylosed facial suture of holaspid phacopids and their  
480 moulting by disarticulation of the cephalothoracic joint (Drage 2019) could be a response to  
481 that issue. In addition to the facial suture displacement along with the visual complex  
482 reduction, blind phacopids have a less curved genal angle, except *Illaenula*. A marginal facial  
483 suture and weakly arched genal angles characterised blind phacopids but these characteristics  
484 are also found among some sighted genera. There were reduced-eye trilobites such as  
485 *Eocryphops* (Holloway 2005), that showed the suture displacement. Blind trilobites are not  
486 associated with a particular morphology of the pygidium as it was the case for the cephalon.  
487 Nevertheless, the morphology of blind phacopids was limited to a particular shape of  
488 pygidium: those with high width/length ratios.

489 The second most important morphological variation in phacopids concerned the curvature  
490 of the genal angle and the cheek width. Large cheeks give a vaulted form to the cephalon.  
491 This kind of cephalic shape was found in other clades such as harpetids, was supposed to  
492 prevent the trilobite from sinking into mud (Richter 1920; Feist & Clarkson 1989). Many  
493 phacopids with the most vaulted cephalon lived indeed in a muddy environment like  
494 *Echidnops taphomimus* (Rustán & Balseiro 2016), *Illaenula struvei* (Basse & Müller 2000),  
495 *Nephranomma sweeti* (Sandford 2003), *Orygmator yanyeani* (Sandford 2000), *Teichertops*  
496 *soetenicus* (Struve 1970) and *Zaplaops zaplensis* (Baldis et al. 1976). However, some  
497 trilobites with a vaulted cephalon occurred in limestone deposits, such as *Lochkovella misera*  
498 (Chlupáč 1977). Consequently, the type of substrate is not the only factor influencing the  
499 shape of the cephalon. Although all phacopids are characterized by a similar shape of  
500 glabella, narrower (tr.) at the base and wider (tr.) at the front, there were glabellar changes

501 associated with cephalic changes. The glabella is wider at its front with a less curved genal  
502 angle for a vaulted cephalon. The base/frontal part width ratios are partly due to the putative  
503 predatory/scavenger habit of phacopids, a forwardly expanding glabella allowing ingestion of  
504 higher volumes (Fortey & Owens 1999). However, Bruton and Haas (2003) claimed that  
505 phacopids were more filtering detritus. This pattern contrasts with the morphological changes  
506 observed during the ontogeny for which the maximal width of the glabella/minimal width of  
507 the glabella ratio increased while the genal spines, and so the curvature of the genal angle,  
508 reduced (Crônier & Fortey 2006; Crônier 2007).

509 The elongation of the pygidium was also a major variation in phacopids. Some genera had  
510 an elongated pygidium with a width/length ratio greater than 2 (e.g., *Trifoliops*) while others  
511 had a ratio less than 1 such as *Enigmatyge* (Feist *et al.* 2016). It is noticeable that the genera  
512 with the most elongated (tr.) pygidium are not the same as those with the largest cephalon.  
513 The pygidium shape was probably less suitable for stabilizing the organism on the seafloor.  
514 The morphology of organisms being the result of trade-offs between different tasks (Shoval *et*  
515 *al.* 2012; Ou *et al.* 2020), the pygidial organization favoured probably other functions than the  
516 balance of the trilobite. For example, the enrolment influenced both cephalon and pygidium  
517 morphology, but it had probably a stronger effect on the pygidium, which was dedicated to  
518 fewer tasks (Oudot *et al.* 2019; Suárez & Esteve 2021). Consequently, there is a decoupling at  
519 the level of innovations between cephalon and pygidia. Finally, although the length of the  
520 pygidial axis also changes between different phacopids, only a short (sag.) postaxial area  
521 characterised the phacopid family, except *Enigmatyge* discussed above.

522

523 *Evolutionary history*

524

525 The shape of the pterygometopid *Calyptaulax*, a sister group of phacopids (Oudot et al. 2019),  
526 is located closed to the edge of phacopid morphologies with a facial suture close to the  
527 posterior border. Its shape is not completely different from phacopid morphologies, being  
528 close to the shape of the oldest phacopid *Sambreusaspis*. Hence, the assumption that  
529 Pterygometopidae is a sister taxa of phacopids seems relevant (Ludvigsen & Chatterton  
530 1982). Similarities between ontogenetic trajectories of this genus and some phacopids (Jacobs  
531 & Carlucci 2019) reinforce this hypothesis. *Calyptaulax* had a facial suture (and therefore the  
532 eyes) near to the posterior border furrow and a vaulted cephalon (Clarkson & Tripp 1982).  
533 From similar ancestral character states, phacopids developed from the Late Ordovician  
534 onwards leading to an increase of their morphological disparity. Although the oldest phacopid  
535 *Sambreusaspis* exhibited a general morphology similar to *Calyptaulax*, the facial suture of  
536 phacopids are relatively close to the lateral margin in the Silurian. This was particularly the  
537 case for *Denckmannites*, *Lochkovella* and *Orygmotos*, the first reduced-eye phacopids  
538 (Chlupáč 1977; Sandford 2000; Crônier & Courville 2003). An eye reduction in trilobites  
539 could be linked to the migration and an adaptation to deeper environments (Feist et al. 2009;  
540 Feist 2019). While *Acernaspis* and *Paciphacops* Maksimova, 1972 lived in shallow  
541 environments (Waisfeld et al. 1988; Owen & Harper 2008; Rustán et al. 2011),  
542 *Denckmannites*, *Lochkovella* and *Orygmotos* lived in a relatively deep environment. The  
543 observed morphological change seems to be related to the invasion of this environmental  
544 niche. However, *Calyptaulax* has proliferated in a deep environment (Owen & Parkes 2000;  
545 Carlucci & Westrop 2012), indicating that this large-eyed morphology is not inconsistent with  
546 the habitat of a basin environment. On its side, the pygidium of phacopids has lengthened  
547 compared to its probable ancestral morphology.

548 The morphological disparity trends corresponding to the cephalon and to the pygidium  
549 shapes, are partly uncorrelated. The constant increase of the morphospace occupancy from the

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

563 During the Pragian–Emsian diversification, the taxonomic richness of phacopids increased,  
564 like many trilobite families (Chlupáč 1994; Bault *et al.* 2021; 2022a). This boost of diversity  
565 was linked to the increase in morphological disparity for both cephalon and pygidia.

566 Competition and niche partitioning within Phacopidae and with other trilobites in this period  
567 of diversification could strengthened the morphological diversification (Cross *et al.* 2022;  
568 Bault *et al.* 2022b). Nevertheless, no important novelties characterised the development of  
569 new phacopids. Only the blind genus *Afrops* exhibits a new cephalon morphology with a  
570 small cephalic shield without an elongated genal angle (Alberti 1983). For pygidia, the main  
571 innovation involved a triangular shape as in *Rhinophacops schizoloma* (Kaneko 1990) or the  
572 elongated (tr.) pygidium as in *Morocops granulops* (Chatterton *et al.* 2006). Nevertheless, the  
573 Emsian was the age of the maximum disparity for both cephalon and pygidia. Contrary to most  
574 of the trilobites for which the peak of morphological disparity occurred usually after the peak



575 of diversity (Foote 1993), phacopids showed a different pattern. The Emsian morphological  
576 disparity peak occurred earlier than the maximum diversity, which followed in the Eifelian  
577 (Crônier & Courville 2003). Decoupling between morphological disparity and taxonomic  
578 diversity is common in the fossil record (Foote 1993) but it was often linked to extinctions  
579 (Bapst 2012; Hopkins 2013; Wan *et al.* 2021). In this case, the Eifelian anoxic events,  
580 associated with sea-level changes, could affect more morphological disparity than diversity.  
581 This pattern differs from mass extinction events for which the impacts are stronger on the  
582 diversity component (Villier & Korn 2004; Oyston *et al.* 2015). The decrease of  
583 morphological disparity might have been caused either by a loss of ecological habitats  
584 (Valentine 1995; Oyston *et al.* 2015) or by an increase of developmental constraint (Gould  
585 1991; Oyston *et al.* 2015).

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

593 An important extinction phase occurred in the Givetian with a strong decrease of both  
594 diversity and morphological disparity. The sea-level changes and the anoxia of the Middle  
595 Devonian events (Walliser 1996, pp 225–250; House 2002) affected all the trilobites  
596 (Lerosey-Aubril & Feist 2012; Bault *et al.* 2022a). The phacopids did not escape these  
597 environmental events and lost more than 60% of their genera. The mid-Givetian Taghanic  
598 event was the most devastating for them (Feist 1991; Crônier & Courville 2003). This crisis  
599 caused a collapse of the morphospace occupation, characteristic of non-random extinctions

600 (Ciampaglio *et al.* 2001). On the contrary, the density of the morphospace was not disturbed  
601 by these events, implying a marginal or lateral extinction (Korn *et al.* 2013). Interestingly, a  
602 lateral extinction of the morphospace affected the cephalon with the disappearance of genera  
603 with well-rounded genal angles and antero-lateral facial sutures such as *Eocryphops* and  
604 *Nandanaspis*. Therefore, the morphospace shifted during the Middle Devonian, while a rather  
605 marginal extinction with no strong change in the morphospace range affected the pygidium  
606 morphospace. The Taghanic extinction event led to the disappearance of genera with a  
607 cephalon characterised by an anterolateral facial suture. Therefore, in the late Givetian all  
608 phacopids only had large eyes. Nevertheless, reduced-eyed trilobites could survive these  
609 environmental changes, in other families such as Tropicocoryphidae (Feist 2003). Abiotic  
610 causes were not the only possible explanations for the Middle Devonian morphological  
611 variations: the increasing predation at that time could reshape the phacopid morphospace  
612 (Brett & Walker 2002; Bault *et al.* 2022a). Meanwhile, two of the largest genera of the family  
613 appeared, it was *Drotops* and *Hypsipariops* Struve, 1982 (Struve 1995). Indeed, the Early and  
614 the Middle Devonian were the times of giant organisms including trilobites (Klug *et al.* 2014).  
615 This trend was hardly explained by single environmental parameters although a latitudinal  
616 influence cannot be excluded (Klug *et al.* 2014). *Drotops* and *Hypsipariops* lived in the mid-  
617 latitudes of Morocco (Struve, 1995), exactly the range of gigantism occurrences.

618 In the Frasnian, morphological disparity remained low. This stage has long been thought to  
619 be poorly diversified, despite Feist and Klapper (2022) proposing four new phacopid genera.  
620 Nevertheless, this was the least populated period in phacopid history. Generic diversity  
621 mainly increased in the mid- and late Frasnian times. Nevertheless, the stagnation of  
622 morphological disparity was accompanied by important morphological changes. For cephalata,  
623 morphospace occupancy shifted to the area indicating the acquisition of an anterolateral facial  
624 suture, underlying the Late Devonian trend toward blindness (Feist 1995, 2019; Crônier &

625 Courville 2003; Crônier *et al.* 2011). This trend was also noticed in other families (Feist &  
626 Clarkson 1989; Lerosey-Aubril & Feist 2012; Schoenemann 2018). As for the Silurian, the  
627 existence of blind phacopids was associated with a life in deeper environments (Feist *et al.*  
628 2009; Feist 2019). The successive transgressions and the long-term sea-level rise in the  
629 second part of the Devonian forced the trilobites to adapt to these new environments  
630 (Lerosey-Aubril & Feist 2012; Crônier & François 2014). Whatever the water depth, an  
631 endobenthic behaviour or a turbid environment with low luminosity could also imply an eye-  
632 reduction (Feist *et al.* 2009). Rustán *et al.* (2011) had precisely identified an increase of  
633 endobenthic behaviour among phacopids in the Devonian due to increasing predation.  
634 Concomitantly to the progressive modification of the eye and the displacement of the facial  
635 suture on the cephalon, the pygidium changed to a more elongated shape in phacopids. The  
636 morphological innovations still developed in the same direction in the Famennian. The  
637 combination of lateral facial sutures and an elongated pygidium contributed to increase the  
638 morphological disparity, particularly for the pygidium. Subsequent to the disastrous  
639 Kellwasser events at the Frasnian–Famennian boundary (Buggisch 1991; Bond and Wignall  
640 2008), trilobites recovered and invaded various habitats and areas (Crônier and François  
641 2014). As the result of this dispersal, morphological disparity increased, as was the case with  
642 the appearance of new niches in the Pragian. Some phacopids recolonized shallower  
643 environments and developed large eyes, such as *Omegops* (Crônier and François 2014).

644 The evolutionary history of phacopids stopped at the end of the Devonian with the  
645 disappearance of the whole order Phacopida (Bault *et al.* 2022a). Their extinction was the  
646 consequence of the Hangenberg event consisting of sea-level changes, carbon cycle  
647 perturbation and temperature oscillations (Kaiser *et al.* 2016). All phacopids vanished  
648 regardless of their shapes, but the predominance of reduced-eyed and blind taxa inhabiting

649 more distal environments probably doomed them. Indeed, this event was devastating for non-  
650 oculated and reduced-eyed trilobites, including Proetida (Lerosey-Aubril & Feist 2012).

651

## 652 CONCLUSION

653

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

674

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

682

683 Author contributions. Conceptualization V.Bault (VB); Data Curation VB; Formal Analysis  
684 VB, C. Monnet (CM); Funding acquisition CCrônier (CC), B. Waisfeld (BW); Investigation  
685 VB; Methodology VB, CC, CM, D. Balseiro (DB), F. Serra (FS), BW, A. Bignon (AB), J.J.  
686 Rustán (JJR); Project administration VB, CC; Resources VB, CM; Softwares CM; Validation  
687 VB; Visualization VB; Writing-Original Draft VB; Writing – Review & Editing VB, CC,  
688 CM, DB, FS, BW, AB.

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1103 **FIGURES**

1104

1105 **Figure 1.** Twelve landmarks and four semi-landmark curves of 30 points defined on the  
1106 cephalon and 8 landmarks and one semi-landmark curve of 24 points on the pygidium.  
1107 Modified from [Crônier \(2013\)](#).

1108

1109 **Figure 2.** Global morphospace for phacopid cephalon computed by performing a PCA based  
1110 on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 49% of the variance; (B)  
1111 the PC3 and PC4 axes explain 18% of the variance. Tribes according to [McKellar &](#)  
1112 [Chatterton \(2009\)](#): Anaspini [Haas, 1998](#) (Brown); Cordapeltini [Struve, 1989](#) (Dark green);  
1113 Cryphopini [Struve, 1989](#) (Orange); Geesopini [Flick & Struve, 1984](#) (Blue); Phacopini [Flick &](#)  
1114 [Struve, 1984](#) (Light green); Reedopini [Struve, 1989](#) (Purple) and *Incertae sedis* (Red). The  
1115 pterygometopid *Calyptaulax* is represented by a black square. Virtual shapes were  
1116 reconstructed by doing the back transformation from the considered PC scores, and then  
1117 reshaped to landmark data.

1118

1119 **Figure 3.** Global morphospace for phacopid pygidium computed by performing a PCA based  
1120 on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 76% of the variance; B)  
1121 the PC3 and PC4 axes explain 12% of the variance. Tribes sensu [McKellar & Chatterton](#)  
1122 [\(2009\)](#): Anaspini [Haas, 1998](#) (Brown); Cordapeltini [Struve, 1989](#) (Dark green); Cryphopini  
1123 [Struve, 1989](#) (Orange); Geesopini [Flick & Struve, 1984](#) (Blue); Phacopini [Flick & Struve,](#)  
1124 [1984](#) (Light green); Reedopini [Struve, 1989](#) (Purple) and *Incertae sedis* (Red). The  
1125 pterygometopid *Calyptaulax* is represented by a black square. Virtual shapes were  
1126 reconstructed by doing the back transformation from the considered PC scores, and then  
1127 reshaped to landmark data.

1128

1129 **Figure 4.** Location of: cephalon (A) and pygidium (B) according visual abilities of phacopids in  
1130 the global morphospace defined according to the four first principal component axes  
1131 performed on Procrustes residuals, respectively PC1 vs PC2 and PC3 vs PC4.

1132

1133 **Figure 5.** Fluctuations of the morphological disparity and taxonomic diversity of phacopids  
1134 through time, respectively based on the cephalon and the pygidium. Number of studied genera  
1135 (A) for cephalon; (B) for pygidium. Morphological disparity of the cephalon: SoR: Sum of  
1136 Range (C); SoV: Sum of variance (E); NDD: Nearest-Neighbour Distance (G). Morphological  
1137 disparity of the pygidium: SoR: Sum of Range (D); SoV: Sum of variance (F); NDD: Nearest-  
1138 Neighbour Distance (H). Solid lines correspond to mean values from 1000 bootstrap  
1139 replicates and shaded areas represent 95% confidence intervals. See text for the explanations  
1140 of the indices. Ages from [Cohen et al. 2013, updated](#).

1141

1142 **Figure 6.** Location of the morphospace occupation on PC1 and PC2 through time. (A and B)  
1143 Average values of PC1 and PC2 on the cephalon. (C and D) Average values of PC1 and PC2  
1144 on the pygidium.

1145

1146 **Figure 7.** Morphological occupation of the (A) cephalon and (B) the pygidium through time  
1147 (PCA based on Procrustes residuals). Circles represent eyed phacopids, crosses represent  
1148 blind phacopids and the square represent the pterygometopid *Calyptaulax*.

1149



1150

1151 **SUPPLEMENTAL FIGURES**

1152

1153 **Table S1:** Description of landmarks and semi-landmark curves.

1154

1155 **Figure S1:** Evaluation of the measurement process bias (blue) and the intra-generic variation  
1156 (red). (A) Phacopid cephalon morphospace and (B) Within sample variance.

1157

1158 **Figure S2:** Global morphospace for phacopid (A) cephalon and (B) pygidium computed by  
1159 performing a PCA based on Procrustes residuals. Numbers correspond to the ID of each genus  
1160 (Appendix S1).

1161

1162 **Appendix S1**

1163 Dataset of all phacopid genera and *Calyptaulax* Cooper, 1930 used in this analyse.

1164

1165 **Appendix S2**

1166 List of the publications used to compile the phacopid dataset.

1167

1168 **Data S1**

1169 Cephalon TPS coordinates for all landmarks and semi-landmarks curves for each specimen  
1170 used in the study.

1171

1172 **Data S2**

1173 Pygidium TPS coordinates for all landmarks and semi-landmarks curves for each specimen  
1174 used in the study.